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Transcranial magnetic stimulation of early visual cortex suppresses conscious representations in a dichotomous manner without gradually decreasing their precision

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ABSTRACT

Transcranial magnetic stimulation (TMS) of early visual cortex can suppresses visual perception at early stages of processing. The suppression can be measured both with objective forced-choice tasks and with subjective ratings of visual awareness, but there is lack of objective evidence on how and whether the TMS influences the quality of representations. Does TMS decrease the precision of representations in graded manner, or does it lead to dichotomous, "all-or-nothing" suppression. We resolved this question by using a continuous measure of the perceptual error: the observers had to perceive the orientation of a target (Landort-C) and to adjust the orientation of a probe to match that of the target. Mixture modeling was applied to estimate the probability of guess trials and the standard deviation of the non-guess trials. TMS delivered 60–150 ms after stimulus-onset influenced only the guessing rate, whereas the standard deviation (i.e., precision) was not affected. This suggests that TMS suppressed representations dichotomously without affecting their precision. The guessing probability correlated with subjective visibility ratings, suggesting that it measured visual awareness. In a control experiment, manipulation of the stimulus contrast affected the standard deviation of the errors, indicating that contrast has a gradual influence on the precision of representations. The findings suggest that TMS of early visual cortex suppresses perception in dichotomous manner by decreasing the signal-to-noise ratio by increasing the noise level, whereas reduction of the signal level (i.e., contrast) decreases the precision of representations.

1. Introduction

Transcranial magnetic stimulation (TMS) provides a unique way to study the causal roles of cortical areas in visual perception and visual awareness. A single TMS pulse on a specific area may interfere with perceptual process, provided that the area has a causal role in that process during the moment of stimulation. Amassian et al. (1989) were the first to show that TMS delivered over the occipital cortex in a specific time window, about 60–140 ms after the onset of the visual stimulus, suppressed the perception of stimuli. This 'classical dip' is one of the most reliable effects in the TMS literature (Kammer et al., 2005; de Graaf et al., 2014). It has been replicated in many studies using both objective forced-choice tasks and subjective ratings of visual awareness (i.e., subjective experience of seeing). Typically, both objective and subjective measures show a parallel decline during ~60–120 ms after the onset of visual stimulus, with the largest suppression around 80–100 ms (de Graaf et al., 2011a, b; Koivisto et al., 2011b, 2012; Jacobs et al., 2012; Railo et al., 2012).

TMS of occipital cortex may impair visual perception also when delivered shortly before the visual stimulus is presented (Corthout et al., 1999a, b, 2000; 2003; de Graaf et al., 2011a; Jacobs et al., 2012), suggesting that the visual cortex must be in a specific kind of preparatory state for the oncoming stimulus to be perceived (Mathewson et al., 2009). Occipital TMS may also deteriorate perception at relatively long latencies (~220–280 ms), but this effect seems to be restricted to processing of complex stimuli (Camprodon et al., 2010; Koivisto and Silvanto, 2012).

Subjective reports by observers suggest that the TMS-induced scotoma is filled-in by the temporally adjacent visual field (Kamitani and Shimojo, 1999; Murd et al., 2010). However, there is no direct evidence in literature on how occipital TMS influences the *quality* of perceptual

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representations. Does it suppress perception in a dichotomous "all-or-nothing" manner, or does it decrease the precision of visual representations gradually? To reveal the influence of occipital TMS on the quality of perceptual representations, we used a mixture modeling method, which was first applied in working memory research (Zhang and Luck, 2008), but has been recently applied also to perception (Asplund et al., 2014; Harrison et al., 2016). The observers were asked to perceive the orientation of Landolt-C and to adjust the orientation of a probe to match that of the original one. The degree of the error between observer's adjustment and the actual orientation was measured. For perceived stimuli, the error values form a Gaussian distribution around the correct value (i.e., error of 0°; Fig. 1A). For unperceived stimuli, the observer must guess and the responses are distributed randomly between −180 and 180°. Mixture modeling was used to estimate the proportion of non-guess ('correct') trials in which the responses came from a circular Gaussian distribution centered on target's orientation and the proportion of guess trials (*g*) where responses came from a uniform distribution. The standard deviation (*sd*) of the distribution of non-guess responses provided the measure of the precision of the perceptual representation.

