Human ability to initiate reflexive eye movements towards unseen targets without the primary visual cortex

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Abstract

Blindsight patients who have a visual field loss due to a lesion in primary visual cortex (V1) can shift their gaze to stimuli presented in their blind visual field, but the extent to which this is a residual capacity that is not affected by the lesion or caused by neural reorganization is open. Using retinotopically navigated transcranial magnetic stimulation (TMS) of primary visual cortex (V1; Experiment 1, $N = 9$) and metacontrast masking (Experiment 2, $N = 13$), we examined the ability of neurologically healthy individuals to make saccadic eye movements to visual stimuli they report being unconscious of. In both experiments we observed that participants could initiate saccades towards targets they reported not seeing, but in TMS experiment, this happened only on a small proportion (~8%) of unconscious trials. Because saccades towards reportedly unconscious stimuli could be initiated despite V1 TMS, the results suggest that the process may be independent of V1. That said, signal detection theoretic measures suggested that in the TMS experiment, saccades towards reportedly unconscious stimuli may have been based on weak conscious experiences. With both TMS and metacontrast masking, reduced visibility of stimuli was associated with slower and less precise gaze shift. Our results indicate that in neurologically healthy individuals, visual stimuli can trigger saccadic gaze shifts even when the target is reported not consciously perceived, although the reliability, accuracy, and speed of such saccades is inferior when compared to saccades initiated in response to consciously perceived targets.

Keywords: Blindsight; Transcranial Magnetic Stimulation; Primary visual cortex; Saccadic eye movements; Superior Colliculus

Introduction

Humans orient themselves towards stimuli using fast eye movements called saccades. This process is automatic, and it is often further assumed that it can be initiated in response to stimuli that are not consciously seen. Some patients with lesions to the primary visual cortex (V1) have been shown to retain their ability to make saccades towards stimuli that they report not seeing. However, the extent that this ability reflects completely unconscious perception, and is present in neurologically healthy individuals, remains open. Here, we use transcranial magnetic stimulation (TMS) of V1 (Experiment 1) and visual metacontrast masking (Experiment 2) to test if neurologically healthy participants can initiate saccadic eye movements towards stimuli they report not seeing.

According to a popular model, whereas the V1 mediates conscious perception of visual stimuli, the superior colliculus (SC) can trigger behavioral responses towards visual stimuli that are not consciously registered (Danckert & Rossetti, 2005). Together with the pulvinar, the SC is often assumed to correspond to the visual system in phylogenetically older species (Schneider, 1969; Tamietto & De Gelder, 2010), on which the geniculo-V1 visual system of primates has developed on (Baldwin et al., 2017). Because saccadic eye movements are initiated by neurons in the deep layers of the SC (Wurtz, 2010), saccades are a prime candidate for actions that can be triggered by unconscious stimuli. In non-human primates, V1 modulates activity in SC, and V1 lesions lead to spatially more imprecise saccades. Yet, despite the lesion, saccadic reaction times to stimuli in the affected hemifield are relatively fast and show less variance when compared to saccades to the intact visual field (Yoshida et al., 2008), suggesting that they are reflexive behaviors. Studying the extent to which the saccadic eye movements are associated with conscious experience of the stimuli is particularly difficult in non-human primates, but evidence suggests that despite the V1 lesion, monkeys may retain a severely degraded form of conscious visual perception of stimuli (Isa & Yoshida, 2021; Yoshida & Isa, 2015).

In humans, V1 lesions typically cause blindness in the corresponding visual field, but stimuli that are presented in the affected visual field may still influence the behavior of these patients – this is known as *blindsight* (Cowey, 2010; Pöppel et al., 1973; Weiskrantz et al., 1974). It is debated whether blindsight is based on completely unconscious visual information (Michel & Lau, 2021; Weiskrantz, 2009), or whether is a form of severely degraded conscious vision (Campion et al., 1984; Ffychte & Zeki, 2011; Phillips, 2021).

Oculomotor responses to stimuli in the blind visual field have been studied relatively extensively in blindsight patients. Pöppel et al. (1973) observed that while patients ($N = 4$) with V1 lesions could not accurately shift their gaze to stimuli presented in the blind field, the endpoints of the saccades were biased by the stimulus presented to the blind visual field across trials. Weiskrantz et al. (1974) observed that a blindsight patient could accurately fixate targets presented 5° from fixation in the blind visual field, but the accuracy of saccades to more eccentric targets were at chance-level. Perenin and Jeannerod (1978) examined six hemidecorticate patients and observed that "the eyes were turned toward the target each time it had to be located" (p. 8), although this could only be precisely measured in two patients. Zihl (1980) studied three patients and observed that two of them could shift their gaze to stimuli presented in the blind visual field. Interestingly, saccades to blind visual field locations were initiated about 100ms faster than saccades to targets presented in the intact visual field, suggesting that they were reflexive and not based on a conscious decision. Barbur et al. (1988) observed that a patient with left visual cortical lesion could initiate rapid saccades towards visual stimuli in the affected hemifield. Rafal et al. (1990) showed that saccades towards the intact visual field could be slowed down by stimuli presented in the blind visual field. This slowing down was only caused by distractors presented in the (monocular) temporal visual field, suggesting that the effect was mediated by the visual pathway to SC. Savina and Guitton (2018) studied two hemidecorticated patients and reported that patients' saccades towards the blind visual field were biased by stimuli presented in the blind field.

The above findings suggest that some patients with blindsight can fixate targets presented in their blind visual field, but there is variation between patients. The individual differences could be due to variation in the extent of the lesion, as lesions that exclusively extend to V1 are rare. Second, blindsight may be partly a learned ability. For example, Zihl (1980) and Roth et al. (2009) observed that training improved the patients' ability to fixate targets in the blind visual field. Finally, blindsight could be due to neural reorganization of white matter pathways after the lesion. Non-human primates (Isa & Yoshida, 2021) and some patients with blindsight show anatomical connections that are not present in patients without blindsight, or neurologically healthy controls (Bridge et al., 2008; Leh, Johansen-Berg, et al., 2006; Leh, Mullen, et al., 2006; Tamietto et al., 2012). This means that studies on blindsight patients leave open the question to what extent V1 contributes to gaze shifts in neurologically healthy individuals (Railo & Hurme, 2021).

