Manifestation of scotomas created by transcranial magnetic stimulation of human visual cortex

Yukiyasu Kamitani and Shinsuke Shimojo

Computation and Neural Systems, California Institute of Technology, MC 139-74, Pasadena, California 91125, USA

Correspondence should be addressed to Y.K. (kamitani@percipi.caltech.edu)

Reduced visual performance under transcranial magnetic stimulation (TMS) of human visual cortex demonstrates suppression whose spatial extent is not directly visible. We created an artificial scotoma (region missing from a visual pattern) to directly visualize the location, size and shape of the TMS-induced suppression by following a large-field, patterned, visual stimulus with a magnetic pulse. The scotoma shifted with coil position according to known topography of visual cortex. Visual suppression resulted in pattern-dependent distortion, and the scotoma was filled in with temporally adjacent stimuli, suggesting spatial and temporal completion mechanisms. Thus, perceptual measurements of TMS-induced suppression may provide information about cortical processing via neuronal connections and temporal interactions of neural signals.

Transcranial magnetic stimulation is a noninvasive technique for stimulating the cerebral cortex by electromagnetic induction with a coil placed on the scalp[1]. In human visual cortex, documented effects are mostly suppressive[2–4], but a small number of studies report TMS-induced phosphenes[5–7]. Suppression is typically characterized by deteriorated performance in discrimination or identification tasks that use briefly presented, small visual targets such as letters followed by a single magnetic pulse[2,3]. However, it is difficult to directly 'perceive' TMS-induced suppression as interruption of aspects of visual perception of a continuous scene. If the range and characteristics of the suppressive effect could be identified in a single instance of perception, one could study the relationship between human perception and neural electrical activity more directly and in greater detail than previously possible. Here we introduce a method allowing visualization of TMS-induced suppression as a region of visual space missing a pattern in a flashed, large-field visual stimulus. Using this method, we found pattern-dependent distortion and filling in of the scotoma with temporally adjacent stimuli, demonstrating the dynamic nature of TMS-induced suppression.

Results

TMS-induced suppression made directly visible

We first asked whether the spatial extent of the TMS-induced suppression could be directly perceived. We reasoned that, if TMS interferes with neural signals projecting onto a limited area of the cortical retinotopic representation, the TMS-induced suppression should be perceived as a gap in pattern vision with a large-field, patterned stimulus. To test this hypothesis, we presented a large, circular grid pattern consisting of vertical and horizontal gratings with 50% contrast (diameter, >13°) on a gray background for 40 ms instead of a small target as used in previous studies (**Fig. 1**). A single magnetic pulse was applied with a delay of ~100 ms from the onset of the visual stimulus (**Fig. 1a**). This delay is effective for the suppression of small visual targets[2].

The coil was 8-shaped, and its center (the intersection of the two windings) was placed a few centimeters lateral from and above the inion (the external occipital protuberance of the skull). Under these conditions, the briefly presented, patterned stimulus appeared with a patch missing from the grid pattern in the lower quadrant of the visual field contralateral to the coil (**Fig. 1b**). The suppressed region generally appeared homogeneous and gray.

Using a mouse, each subject drew an ellipse on the computer screen to match the perceived suppressed region (see Methods for phenomenology of preliminary observations and detailed procedure). The data of five repeated trials were converted to a reconstructed percept as shown in Fig. 1b. Regions with reduced pattern contrast represent areas included in the ellipse (suppressed region) in a higher proportion of trials. The size of the suppressed region varied substantially across six subjects (1.2°–5.6°, long axis). When the delay of the magnetic stimulation was systematically varied, the suppressed region was observed only between 60 and 180 ms, peaking at delays of 80–120 ms (**Fig. 1c**), roughly in agreement with a previous study using small letters[2]. The results of control conditions using other scalp locations or catch trials provided evidence against artifacts (see Methods).

