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The neural basis of the Enigma illusion: A transcranial magnetic stimulation study

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ABSTRACT

The aim of this study was to test the role of the visual primary (V1) and the middle temporal area (V5/MT) in the illusory motion perception evoked by the Enigma figure. The Enigma figure induces a visual illusion that is characterized by apparent rotatory motion in the presence of a static figure. By means of repetitive transcranial magnetic stimulation (rTMS) we show that V5/MT is causally linked to the illusory perception of motion. When rTMS was applied bilaterally over V5/MT just prior to presentation of the Enigma figure, the perception of illusory motion was disrupted for approximately 400 ms resulting in a delayed illusion onset. In contrast, rTMS applied over V1 did not have any effect on the illusory perception of motion. These results show that V5/MT, a visual cortical area associated with real motion perception, is also important for the perception of illusory motion, while V1 appears not to be functionally involved in illusory motion perception.

1. Introduction

Enigma, devised by Leviant (1981 – Palais de la Découverte, Paris) is a figure that elicits the spontaneous perception of rotary motion in the absence of real motion. The image consists of a black and white ray pattern with narrowly spaced radial lines, onto which three chromatic rings are superimposed (Fig. 1). The presence of illusory motion seen on the rings suggested the name "The Enigma". The illusory motion of the annuli alternates between clockwise and counter-clockwise rotation (Gori, Hamburger, & Spillmann, 2006; Leviant, 1996).

Enigma is a peculiar motion illusion which makes this figure very interesting to study. While most other motion illusions represent a misperception of motion direction (Gori & Hamburger, 2006; Gori & Yazdanbakhsh, 2008; Gori, Giora, & Stubbs, 2010; Pinna & Brelstaff, 2000; Wallach, 1935; Yazdanbakhsh & Gori, 2008), the illusory motion in the Enigma figure is present under static viewing conditions; that is, no motion of the observer or of the stimulus is necessary to perceive the illusory rotary motion. Another motion illusion, the Rotating Snakes (Kitaoka and Ashida, 2003), elicits motion under static viewing conditions, but it does not show motion reversals as the Enigma figure does. All of these characteristics make the Enigma figure a very unique and intriguing motion illusion.

Several hypotheses have been formulated on the mechanisms underlying the illusory motion induced by the Enigma figure. Gregory (1993, 1995) proposed an explanation in terms of fluctuations in the eye accommodation ("hunting for accommodation") and fixational eye movements (FEMs) (Gregory, 1994; Mon-Williams & Wann, 1996), suggesting that these factors may account for the illusion induction. Zeki, Watson, and Frackowiak (1993) showed by means of positron emission topography (PET) that when participants perceived illusory motion, the regional cerebral blood flow (rCBF) increased in the same brain areas that were active when participants were looking at a physically moving stimulus (V5/MT, an extrastriate area highly involved in visual motion processing (Born & Bradley, 2005) and adjacent motion areas, such as V3a, V3b and MST), suggesting therefore that the illusory motion could be mediated by the same neurons as real motion. Moreover, in addition, during the illusory motion observation, the authors reported rCBF increases in other areas outside the visual cortex (right frontal operculum and right anterior cingulate gyrus), which

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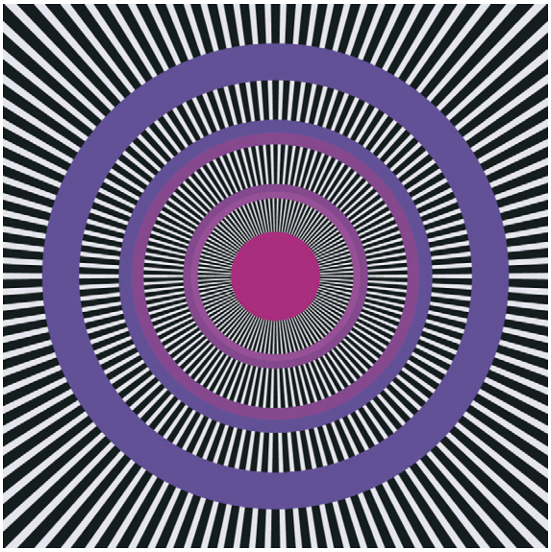

Fig. 1. The Enigma figure drawn by Leviant (1981).