Early visual cortex (V1-V3) TMS can be used suppress the visibility of a briefly presented stimulus (Amassian et al., 1989; de Graaf et al., 2014). This allows the examination whether blindsight-like behavior can be detected in neurologically healthy individuals (known as "TMS-induced blindsight"). While studies do not provide support for a completely unconscious TMS-induced blindsight of visual features such as color or orientation (Hurme et al., 2020; Koivisto et al., 2021; Lloyd et al., 2013; Railo et al., 2014), neurologically healthy participants may be able to detect the presence or roughly localize a visual stimulus they report not consciously seeing (Christensen et al., 2008; Hurme et al., 2017; Railo & Koivisto, 2012; Ro, 2008, reviewed in, Railo & Hurme, 2021). Ro et al. (2004) reported that distractor stimuli whose visibility was suppressed due to TMS delayed saccadic eye movements to visible targets. However, a test of neurologically healthy individuals' ability to initiate a saccade towards a target whose conscious visibility has been suppressed by V1 TMS is lacking.

The aim of the present study was to see if saccadic eye movements can be initiated towards a target participants report not consciously seeing. We presented visual stimuli to the left or right

visual field and asked participants to rapidly shift their gaze to the target. After this, the participants rated how well they saw the stimulus. In Experiment 1, conscious visibility of the stimulus was manipulated by TMS to left or right V1. If the saccade control system can initiate gaze-shifts without the V1, the participants should be able to shift their gaze towards the target location even when stimulus visibility is suppressed by V1 TMS. Experiment 2 is otherwise identical to Experiment 1, but stimulus visibility was manipulated using visual metacontrast masking.

EXPERIMENT 1: TMS

Materials and Methods

Participants

Twelve University of Turku students between ages of 21–46 (11 women, M_{age} = 27, SD_{age} = 7) participated in the study. The visual areas of these individuals had been previously mapped with functional magnetic resonance imaging (fMRI). All the participants had normal or corrected-to-normal vision. Participants were paid a small monetary fee for taking part in the experiment.

The study was approved by the ethics committee of the Hospital District of Southwest Finland and was conducted in accordance with the Declaration of Helsinki and with the understanding and written consent of each participant.

Apparatus

Magnetic Resonance Imaging

MRI was performed in Turku PET-center using 3T Philips MRI. A high-resolution (voxel size = 1 mm^3) T1-weighted anatomical image of the whole head was acquired (3D TFE) for each participant. Visual cortical areas were mapped with fMRI, using a modified version of the multifocal procedure (Henriksson et al., 2012) described by Vanni et al. (2005). The multifocal visual stimuli were presented in the scanner using VisualSystem HD (NordicNeuroLab, Bergen,

Norway) video goggles (1920 × 1200 resolution) and Presentation software (Neurobehavioral Systems, Inc., Albany, CA, USA). For the retinotopic mapping, the major imaging parameters were repetition time of 1,800ms, echo time of 30ms, flip angle of 60°, field of view of 250mm, matrix of 96 × 96, and a 2.5mm^3 voxel size. Twenty-nine slices were acquired in interleaved order. Standard preprocessing with slice-time and motion correction was followed by estimation of general linear model with SPM8 Matlab toolbox.

Transcranial Magnetic Stimulation

TMS was delivered using MagVenture MagPro X100 stimulator and a liquid cooled 65 mm figure-of-eight coil (Cool-B65). TMS intensity was set to 85% of maximum stimulator output. Stimulation location was neuronavigated based on the individual participants' MRIs using Localite TMS Navigator 3.0.48 navigation system. The targeted stimulation areas in V1 were defined individually based on retinotopic maps of the visual cortex. The two stimulation targets were the left and right hemisphere V1 locations corresponding to receptive fields that process the location where the visual stimulus was presented. Anatomically these correspond to locations in the upper bank of the calcarine sulci. Left and right hemisphere locations were stimulated in alternating experimental blocks (order counterbalanced).

Eye-Tracking

Eye movements were recorded monocularly using EyeLink 1000 Plus (SR Research Ltd., Ontario, Canada) at 1000 Hz sampling frequency. Participants were seated 82 cm from the screen, and a chin rest is used to stabilize the head.

Stimuli and Task

In the experiment, participants were presented with visual stimuli 2° from the fixation cross (which was in the center of the monitor) in the bottom left and right quadrants in random order. The stimuli were dots presented against a light grey background (75 cd/m^2) for one screen refresh. The

stimuli size was set to 0.20° but increased if the participant reported that they saw the stimuli in less than 80% of the practice blocks ran before the actual experiment (across the participants, stimulus size was, $M = 0.22°$, $SD = 0.02°$). The measured luminance of the grey stimulus was on average 51 cd/m^2. These visual stimulation parameters roughly correspond to those used by Railo & Koivisto (2012). The experiment was run in MATLAB (version R2014b), and the stimuli were presented on a 24" VIEWPixx /Lite LCD-monitor with refresh rate of 120Hz and a resolution of 1920 × 1080 pixels.

TMS pulse was delivered 100 ms after the visual stimulus onset, as previous studies have shown that this stimulus onset asynchrony (SOA) suppresses conscious perception reliably (de Graaf et al., 2014). Moreover, the study by Hurme et al. (2017) suggests that earlier TMS SOAs may disturb unconscious visual processing by interfering with feedforward visual activity in V1. Because the visual stimulus was presented to either the left or the right visual field, the stimulated cortical area was either contralateral or ipsilateral with respect to the visual stimulus. The contralateral trials were the experimental trials where strong suppression by TMS is expected, and the ipsilateral trials are control trials.

After the pulse, the participants indicated where the stimulus was presented by moving their eyes as fast as possible to the location where the stimuli appeared or kept their eyes in central location if they did not perceive any stimulus. Participants were given 900ms time to give their answer. Then the participants are asked to rate the subjective visibility of the stimuli on a four-step scale (Ramsøy & Overgaard, 2004; Sandberg et al., 2010). The definitions of the four alternatives were carefully explained to the participants. The lowest alternative (0) means that the participants *did not see the stimulus at all*. The second lowest option (1) means that the participant felt that they *detected a small glimpse of the stimulus*. During the instructions, it was emphasized that if the participant felt that they saw anything related to the stimulus (no matter how weak), they should always choose the second lowest option. That is, the lowest alternative was reserved only for trials

where the participant feels confident that they did not see the stimulus at all – throughout the manuscript we refer to these trials as "unseen" or "unconscious". The third option (2) indicates that the participant *perceived the target pretty well, but not perfectly*, and the highest rating (3) corresponded to *perfectly seen stimulus*. The responses were given using a numeric keypad on a keyboard.

