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11 **What Can TMS Tell Us About Visual Awareness?**
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26 Running head: TMS and awareness
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Abstract

TMS of the primary visual cortex (V1) produces suppression of visual processing in retinotopically specific regions of the visual field. Despite this TMS-induced unawareness of visual events, several studies have now demonstrated a tremendous amount of unconscious visual processing without V1. These investigations of visual awareness with TMS provide a unique opportunity to examine the role of different brain regions in visual processing with and without awareness.

What Can TMS Tell Us About Visual Awareness?

With our eyes open, we usually have the impression that we are consciously aware¹ of our visual environment. For example, we may appreciate and avoid obstacles in our path, examine the colour or pattern of the shirt of a passerby, or actively search for a missing pen by sequentially inspecting an array of items on a desk. Thus, at any given moment, we are typically conscious of some, albeit limited, aspect of our visual environment. How does the human brain achieve such a seemingly simple, yet truly remarkable feat?

Patients with focal brain damage have offered unique and some of the most definitive insights into the underlying neural basis of cognition. From decision-making impaired and personality disordered Phineas Gage (Damasio et al., 1994), to blindsight patients DB and GY (Weiskrantz, 1996), to one of our recent patients SR, whose small ventrolateral thalamic lesion has left her with an acquired auditory-tactile synesthesia (Ro et al., 2007), these lesion studies have demonstrated causal roles that different brain regions play in different sensory and cognitive functions. However, such detailed investigations of brain-damaged patients have also frequently revealed a remarkable degree of alterations in cognitive function over the many years of testing after brain damage. For example, after decades of testing, GY appears to have some improved abilities to at least report some visual events in his affected field (Covey, 2004), perhaps due to extensive practice, and SR now reports the ability to feel sounds primarily in the

¹ Throughout this review, the terms consciousness and awareness will be used interchangeably to refer to the subjective perceptual experience of a visual event. In other words, visual awareness will refer to visual information that is represented at the forefront of our thought and can be instantly described or reported without a change in focus or shift of attention. Metaphorically, and along the lines of various models of consciousness that have been advanced, visual information that we are aware of is therefore information that is on a “global workspace,” is on the stage of a “Cartesian theatre,” or has “fame in the brain” (Baars, 2002; Dehaene and Naccache, 2001; Dennett, 2001). In contrast, the terms unconscious and unaware will be used to refer to the lack of a subjective perceptual experience of a visual event, regardless of whether or not that event has been processed by the visual system.