are not usually activated when participants are exposed to real motion. Therefore, also these brain regions could be candidates for mediating perception of the Enigma figure. Based on these results, Zeki et al. (1993) argued that the generation of illusory motion may depend on the activation of frontal areas that are not active during exposure to real motion, thus excluding retinal influences in the illusion perception. On the other hand, a computational model consistent with available neurobiological evidence was proposed by Fermuller, Pless, and Aloimonos (1997) that attempts to make both FEMs and cortical activation necessary for the perception of motion induced by the Enigma figure. Their model proposes that eye movements are necessary to trigger the illusory rotation in the Enigma figure but that high-level cortical processes are mainly responsible for the illusion. Recently, Hamburger (2007) and Kumar and Glaser (2006) claimed that the illusory motion in the Enigma figure is not the result of motion of the image on the retina due to microsaccades but rather has a strictly cortical origin. Gori et al. (2006) provided data supporting the cortical role of this illusory phenomenon without excluding the possibility that FEMs were involved in the generation of the illusion. These authors highlight a clear regularity in the reversals that suggests the presence of a neural saturation mechanism at the cortical level. Moreover, they showed how real motion can influence illusory motion, suggesting that real and illusory motion interact at some point along the motion-processing pathway. On the other hand, Troncoso, Macknik, Otero-Millan, and Martinez-Conde (2008) convincingly demonstrated that small eye movements are a necessary condition to perceive the illusory motion. These authors set out to resolve the long-standing debate as to whether the initial neural processes that ultimately lead to the perception of the Enigma illusion arise in the eye or in the brain. Because the illusion was found to be strongly dependent on small eye movements, the answer seems to be that the illusion perception starts in the eye, rather than in the brain, even if the brain is necessarily involved in the illusory perception. Troncoso et al. (2008) found, indeed, that the rate of microsaccades increased just before the reported perception of faster illusory motion, compared with a decrement in the rate of microsaccades when the participants reported slower or no illusory motion during a prolonged viewing of the Enigma figure. Therefore, although a full explanation of how the illusion arises is still a controversial topic, it seems reasonable that, even though the FEMs probably trigger the illusion, the cortex plays a pivotal role in the perception of the illusory motion.

In the present study, we aimed at assessing the role of the visual cortex in the perception of the Enigma figure illusion by using transcranial magnetic stimulation (TMS). TMS is widely employed in neuroscience in order to provide more direct evidence of the relationship between a brain area and a cognitive process with respect to the correlation approach typical of brain imaging techniques. In addition, it has been widely used as a tool for studying the underlying neural circuits involved in motion processing and a number of TMS studies have shown that interfering with the normal activity of the V5/MT area significantly affects motion perception (Beckers & Homberg, 1992; Campana, Cowey, & Walsh, 2002, Campana, Cowey, & Walsh, 2006; d'Alfonso et al., 2002; Hotson & Anand, 1999; Laycock, Crewther, Fitzgerald, & Crewther, 2007; Ruzzoli, Marzi, & Miniussi, 2010; Sack, Kohler, Linden, Goebel, & Muckli, 2006; Stevens, McGraw, Ledgeway, & Schluppeck, 2009). Despite methodological differences in the various TMS studies, there is agreement about defining two cortical windows of activation of V5/MT in visual motion processing (d'Alfonso et al., 2002; Laycock et al., 2007; Sack et al., 2006; Stevens et al., 2009): an early activation beginning approximately 60 ms prior to stimulus presentation and a late temporal window of activation beginning approximately 130 ÷ 150 ms after stimulus presentation (Stevens et al., 2009). In the first experiment of the present study, we varied the time window in which repetitive TMS (rTMS) was delivered over V5/MT, either before or after the appearance of the Enigma figure in order to define the temporal window in which perception of the Enigma illusion could be affected. In the second and third experiment, in view of the numerous feedforward and feedback projections existing between V1 and V5/MT (Born & Bradley, 2005) we explored the role of the V1 cortex in the perception of the illusion.

2. Experiment 1: rTMS over V5/MT

2.1. Materials and methods

2.1.1. Participants

Sixteen naïve healthy participants (seven males, 20 ÷ 28 years old), took part in the experiment as paid volunteers. All of them had normal or corrected to normal visual acuity. None of them had neurological, psychiatric or other relevant medical problems or any contraindication to rTMS (Rossi et al., 2009). All participants gave informed consent and the experimental protocol was approved by the Ethics Committee of IRCCS San Giovanni di Dio, Fatebenefratelli, Brescia, Italy.

2.2. Stimuli and apparatus

Stimuli were displayed on a 19-inch monitor with a refresh rate of 60 Hz that was generated with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1024 × 768. Each pixel subtended ~1.9 arcmin. The grayscale Enigma illusion used by Hamburger (see Fig. 2A in Hamburger, 2007) served as stimulus (Fig. 2A). As a control stimulus (Fig. 2B), the same version of the Enigma figure was used, except that the radial lines were replaced by a black homogeneous background (see Fig. 2I in Hamburger, 2007). According to Hamburger (2007), this stimulus does not induce illusory motion. Both Enigma and control figures had a Michelson contrast of 98%. The figures subtended 15.4 × 18.3° of visual angle and were presented at the center of the screen. A black central fixation point (0.22°) overlapped with the center of the figures.

2.3. TMS protocol

TMS was applied simultaneously and bilaterally over V5/MT using two Magstim Super Rapid Magnetic Stimulators (50 Hz—biphasic, four boosters) and two figure-of-eight coils (custom double 50 mm; Magstim Company Limited, Whitland, UK). The participants wore a close-fitting skullcap on which the