Procedure

Upon arrival the participants were naïve to the purpose of the experiment, and the specific nature of the task was explained to them only after the experiment. First, each participant signed an informed consent form. After that the eye-tracking and TMS systems were introduced to them, and the experimental procedure was explained. The participants then completed a practice block of 20 trials to get familiar with the task and to determine whether the stimulus size was adequate for the participant. The practice block was repeated until the participant felt comfortable with the task and could correctly indicate the target location on more than 80% of the trials.

Before each experimental block, the eye-tracker was set up and calibrated using a three-point calibration screen. After successful calibration ($M_{\text{error}} < 0.5°$ in visual angle, error in each point < 1°), the stimuli were presented in the blocks of 70 trials. Each experimental block included 20% of catch trials (i.e., no target stimulus was presented). A TMS pulse was delivered on each trial. The experimental set-up is schematically presented in Figure 1. We aimed to complete at least eight experimental blocks (i.e., 560 trials) with each participant within a 120-minute experimental session. Participants were given the possibility to rest after each experimental block. On average the participants completed 8.25 blocks or 577.50 trials ($SD_{\text{blocks}} = 0.87$, $SD_{\text{trials}} = 60.62$).

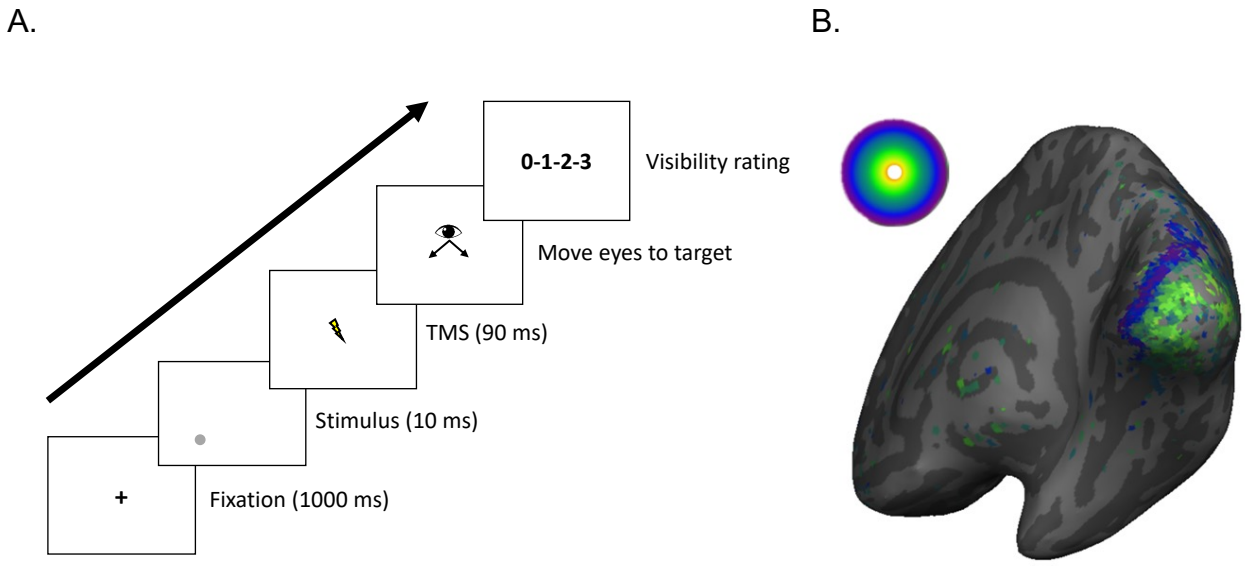

Figure 1. (A) A schematic presentation of the stimuli and the experimental procedure. (B) TMS pulses were targeted based on retinotopically mapped visual cortical areas (here color represents eccentricity, overlaid over inflated right hemisphere; visualized using FreeSurfer software).

Data Preparation and Analysis

Saccadic answers were determined for each trial as follows. The saccade needed to cross the vertical and horizontal halfway point between the fixation cross and stimulus location. These thresholds are visualized in Fig. 2A with dashed lines. If multiple saccades were present during the trial, only the first saccade after stimulus presentation that crossed these thresholds was considered. This procedure yields binary measure of whether the participant made a saccade to *either* target location. We call this measure "saccadic reaction". It enables us to examine if visual stimuli participant report not seeing yield saccades, irrespective of whether the gaze shift was towards the correct location. Second, another binary measure was created to indicate whether the answer was done in the direction of the stimulus (i.e., correct answer) vs the opposite location (i.e., wrong answer). This measure was used to calculate, for each participant, the mean proportion of correct saccadic responses. Third, we also calculated the distance in visual degrees between the saccade end

location and the target location (called "saccadic precision"). This gives us a continuous measure of the saccade accuracy. Last, saccadic reaction times were calculated relative to the onset of the stimulus.

Data were analyzed with the R statistical software (Version 4.1.2; R Core Team, 2021). We analyzed *saccadic reactions to unconscious targets* by calculating signal detection theoretic sensitivity (d') and criterion (c). A hit was defined as a saccade landing to either stimulus location when a stimulus was presented (but reported not seen). False alarms were trials where the participant made a saccade to either target location when no stimulus was presented (and visibility rating = 0). Second, the participants' sensitivity (d') and criterion (c) to *report conscious perception* of the target was calculated. A hit was defined as a visibility rating > 0 when a stimulus was presented. False alarms were trials where the participant reported seeing a target (rating > 0) when no stimulus was presented.

Saccadic precision, and *saccadic reaction times* were analyzed with linear mixed-effects models using the *lme4* package (Bates et al., 2015). Data for saccadic precision, and saccadic reaction time were skewed and were logarithmically transformed prior to analyzes (best fitting transformation was selected for the data using Box-Cox Power transform). Moreover, extreme reaction times (> |2.5 SD|) were filtered prior to the analyzes (2.86% of the trials were filtered). Visibility of the stimulus was fitted into the models as centered continuous variable and trial type (ipsilateral vs. contralateral TMS), were fitted into all the models as repeated contrast coded (see Schad et al., 2020 for more detail) fixed factor. In the models, random effects were kept maximal (Barr et al., 2013). The exact degrees of freedom are difficult to determine for the t statistics estimated by mixed-effects models, leading to problems in determining p-values (Baayen et al., 2008). Statistical significance at the .05 level is indicated by the values of $t > |1.96|$. The data and the R-scripts are made available using Open Science Framework https://osf.io/6wncf/

Results

General Overview of Task Performance

When a stimulus was presented, the participants reported seeing it (i.e., visibility rating > 0) on average on 87% of trials. When no stimulus was presented, the participants reported seeing it on about 12% of trials. TMS interfered with the participants conscious perception of the stimulus: When the visual stimulus was contralateral to the TMS stimulus location, the average (non-binarized) visibility rating was lower (M = 1.15, SD = 0.35) in comparison to ipsilateral trials (M = 1.48, SD = 0.35), $t(11) = -2.30$, $p = .042$, $d = 0.94$ (see Fig. 2B).