Consistency with cortical retinotopy

To further validate our technique, we shifted the coil position and compared the results with the known anatomy of visual cortex (**Fig. 2**). Note that this technique allows determination of a suppressed region with high resolution with only a single trial, whereas many trials are required for characterization based on performance in discriminating or identifying small visual targets at various locations[2,4,7]. When the coil was shifted to the contralateral, symmetrically positioned spot (0 to 1 in **Fig. 2a**), the suppressed region moved to the contralateral visual field (**Fig. 2b**) as in previous TMS studies[2,4,7]. The suppressed location did not change significantly with changes in the vertical coil

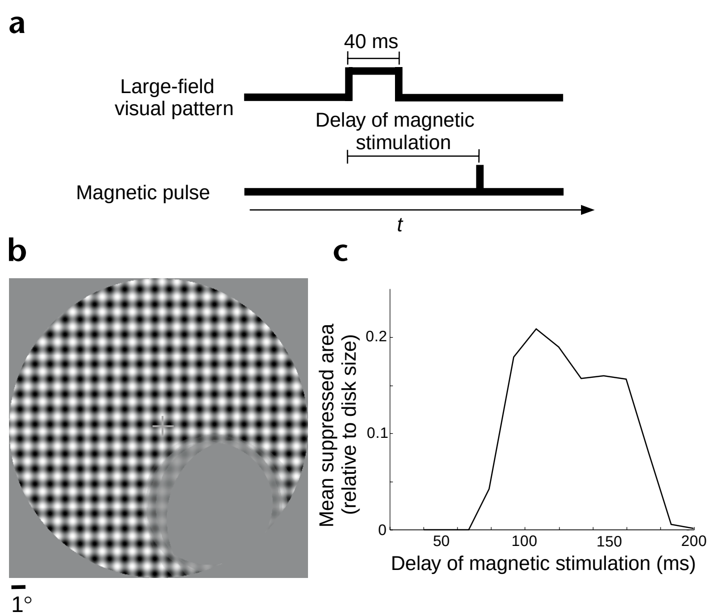

Fig. 1. Locally suppressed region in a large-field patterned stimulus. **(a)** Time course of the presentation of the large-field patterned stimulus and the magnetic stimulation. The duration of the magnetic stimulation was less than 1 ms. The delay of the magnetic stimulation refers to the time from the onset of the visual stimulus to that of the magnetic stimulation. **(b)** Reconstructed percept obtained when a grid pattern (0.9 cpd; diameter, 21°) was presented, followed by a magnetic pulse delivered by an 8-shaped coil placed on the left occipital lobe (2 cm to the left of and above the inion), with a delay of 106 ms (subject OK). See Methods for the details of the method of reconstructing the percept. Note that the subject shown here tended to perceive a larger suppressed area centered in the periphery, compared to the other subjects. **(c)** Mean suppressed area as a function of the delay of the magnetic stimulation (subject OK). The conditions were identical to those mentioned above except for the delay.

position (0, 2 and 3), and suppression was rarely perceived in the upper visual field[4,7]. This may be because lower portions of the visual cortex representing the upper visual field are farther from the scalp as observed in magnetic resonance images. The lateral shift within the hemisphere (0 to 4) increased foveal suppression, consistent with the anatomy in that the map of the foveal visual field is located in superficial regions of cortex and extends laterally[8]. In general agreement with previous studies, these results confirmed that the visualized suppressed region indeed reflected interference of TMS with the activity of the cortical retinotopic representation rather than an artifact caused by muscular contraction or the sound generated by the coil. The effect of laterally shifting the TMS site within the hemisphere, however, had not been previously found. The exact cortical site of stimulation was unclear (V1, V2/V3 or both); it might be identified by combining location of the suppression with a cortical retinotopic map obtained with functional magnetic resonance imaging[9,10] for each subject.

Pattern-dependent distortion of suppresion by TMS

The agreement of our findings with previous studies provides support for the validity and efficiency of our technique in identifying the suppressive effect of TMS. This technique also allowed direct perception of the shape as well as location and size of the suppressed region. Some unique aspects of the TMS-induced suppression visualized with this method suggest that the percept of the suppressed region reflects more than the mere geometry of the visual cortical map and the induced electric field.