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3 contralesional half of her body (Ro et al., 2007). Although such sensory changes may provide
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5 important information about some of the neural mechanisms of plasticity, since changes likely
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7 reflect reorganisation of brain function over time, they also complicate examinations of sensory
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9 processing and visual awareness.
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13 Unlike in patients with brain damage, however, examining brain function, and in
14
15 particular, visual awareness with TMS provides a unique opportunity to examine the effects of
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17 reversible visual cortex disruption on visual information processing (see Figure 1). In addition to
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19 providing a within-subject control, the use of TMS also drastically reduces or eliminates any
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21 opportunities for long-term neural plasticity. Thus, the precise contributions of different cortical
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23 regions towards visual awareness can be readily elucidated with TMS. Taking this approach,
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25 Amassian and colleagues (Amassian et al., 1989) first showed that visual processing could be
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27 suppressed when TMS is delivered over the occipital cortex within a brief time window after the
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29 onset of a briefly flashed visual stimulus (for a recent review, see Kammer, 2007). Subsequent
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31 studies have shown that motion perception can be disrupted with TMS of the human analogue of
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33 the middle temporal (MT) area of the monkey (Beckers and Homberg, 1992; Beckers and Zeki,
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35 1995; Hotson et al., 1994; Walsh et al., 1998). Furthermore, TMS of the posterior parietal cortex
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37 can produce visual extinction of a contralateral visual target during double simultaneous
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39 stimulation (Pascual-Leone et al., 1994; but see Chambers et al., 2006), a consequence of
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41 ipsilateral hyperorienting towards sensory events after parietal TMS (Seyal et al., 1995; Hilgetag
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43 et al., 2001, Chambers, 2006). These earlier studies demonstrate that TMS can be systematically
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45 used to produce unawareness of visual events and provide converging and replicating evidence
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54 with patient studies.
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3 More recently, several studies have been providing the mechanisms in which the primary
4 visual cortex leads to visual awareness. By using single-pulse TMS, which can provide excellent
5 temporal as well as spatial information regarding brain function, it has been suggested that
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7 interhemispheric connections (Silvanto et al., 2007) and especially feedback projections to V1
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9 (Pascual-Leone and Walsh, 2001; Silvanto et al., 2005a; Silvanto et al., 2005b; Ro et al., 2003)
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11 are important for visual awareness, as studies using other techniques have also suggested (Hupe
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13 et al., 1998; Lamme and Roelfsema, 2000; Fahrenfort et al., 2007; Super et al., 2001). For
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15 example, in one of our studies we have demonstrated using metacontrast masking in conjunction
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17 with TMS that feedback of information to V1 is critical for visual awareness (Ro et al., 2003).
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19 When TMS was applied after a visual target and subsequent mask, visibility of the mask was
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21 suppressed by the TMS. Importantly, the magnitude of this mask suppression was greater in
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23 comparison to trials when a preceding visual target was not presented, indicating that the prior
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25 visual target information was interacting with and affecting later processing of the mask in V1.
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27 Since visibility of the preceding visual target was better when the mask was suppressed by the
28
29 TMS, our results cannot be explained by processing solely within V1, but rather indicate that
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31 feedback activity to V1 is essential for visual awareness.
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41 In addition to feedback activity for visual awareness, recent studies are also suggesting
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43 that low levels and phase of alpha activity in V1 are also important indicators of awareness of
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45 visual events. In a recent study, we have provided evidence that pre-stimulus alpha levels and
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47 phase can predict visual awareness of a metacontrast-masked target (Mathewson et al., under
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49 review). When alpha activity is low and in phase with target stimulus presentation, visibility of a
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51 masked target is increased in comparison to trials with high and out of phase alpha activity. Our
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53 results dovetail with a recent study demonstrating that TMS-induced phosphenes are more
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3 visibile when levels of alpha activity are low (Romei et al., 2008). As a whole, these
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5 investigations of visual awareness with single-pulse TMS provide new and important insights
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7 into the critical and essential role of V1 in visual awareness.
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11 Even when TMS over V1 is used to induce visual unawareness and suppression, there is
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13 now strong evidence that visual information can be processed unconsciously. As in patients who
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15 have primary visual cortex damage with above-chance discrimination abilities, subjects who
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17 have visual cortex suppressed with TMS, and are therefore transiently blind, are still able to
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19 process information at remarkably high levels without any awareness. For example, in one
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21 study, despite unawareness of the orientation of a line in one experiment and unawareness of the
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23 colour of a dot in another experiment, subjects were nonetheless able to guess at well-above
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25 chance levels the orientation and colour of these stimuli presented within their TMS-induced
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27 scotomas (Boyer et al., 2005; also see Jolij and Lamme, 2005 for a demonstration of affective
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29 blindsight). Since this orientation and colour information could not have been processed within
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31 the suppressed primary visual cortex or the superior colliculus, the latter of which cannot process
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33 colour or orientation information, these results implicate a geniculostriate pathway that
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35 bypasses V1 and projects directly from the lateral geniculate nucleus (LGN) into extrastriate
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37 cortex, likely area V4. A direct anatomical pathway from LGN to V4 has been demonstrated in
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39 lower primates (Fries, 1981; Yuki and Iwai, 1981), with our TMS results implicating the
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41 existence of such a pathway in humans as well. Our results further suggest, however, that
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43 information relayed through this pathway is unconscious, at least without a functioning V1.
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52 In another study using TMS to examine unconscious visual processing, we have shown
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54 that unconscious visual information can nonetheless affect saccadic eye movements (Ro et al.,
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56 2004). On the critical trials of that study, we presented a visual distractor within a TMS-induced
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3 scotoma. Despite unawareness of that distractor due to TMS over primary visual cortex, saccades
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5 to peripheral targets were significantly delayed when these “blind” distractors were presented.
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7 Importantly, manual button press responses were not affected by the unconscious distractors,
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9 implicating a role of the superior colliculus, via the retinotectal pathway and involved with
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11 saccade generation (Munoz and Wurtz, 1995b, 1995a; Robinson and McClurkin, 1989), in these
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13 effects.
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18 In a more recent study, I examined whether this unconscious visual information within
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20 the retinotectal pathway may be relayed to and processed at higher cortical levels (Ro, 2008).
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22 Anatomical studies have shown projections from the superior colliculus into the posterior
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24 parietal cortex via the pulvinar (Kaas and Huerta, 1988). Since the posterior parietal cortex is a
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26 part of the dorsal processing stream shown to be involved with visually guided reaching
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28 (Goodale and Milner, 1992; James et al., 2003; Pisella et al., 2000), we assessed whether visually
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30 guided reaching could be affected by unconscious visual distractors. As with saccades, reaching
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32 towards peripheral targets was affected by distractors that were rendered unconscious by TMS of
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34 the primary visual cortex. These results suggest that visual information within the dorsal stream
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36 is also unconscious, as others have also demonstrated (Goodale et al., 1991).
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43 Taken together, these investigations using TMS to examine visual awareness have
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45 provided rich and previously unobtainable information regarding the neural mechanisms for
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47 conscious and unconscious vision. In addition to pinpointing the areas of cortex necessary for
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49 visual awareness, TMS has provided important temporal processing information for visual
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51 awareness, as well as the functional nature of different visual anatomical projections. Future
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53 studies using TMS to examine the visual system should provide further details about the different
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55 brain regions, anatomical pathways, and processing mechanisms for visual awareness.
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Figure Caption

Figure 1. A depiction of the effects of TMS of the visual cortex on visual information processing. When a single TMS pulse is applied over the visual cortex, the induced current transiently suppresses vision, as illustrated in the top portion of the figure. Before the TMS and shortly after it, vision is or returns to normal (bottom portion), allowing for within-subject comparisons of normal and disrupted primary visual cortex function.

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Figure

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