The proportion of saccadic reactions (to either stimulus location) is presented in Table 1 and is visualized in Fig. 2A. The participants made a saccadic reaction on average 69% of the trials when a stimulus was presented, and they reported seeing it. The proportion of saccadic reactions was about the same between contralateral and ipsilateral TMS, $t(11) = -0.82$, $p = .428$, $d = 0.12$ (see Table 1/Fig. 2C). Of the saccadic reactions, 98% were made towards the correct location (i.e., location in which the stimulus was presented) when the participants reported seeing the stimulus. There was no difference on saccadic reactions between ipsilateral and contralateral conditions, $t(11) = -1.00$, $p = .340$, $d = 0.15$ (see Table 1/Fig. 2D).

Table 1

Proportion of saccades in different experimental conditions

Visibility	Trial	TMS	*N* (total)	Saccadic Reactions			Proportion of Correct Saccades		
				N	*M*	*SD*	*N*	*M*	*SD*
Unseen	Catch		765	33	.04	.20	-	-	-
	Stimulus	Contralateral	534	38	.07	.27	21	.04	.19
		Ipsilateral	359	31	.09	.28	26	.07	.26
Seen	Catch		81	21	.26	.44	-	-	-
	Stimulus	Contralateral	1674	1105	.66	.47	1094	.65	.48
		Ipsilateral	2172	1454	.67	.47	1449	.67	.47

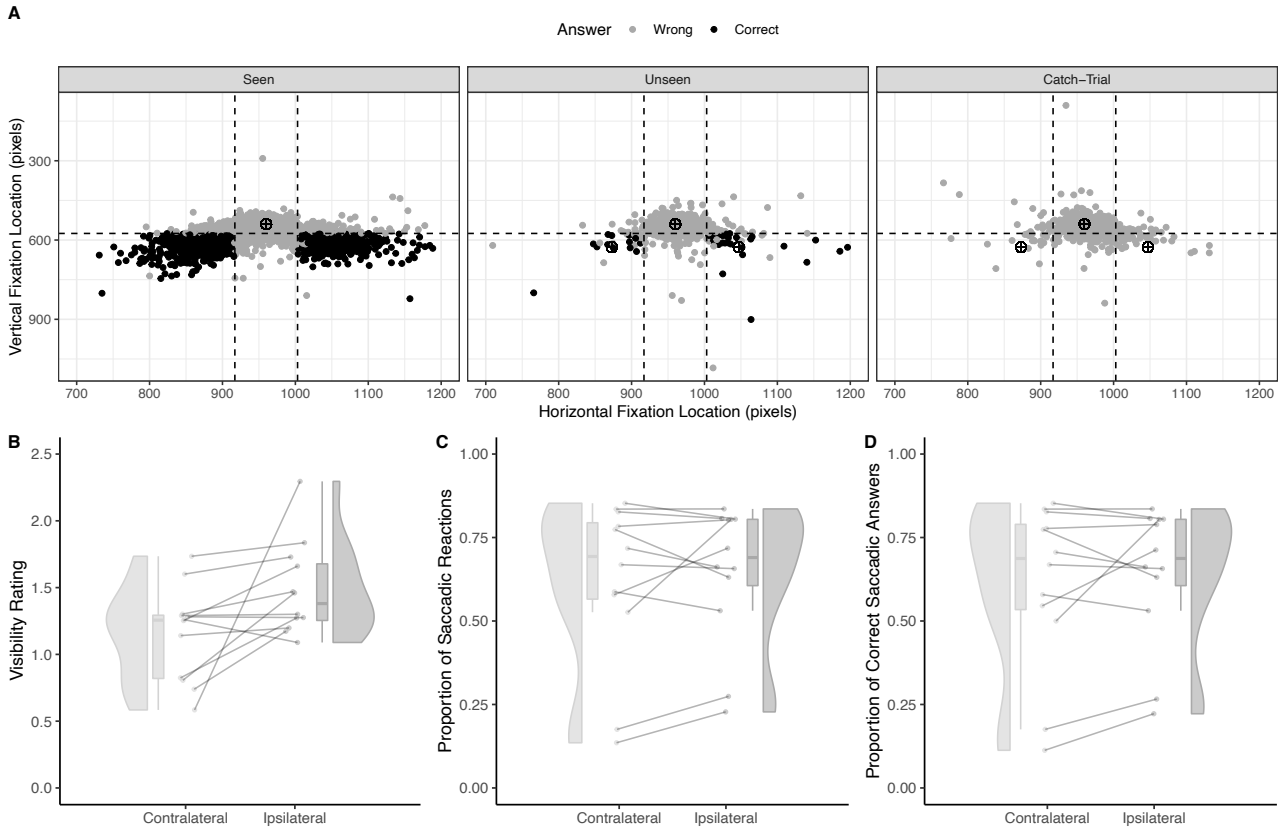

Figure 2. Saccades to targets in different experimental conditions. A) All the saccade landing locations. X-axis and Y-axis presents landing position in pixels. Circled crosses indicate the fixation point location, and target locations. Dashed lines indicate horizontal and vertical thresholds used to determine if the saccade was counted as an answer or not. B) Average visibility ratings in contralateral and ipsilateral conditions. C) Proportion of saccadic reactions in contralateral and ipsilateral conditions. D) Proportion of saccadic reactions launched to correct direction in contralateral and ipsilateral conditions. In panels B-D, the lines in the middle represents direction of the change for each participant between the conditions.

Ability to Make Saccades Towards Unseen Targets

When the participants reported not seeing the target (i.e., lowest visibility rating), they made saccadic reactions to either target location on 7.7% of trials when a stimulus was presented. This shows that by-and-large, the initiation of saccades required conscious perception. But did the participants make more saccadic reactions when a stimulus was presented (but they reported not seeing it), compared to catch trials (where no stimulus was presented), indicating that the unconscious target influenced their behavior? Our aim was to examine the frequency of saccades to unconscious stimuli separately during ipsilateral and contralateral TMS. However, because the participants made so few responses to targets, they reported not seeing, we combined the contralateral and ipsilateral conditions to maximize the number of unconscious trials. Three participants had so few saccadic reactions to unconscious stimuli (0–2) that they were excluded from the analyses.