When horizontal and vertical gratings (100% contrast) were substituted for the grid pattern, we found that the shape of the suppressed region depended on the pattern (**Fig. 3**). The suppressed region was perceived as horizontally compressed when a horizontal grating was presented (**Fig. 3a**) and vertically compressed when a vertical grating was shown (**Fig. 3b**) relative to the suppressed region seen with a grid (**Fig. 3c**). In one subject, however, the suppressed region tended toward a horizontally compressed shape regardless of the pattern. For the subjects who perceived this anisotropic distortion, the aspect ratio ranged from 1.3:1 to 3.2:1. To see if the distortion resulted merely from the short duration of the visual stimulus, we presented gratings containing a circular, gray patch comparable in size to the suppressed region for 40 ms without TMS. In this case, little distortion was observed. Therefore, the anisotropy was not simply due to the brief presentation of the visual stimulus.

Relative to that perceived with the grid pattern, the suppressed regions in the gratings were generally more compressed along the stripes than elongated in the directions perpendicular to them; that is, the stripes in the gratings seemed to extend into the suppressed region. In addition, the suppressed region in the grid pattern did not match the superposition of those observed with horizontal and vertical gratings, even when the contrast of the horizontal and vertical gratings was reduced to 50% for a better comparison with those composing the grid.

The anisotropic distortion may simply reflect the elliptical shape of the classical receptive fields of cells tuned to the pattern's orientation that are inhibited by the magnetic stimulation. However, the receptive fields of most simple cells are elongated along, rather than perpendicular to, the preferred orientation[11]. Therefore, TMS would be expected to affect an elongated region parallel to the pattern orientation. Additionally, classical receptive field shape would not explain differences of the suppressed region

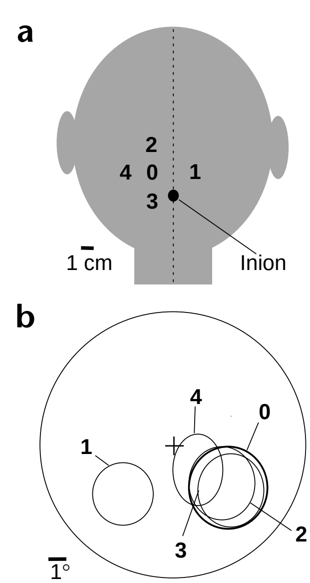

Fig. 2. Mapping of visual cortex. **(a)** Positions of the center of the coil. The center of the coil was shifted from the base position (0, 2 cm above and left of the inion) to the contralateral, symmetrical position (1), to the upper and lower positions by 2 cm (2, 3), and to the lateral position by 2 cm (4). **(b)** Suppressed regions for the different coil positions (subject YK). Each ellipse represents the mean position and the mean lengths of the axes of the ellipses drawn by the subject. The visual stimulus was a grid pattern (1.5 cpd) presented for 40 ms. The delay of the magnetic stimulation was 106 ms.