If TMS of early visual areas degrades the precision of representations, then *sd* should be increased. Alternatively, if TMS disrupts the representations dichotomously, it should increase the proportion of guess responses (*g*) without affecting precision (*sd*). It is also not clear whether the influence of TMS on representations is qualitatively similar at different time windows. Therefore, we stimulated early visual cortex in time windows ranging from 30 ms before the visual stimulus was presented to 120 ms and 180 ms after its onset. TMS may decrease the signal-to-noise ratio by increasing the noise in the visual system (Ruzzoli et al., 2010; Schwarzkopf et al., 2011; Rahnev et al., 2012). In other words, single-pulse occipital TMS may interfere with visual perception by increasing the noise level, without necessarily decreasing the strength of the signal, and thereby it decreases the signal-to-noise ratio (Ruzzoli et al., 2010; Schwarzkopf et al., 2011; Rahnev et al., 2012). Noise may have a dichotomous effect on perception: a masking study (Agaoglu et al., 2015) made use of the mixture modeling and showed that visual noise mask influenced perception dichotomously by increasing the probability of guessing, without affecting the deviation of perceptual errors, whereas metacontrast decreased the quality of representation gradually. Thus, under the assumption that increase of noise produces dichotomous suppression, we can predict that TMS will have a dichotomous influence on perception. For comparison, we performed another experiment manipulating the contrast of the visual stimulus to test how reduction of the strength of the signal influences the quality of perception.

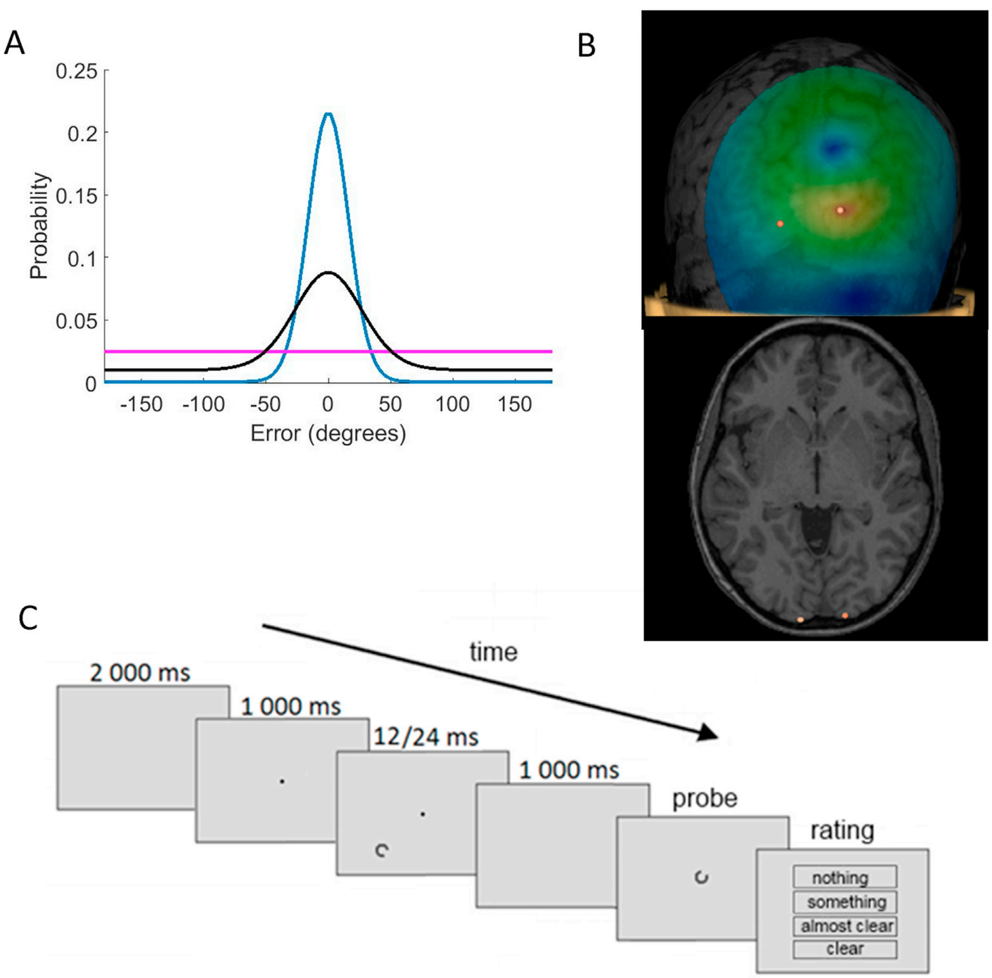

Fig. 1. A. Mixture modeling. When the stimulus is perceived, the reported stimulus values are near the correct value (blue line). When the stimulus is not perceived, the observers' reported values are guesses which are distributed randomly and they do not form a Gaussian distribution around the correct value (pink line). Usually the observers make both types of responses and the data consists of mixture of both type of trials (black line). B. The stimulation areas in the brain of one of the participants are indicated with the orange spots. The colors red-yellow-green (up) describe the modelled strength of the electric field in descending order. C. An example trial. The target stimulus, Landort-C, was presented in random orientation to the left or right lower visual field. One second after the offset of the target, the probe was presented to the fixation in randomized orientation. The participants adjusted the orientation of the probe to match that of the target and rated their subjective awareness of the target.

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