When the participants reported not seeing the target, they made saccadic reactions more often when a stimulus was present than when no target was presented, $t(8) = -2.43$, $p = .041$, $d = 0.97$ (see Fig. 3A). Moreover, when the participants made saccadic reactions and reported not seeing the stimulus, they were able to shift their gaze reliably towards the correct target location (one-sample t test against 50%: $M = 0.68$, $SD = 0.17$), $t(8) = 3.31$, $p = .011$, $d = 1.73$ (Fig. 3B). Participants who were better at in general initiating saccadic reactions to stimuli they reported not seeing, were also better at making saccades to the correct location, $r = .83$, 95% CI [.38, .96] (see Fig. 3C).

We repeated the analysis on saccadic reactions to unconscious targets by calculating signal detection theoretic sensitivity (d') and criterion (c). Although sensitivity for reacting to the unconscious target was low, (M = 0.50, $SD = 0.51$), participants were able to discriminate stimulus from catch trials when they reported not seeing any target (one-sample t test against 0: $t(8) = 2.96$, $p = .018$, $d = 0.99$). Response criterion was relatively high (M = 1.49, $SD = 0.35$), indicating that the

participants were conservative in making saccadic reactions to targets they reported not seeing (i.e., the participants attempted to minimize false alarms).

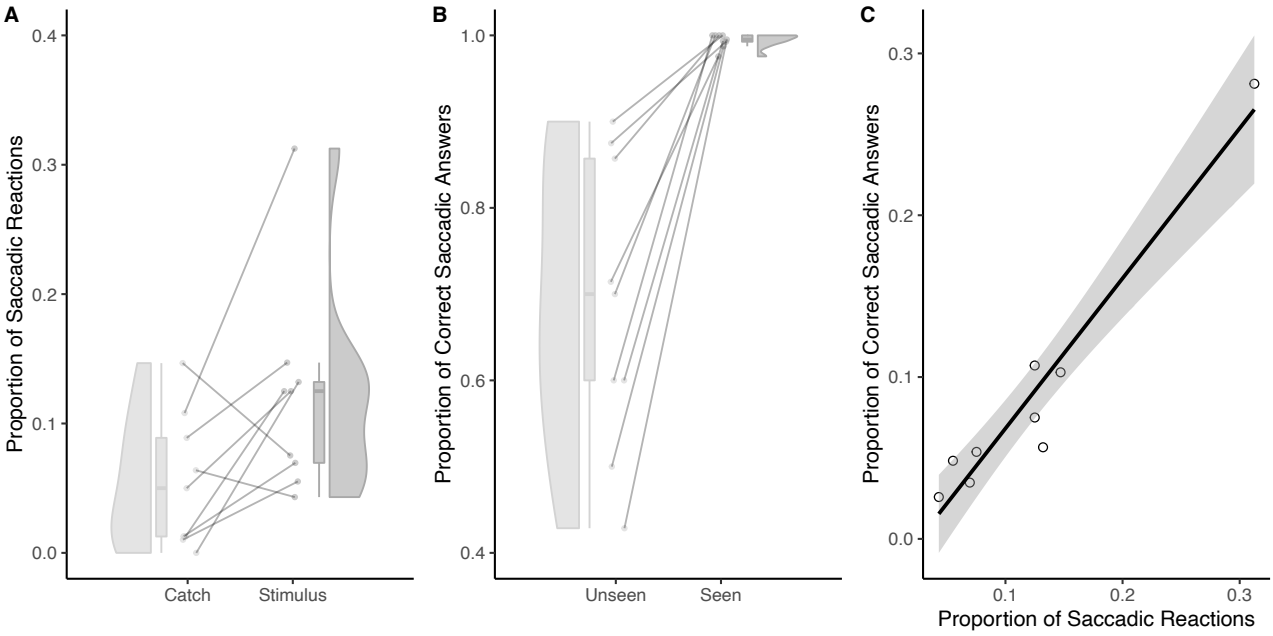

Figure 3. Saccadic reactions as a function of conscious perception of the target. Lines present direction of the effect for each participant. A) Proportion of saccadic reactions (to either stimulus location) when participants report not seeing the target at all (i.e., visibility rating = 0). B) Proportion of saccades towards the correct target location (of the saccades made) when the participants reported seeing (visibility rating > 0) or not seeing the target (visibility rating = 0). C) Relationship between proportion of saccadic reactions to unseen trials and the proportion of trials when the saccade was made to correct direction (i.e., towards the stimulus location). Shaded area represents 95% CI.

To further elucidate the relationship between conscious perception and saccadic reactions, we calculated the participants' sensitivity (d') and criterion (c) to *report conscious perception* of the target. The participants' sensitivity to report conscious perception of the target showed moderate correlation with the proportion of reactions towards the correct direction when participants reported not seeing the target, r = .55 95% CI [-.29, .89]. This indicates that the participants who were less sensitive to subjectively detect the stimulus were less successful at launching saccades towards stimuli they reported not seeing (Fig. 4A). Criterion to report conscious detection of the target also showed moderate correlation with the proportion of reactions towards the correct direction, r = .47, 95% CI [-.29, .86] (see Fig. 4B). This indicates that higher response criterion was related to better

ability to unconsciously launching saccades towards correct stimulus location when the saccadic reaction was made. As the proportion of saccadic reactions (to either direction) correlated strongly with the proportion of correct saccades (Fig. 3C), only correlations with correct answers are reported.

The sensitivity of making saccadic reactions when the stimulus was presented but reported unseen, showed moderate correlation with the sensitivity of consciously perceiving the stimulus, r = .62, 95% CI [-.07, .91] (see Fig. 4C for illustration). Response bias (i.e., c) on whether stimulus was seen vs. not showed moderate correlation with response bias measure of making saccadic reactions, r = .46, 95% CI [-.30, .86] (see Fig. 4D for illustration).