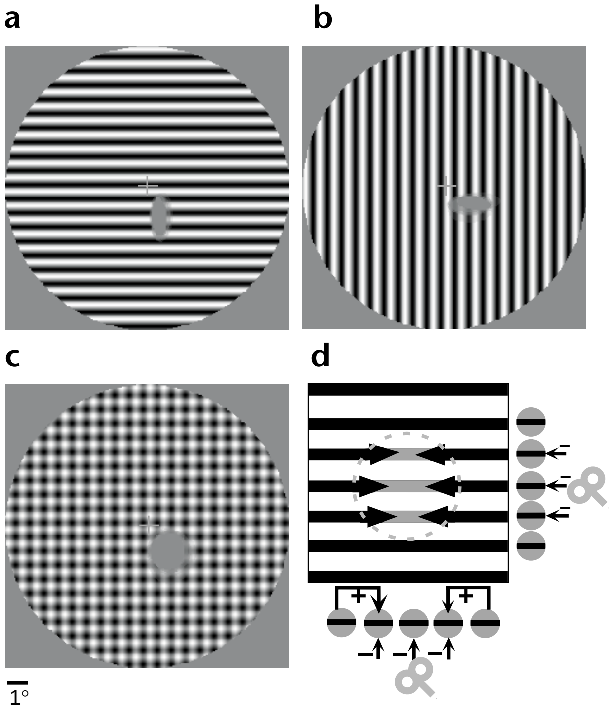

Fig. 3. Anisotropic suppressed region in oriented patterns. **(a–c)** Reconstructed percept of subject PD for horizontal **(a)** and vertical **(b)** gratings, and a grid pattern **(c)**. The visual stimulus was presented for 40 ms, and the magnetic stimulation was delayed 106 ms. Note that this subject saw smaller suppressed regions than the other subjects. **(d)** Hypothetical mechanism for the anisotropic distortion of the suppressed region. A horizontal grating is shown with horizontally tuned neural units aligned vertically (right) and horizontally (bottom). The central gray circle represents the visual space corresponding to the cortical area directly affected by the magnetic stimulation. Long-range facilitatory connections among collinearly aligned units (**+** in the bottom row) mask inhibition by inputs caused by TMS (**–**); thus, the suppressed region appears compressed along the stripes.

in the grid pattern from the superposition of those seen with horizontal or vertical gratings without assuming some nonlinear interactions among receptive field mechanisms.

A more satisfactory account may be provided in terms of long-range facilitatory connections and nonlinear interactions among classical receptive field mechanisms with a similar preferred orientation and collinear alignment. The mechanisms are suggested by anatomical[12], electrophysiological[13,14] and psychophysical[15] studies, and may be involved in various kinds of completion phenomena. The long-range facilitation by collinear stimuli, most pronounced in cells firing at near-threshold level[14], may counter inhibition triggered by magnetic stimulation. As facilitation occurs only along the stripes, it produces the anisotropic shape of the suppressed region (**Fig. 3d**). The large, round suppressed region observed in the grid pattern may reflect attenuation of the facilitatory effect between collinear lines by the presence of orthogonal ones as observed in monkey V1 (ref 13), which would inhibit extension of the perceived stripes.

To further confirm the compression of the TMS-induced suppression along stripes, we compared the suppressed areas within radial, concentric and grid patterns (**Fig. 4**; see Methods for stimuli). The centers of the radial and concentric patterns were positioned at the center of the suppressed region determined with the grid pattern in each subject. We predicted that the suppressed area in the radial pattern would be smaller than those in the other patterns because of the extension of stripes toward the center of the suppressed region. Four subjects showing anisotropic distortion with the horizontal and vertical gratings judged the area of the suppressed region smallest in the radial pattern (**Fig. 4a**) and largest in the grid pattern (**Fig. 4c**). The ratio of the suppressed area in the radial pattern to that in the grid pattern ranged from 0.51:1 to 0.85:1, confirming that the TMS-induced suppressed region was compressed along stripes. The larger size of the suppressed area in the grid pattern may indicate strong inhibition of stripe extension in the presence of the orthogonal stripes.

Filling in of TMS-induced suppression in time

An important question still remains: why was the suppressed region visualized as gray? This may reflect a ‘default value’ in perception corresponding to suppressed neural activity. However, as gray fields were presented both before and after the flashed visual stimulus, it may also be possible that the gray resulted from filling in with the visual features temporally adjacent to the flashed stimulus. To address this issue, we presented colored rather than gray homogeneous fields for more than one second both before and after a flashed grating (**Fig. 5**). Because it was perceived less clearly when presented between colored fields, the grating was presented longer (80 milliseconds) than in the previous experiments. After drawing the suppressed region, the subject selected the perceived color of the suppressed region from a gradient scale between gray and the colors of the homogeneous fields. When the grating was presented between red fields and followed by a magnetic pulse, the suppressed region appeared close to red (**Fig. 5a**), suggesting that the suppressed region was filled in with temporally adjacent stimuli. Temporal filling in may explain why it is difficult to perceive TMS-induced suppression when viewing a continuous scene: interruptions of neural signals by TMS may be quickly filled in with the same local feature, obscuring the gap.