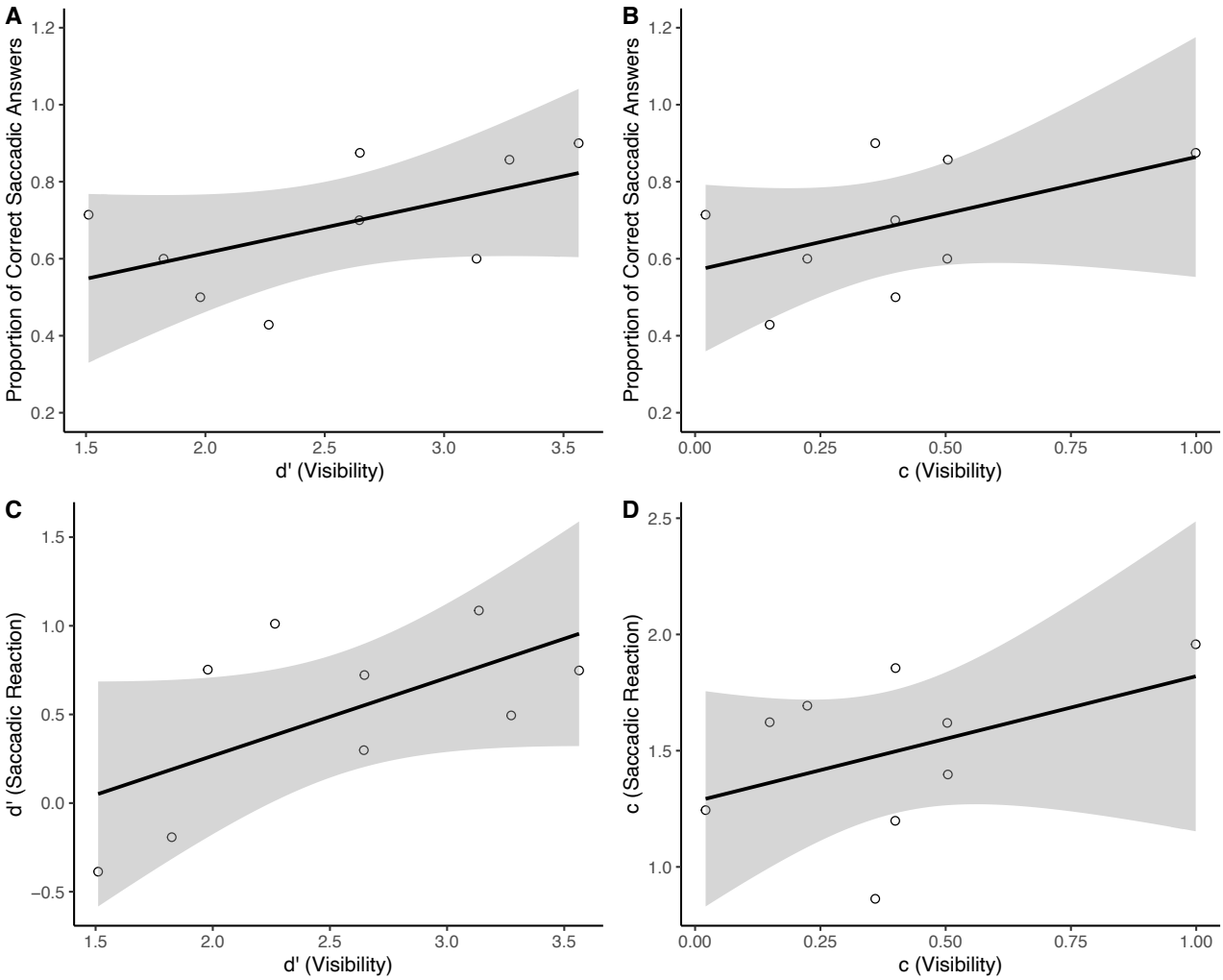

Figure 4. Association between saccades made in response to unconscious targets, and sensitivity to consciously detect the stimulus. Panel A represents correlation between the sensitivity of

consciously detecting the stimulus and proportion of correct saccadic answers (of all the saccadic reactions) in unconscious trials. Panel B represents correlation between criterion for reporting conscious perception and proportion of correct saccadic answers (of all the saccadic reactions) in subliminal trials. Panel C represents correlation between the sensitivity of subjectively detecting the stimulus and sensitivity of reacting for the stimulus. Panel D represents correlation between criterion for reporting conscious perception and criterion of making saccadic reaction. In all the panels, the grey area represents 95% CI.

Precision of Saccadic Reactions and Saccadic Reaction Times

Descriptive statistics for the precision and reaction time of the saccadic reactions are presented in Table 2. Here, precision refers to the distance from saccade landing position to the target position. Linear mixed-effects model on the *precision of the saccade* (when the stimulus was presented and the answer was correct; see Table 3), revealed a main effect of *Visibility*, indicating that distance between saccade landing location and stimulus location decreased while the visibility rating increased (see Fig. 5A). The model did not show an effect of trial type (contralateral vs. ipsilateral), or interaction between Visibility and trial type.

Table 2

Descriptive statistics for precision and reaction times of the correct saccadic reactions

		Distance from stimulus location		RT (ms)	
TMS	Visibility	*Mean*	*SD*	*Mean*	*SD*
Contralateral	Uneen	1.20	1.07	426	148
	Seen	0.65	0.38	389	93
Ipsilateral	Unseen	0.82	0.66	431	133
	Seen	0.64	0.61	395	90

Note. Distance from stimulus location is reported as visual degrees.

Table 3

Model for precision of the saccadic reaction

Random Effects	*n*	*Variance*	*SD*
Participant (Intercept)	9	0.06	0.25
Participant (TMS location)		0.0003	0.02
Residual		0.34	0.58
Fixed Effects	*Estimates*	*95% CI*	*t*
Intercept	-0.57	-0.74 – -0.41	**-6.77**
TMS Location (contralateral vs. ipsilateral)	-0.02	-0.04 – 0.03	-0.70
Visibility	-0.04	-0.06 – -0.01	**-2.73**
TMS Location (contralateral vs. ipsilateral) × Visibility	0.01	-0.04 – 0.06	0.40

Note. $t > |1.96|$ are bolded. *N* of observations = 2097.

The model on *saccadic reaction times* (when the stimulus was presented and the answer was correct; see Table 4), showed that higher stimulus visibility was associated with faster saccadic reactions (see Fig 5B). The model did not reveal an effect of trial type (Contralateral vs. Ipsilateral), or interaction between Visibility and TMS Location.

Table 4

Model for saccadic reaction times.

Random Effects	*n*	*Variance*	*SD*
Participant (Intercept)	9	0.01	0.10
Participant (TMS location)		0.002	0.05
Residual		0.04	0.19
Fixed Effects	*Estimates*	*95% CI*	*t*
Intercept	5.96	5.89 – 6.03	**176.10**
TMS Location (contralateral vs. ipsilateral)	0.01	-0.02 – 0.05	0.65
Visibility	-0.07	-0.08– -0.06	**-15.78**
TMS Location (contralateral vs. ipsilateral) × Visibility	-0.00001	-0.02 – 0.02	-0.01

Note. $t > |1.96|$ are bolded. *N* of observations = 2037

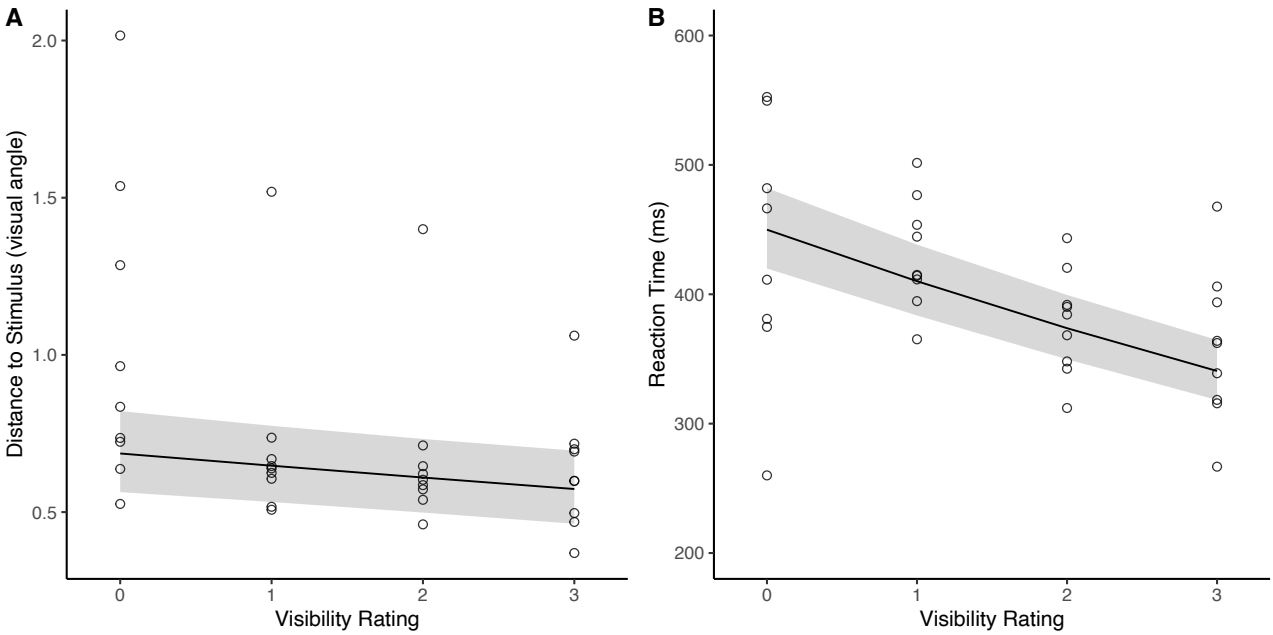

Figure 5. Precision of saccadic reactions and saccadic reaction times. A) Model estimates for effect of visibility to saccade accuracy. Figure values are back transformed from log transformed estimates. B) Model estimates for saccadic reaction times. For illustration purposes, model estimates are back transformed from log values. In both panels, shaded area represents 95% CI. Circles represent observed means for each participant.

Discussion

The results of Experiment 1 suggest that, in general, participants' ability to reliably initiate saccades towards a target requires conscious perception of the target, and lower visibility ratings are associated with more imprecise and slower saccadic reactions. On minority of trials (on average 7.7%) the participants did initiate saccades towards stimuli they reported not seeing, but this ability correlated with the participant's sensitivity to consciously detect the target (as estimated by d'). Because of the small number of saccades towards unconscious targets we were not able to directly test the role of contralateral V1 in triggering saccades to unseen targets.

EXPERIMENT 2: Metacontrast masking

To further test ability to initiate saccades towards targets individuals do not see, we ran an experiment where stimulus visibility was manipulated using a metacontrast mask instead of TMS. The experimental set-up is otherwise identical to the TMS experiment reported above. Metacontrast masking is assumed to interfere with target-related feedback activity, while leaving feedforward activity (in V1, and other areas) largely intact (Breitmeyer & Ogmen, 2010; Macknik & Livingstone, 1998; Railo & Koivisto, 2012). If participants are able to initiate saccade towards targets, they report not consciously seeing, we should observe reflexive saccades towards the reportedly unseen targets.

Materials and Methods

Participants

Thirteen University of Turku students (12 women, M_{Age} = 23, SD_{Age} = 3.70) took part to the experiment for a course credit. All the participants had normal or corrected-to-normal vision. The study was approved by the ethics committee of the Hospital District of Southwest Finland and was conducted in accordance with the Declaration of Helsinki and with the understanding and written consent of each participant.

Stimuli and Task

The schematic presentation of the stimuli and the experimental procedure are illustrated in the Figure 5. The mask comprised of two black annuli (line width = 0.07°) with the same inner diameter as the outer diameter of the stimuli that were presented for one screen refresh. The SOA between target and mask onset set was determined during practice trials, and it was set so that each participant would be able to consciously perceive about the same out of the stimuli as in the Experiment 1. The SOA was on average 36ms (*SD* = 9ms). During the experimental session, on

average 7.9 blocks were presented for the participants, with each block comprising of 50 trials (total number of trials was, on average 396.15 trials per participant (SD_{blocks} = 1.12, SD_{trials} = 55.76).

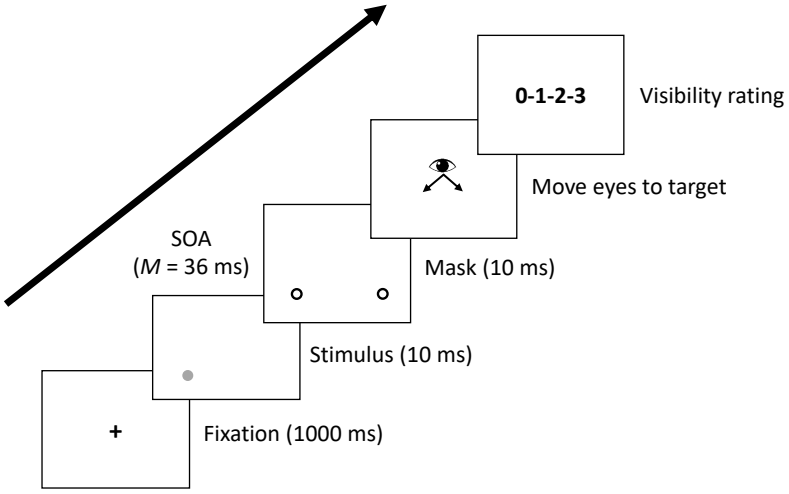

Figure 5. A schematic presentation of the stimuli and the experimental procedure of the Experiment 2.