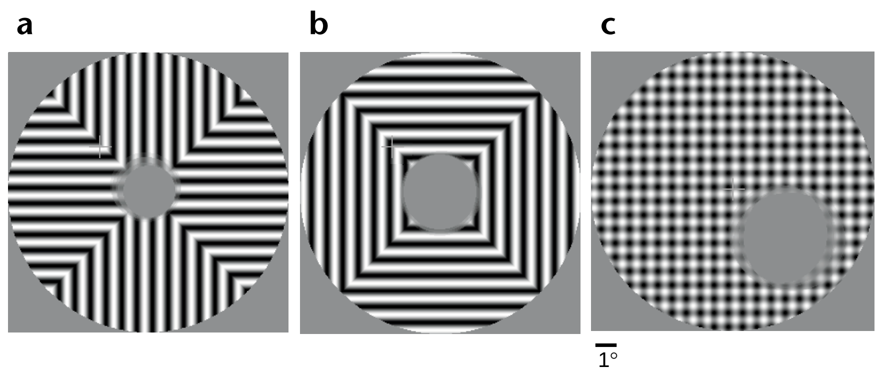

Fig. 4. Compression of the suppressed region in a radial pattern. **(a–c)** Reconstructed percept of a representative subject (SS) for radial **(a)**, concentric **(b)** and grid **(c)** patterns. The radial and concentric patterns were presented away from the fixation point such that the suppressed region was observed in the center of the patterns. The visual stimulus was presented for 40 ms, and the delay of the magnetic stimulation was 106 ms.

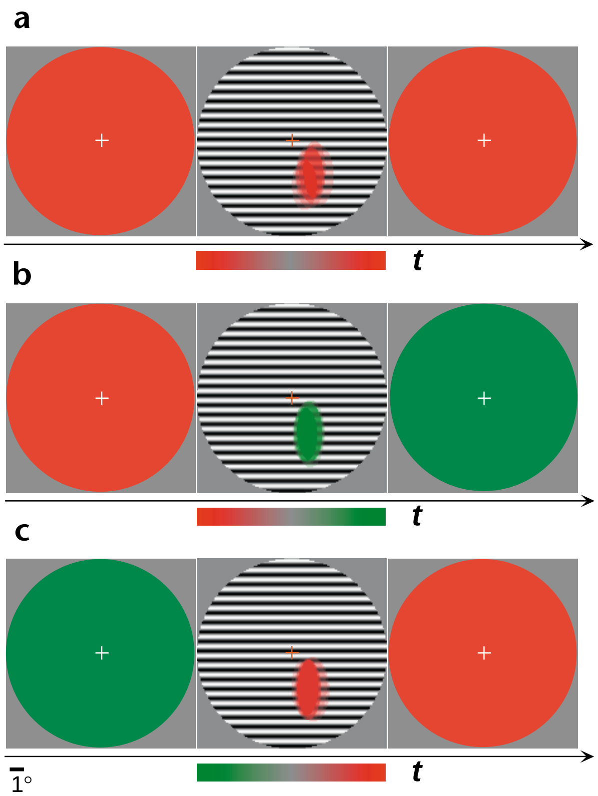

Fig. 5. Filling in of the suppressed region in time. **(a–c)** Reconstructed percept in a flashed grating (middle) and colored fields presented before (left) and after (right) the grating (subject SS). The grating was flashed for 80 ms between colored fields presented for more than 1 s. A magnetic pulse was applied after a delay of 106 ms. After drawing the suppressed region, the subject reported its perceived color by selecting one from a gradient scale of gray and red/green as shown below the middle panels. The color for each pixel was averaged over repeated trials. Note that as the presented grating was horizontal, the suppressed regions were horizontally compressed.

Next, to see whether the filled-in information was from the preceding or subsequent backgrounds, homogeneous fields of red or green were presented before and after the grating (**Fig. 5b** and **c**). Subjects consistently reported the color of the suppressed region to be closer to that presented after the grating, though apparent color saturation varied across subjects. Results were similar over the range of delays of the magnetic stimulation that produced clear, localized suppression. As is observed in backward masking[16,17], the subsequent stimulus affected perception of the previous one. This might be reasonably explained by assuming that, without magnetic stimulation, the grating masks and thus delays perception of the following colored stimulus; magnetic suppression of this forward masker may lead to backward filling in with the following color. Thus, this finding seems analogous to the finding that TMS can block backward masking of a visual target by suppressing the masking stimulus[18]. However, note that in this 'unmasking', the backward masker is suppressed by TMS, whereas we assume suppression of a forward masker. Furthermore, 'unmasking' does not necessarily imply temporal filling in of the suppressed region. Our finding suggests that percepts in the suppressed region may indicate not only loss of neural signals but also dynamic reorganization among temporally adjacent neural signals to replace them. Determining the generality of backward temporal filling in in terms of the temporal sequence and the type of visual stimuli (see Methods) will require additional studies.

Discussion

We have shown that TMS-induced suppression can be visualized as a local loss of pattern within a large-field visual stimulus. The dynamic nature of this visualized suppression was also demonstrated by orientation-dependent spatial distortion and filling in with temporally adjacent stimuli. These phenomena suggest neural mechanisms for spatial and temporal completion of weak or absent information. As subjects did not see phosphenes when TMS was applied without a flashed visual stimulus (see Methods), the visualized suppression cannot be regarded as masking by such an excitatory effect[19]. Furthermore, as demonstrated by temporal filling in, the percept in the suppressed region was highly dependent on temporally adjacent stimuli, whereas visual signals like phosphenes would be invariant for different temporally adjacent stimuli.

These perceptual phenomena suggest at least two stages of neural correlates. First, the suppressed region reflects the local and immediate interference of the induced electric field with the membrane potential of neurons and resulting inhibition of action potentials. Second, pattern-dependent distortion and temporal filling in of the suppressed region both suggest that the percept of the suppressed region may also reflect dynamic interactions of neural signals in visual cortex triggered by the initial reaction to the induced electric field.

In conclusion, we demonstrated three points. First, direct visualization of the spatial extent of TMS-induced suppression allowed study of the relationship between human perceptual experience and the electrical activity in the early visual cortex more directly and in greater detail than in previous studies. Second, the results obtained with this technique showed that the visualized suppression reflects more than the mere geometry of the visual cortical map in the occipital lobe, suggesting the interference of TMS with cortical processing via neuronal connections and temporal interactions of neural signals. Last, our results also suggest ways in which cortical units such as orientation-tuned cells interact to produce a percept.

Methods

Magnetic stimulation. A Magstim Model 200 magnetic stimulator with a 70-mm double coil (Magstim, Wales, UK) was used (2.2 T maximum output at the coil surface; monophasic pulse; duration, 1 ms; rise time, 100 µs). The power was adjusted to a value slightly above the threshold to produce an effective suppressed region for each subject (70–90% maximum power). The center of the coil (the intersection of the two windings) was placed 2–5 cm lateral to and above the inion (most typically, 2 cm to the left of and above the inion). The coil was oriented to induce an electric field at 45° in the left hemisphere and 135° in the right (upward and toward the midline[20]). The use of TMS was approved by the human subject internal review board at the California Institute of Technology. Informed consent was obtained from all subjects.

Visual stimuli. A large patterned disk (diameter, >13°) was presented briefly (40 or 80 ms) on a gray background (22.3 cd per m^2). The size of the disk was adjusted for each subject such that the suppressed region was mostly included in the disk. The grid pattern was composed of superimposed horizontal and vertical sinusoidal gratings with 50% contrast. Separately presented horizontal and vertical gratings had 100% contrast. As spatial frequency of a true radial pattern varies with the distance from the center, the center and the periphery would thus appear asynchronously when the pattern was flashed, confusing the perception. Therefore, radial and concentric patterns were actually composed by rearranging the horizontal and vertical gratings as shown in Fig 4a and b. With radial and concentric patterns, the disk was shifted such that the suppressed region was seen in its center; with other patterns, a fixation point was placed in the center of the disk. The spatial frequency of the patterns was typically 1.5 cycles per degree (cpd; range, 0.45–3 cpd). A lower spatial frequency was used for those who perceived a suppressed region centered in the periphery. In the last experiment, homogeneous red or green rather than gray disks (18.0 cd per m^2) were presented before and after a flashed grating for more than one second. In a separate session, patterned disks preceded and followed a homogeneous one. However, the patterned disks were so salient that they obscured the flashed homogeneous disk, preventing a clear percept of the localized suppression and its visual features. Visual stimuli were presented on a CRT monitor (Sony Multiscan20seII) with a frame rate of 75 Hz, and controlled by a personal computer (Apple Power Macintosh 7600).

Preliminary observations. Of 21 observers, including the 6 experimental subjects, only 2 perceived phosphenes when TMS was applied without a flashed visual stimulus, whereas 5 of them could see neither phosphenes nor a locally suppressed region in the pattern. All others (14) perceived a locally suppressed region, though some initially required 20–30 trials to clearly and consistently perceive it, but did not perceive phosphenes. Regardless of observers' knowledge of brain anatomy, the suppressed region perceived with effective delays of the magnetic stimulation was unanimously reported to appear in the contralateral lower visual field, making cognitive artifacts unlikely. Individual differences may be attributed to variable susceptibility to artifacts such as blinks, neck or eye movements and noise generated by the stimulator. Anatomical variability in orientation and proximity of visual cortex to the scalp may also contribute to such differences[21]. Scalp stimulation at locations other than the occipital lobe, such as the frontal or temporal lobes, did not produce localized suppression of the pattern, but often elicited blinks and eye movements leading to general suppression of visual responses.

Subjects. Six subjects, including the authors, were studied in all experiments except for that using the radial and concentric patterns; four participants were used in this experiment. All had normal or corrected-to-normal visual acuity and had never suffered from neurological diseases. The subjects except the authors did not know the purpose of the experiments, though they had elementary knowledge of brain anatomy. In the preliminary observations, none perceived phosphenes when TMS was applied alone, but with appropriate conditions, they began to perceive a locally suppressed region within a few trials.

Experimental procedure. After the visual stimulus was flashed and followed by a magnetic pulse, the visual stimulus appeared again on the screen. Using a mouse, the subject drew an ellipse on the screen to match the region missing the pattern; if the suppressed region was not observed, the subject indicated this by clicking the mouse. Five trials were repeated for each condition. In drawing the ellipse, the subject adjusted the position and the lengths of the horizontal and vertical axes. This small number of parameters adequately represented the percept, as observers usually reported the suppressed region not to be dented, angular or very obliquely oriented. In the last experiment, after drawing an ellipse, the subject selected the perceived color in the suppressed region with the mouse. The ellipse color changed with the horizontal position of the mouse, corresponding to the degree of the mixture of gray and the colors presented before and after the grating. As yellowish color was not reported in the preliminary observation, the mixture of red and green was not used. The delay of the magnetic stimulation was typically set to the value that caused the maximum area of suppression when a grid pattern was used and the delay was systematically varied (106 or 120 ms for the subjects studied here). In some catch trials, ineffective delays (0 or 40 ms delay) were used as a control for false alarms or cognitive artifacts. In most of these trials, subjects reported the absence of a locally suppressed region.

Reconstruction of percept. For each pixel, the ratio of trials where the pixel was included in the elliptical suppressed region was calculated. Contrast of the pattern was then modulated by ⟨1 – ratio of suppression⟩. Thus, the region included in the ellipse for most trials looks homogeneous, whereas the region mostly outside the ellipse has higher contrast. This transformation of the original data allowed us to visualize approximately what the subject perceived and assess its consistency over trials. For the last experiment, the color for each pixel was averaged over trials.

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