Procedure and Apparatus

The apparatus and experimental procedure were the same as in the Experiment 1.

Data-analysis

Data were analyzed similarly as in the Experiment 1.

Results

General Overview of Task Performance

The proportion of saccadic reactions (i.e., first saccade made after stimulus onset) to either target location is presented in Table 5, and the end location of the saccadic reactions are illustrated in Fig 6A. When a stimulus was presented, the participants reported seeing it (visibility rating > 0)

on average on 80% of trials. This is very similar to Experiment 1. When no stimulus was presented, the participants reported seeing a stimulus on 39% of trials, on average. This number of false alarms is clearly higher than in Experiment 1, and likely due to the fact that the visual mask stimuli made it difficult for participants to accurately detect visual stimuli.

Table 5

Proportion of saccadic reactions

Visibility	Trial	*N* (total)	Saccadic Reactions			Correct Saccadic Answers		
			N	*M*	*SD*	*N*	*M*	*SD*
Not Seen	Catch	555	337	.61	.49	-	-	-
	Stimulus	793	520	.66	.48	354	.45	.50
Seen	Catch	353	280	.79	.41	-	-	-
	Stimulus	3087	2639	.85	.35	2375	.77	.42

Ability to Make Saccades Towards Unseen Targets

When no stimulus was presented, participants made a saccadic response to either potential target location on average on 85% of trials when they reported seeing, and 66% of trials when they reported not seeing a stimulus. This indicates that the visual masks attracted the gaze. From the perspective of unconscious processing, the key question is whether participants launch saccadic eye movements more often when a stimulus they report not seeing is present on the screen, when compared to the catch trials. The analysis showed that there were no difference between reaction towards catch vs. stimulus trials, $t(12) = -0.61$, $p = .552$, $d = 0.10$ (see Fig 6B). However, when the stimulus was presented, but the participant reported not seeing it, they were nevertheless able to initiate saccade towards the correct target location in higher than guessing-level accuracy ($M = 0.63$, $SD = .20$), $t(12) = 2.40$, $p = .033$, $d = 0.67$ (see Fig 6C). Similarly to the Experiment 1, the

proportion of saccadic reactions when the participants reported not seeing a stimulus (to either stimulus location) and proportion of reactions to correct location had high positive correlation with each other, r = .77, 95% CI [.38, .93] (see Fig. 6D).

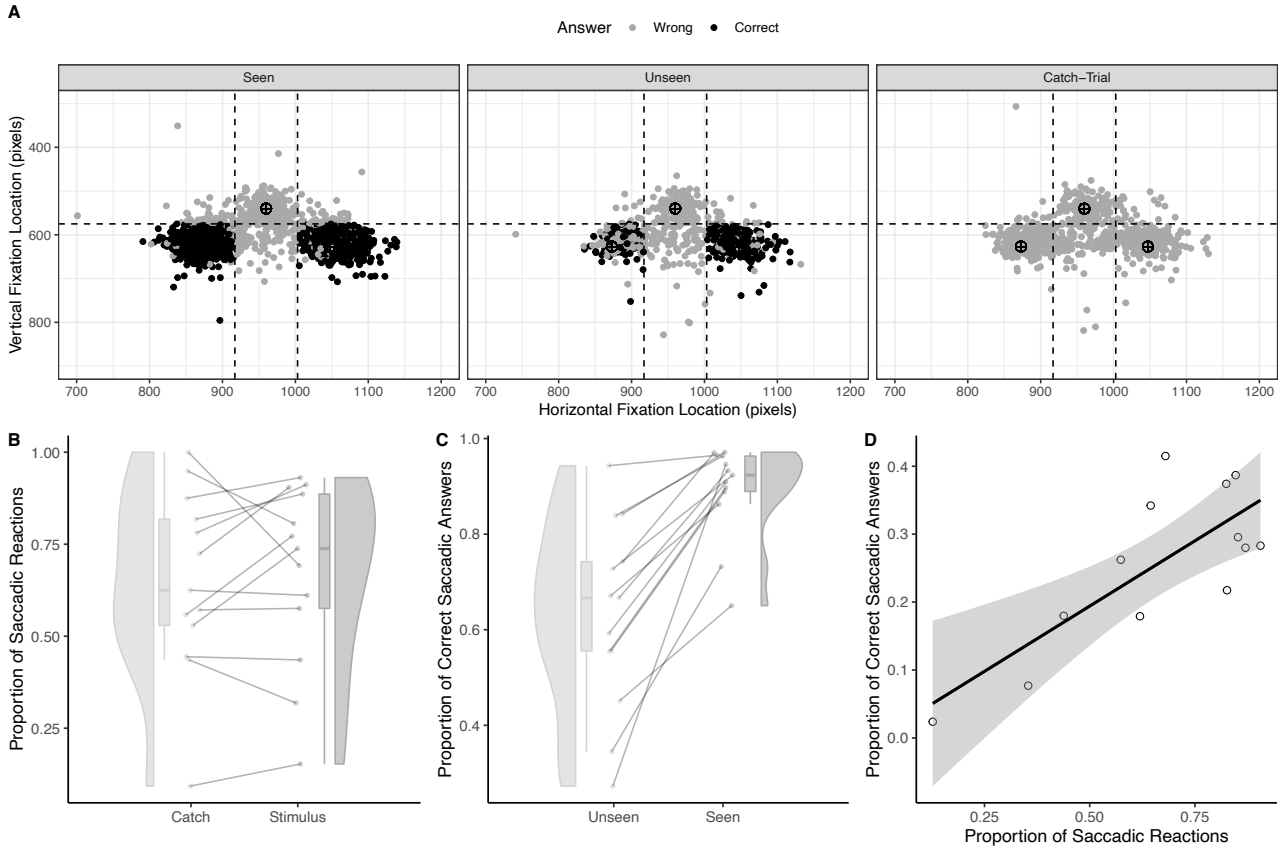

Figure 6. Saccadic responses in different experimental conditions. A) All the saccade landing locations. X-axis and Y-axis presents landing position in pixels. Circled crosses indicate the fixation point location, and target locations. Dashed lines indicate horizontal and vertical thresholds used to determine if the saccade was counted as an answer or not. B) Proportion of saccadic reactions (to either stimulus location) when participants report not seeing the target at all (i.e., visibility rating = 0). C) Proportion of saccades towards the correct target locations when participants reported seeing (i.e., visibility rating > 0) and not seeing the target (i.e., visibility rating = 0). D) Relationship between number of saccades and number of saccades made to correct direction (i.e., towards stimulus location). Shaded area represents 95% CI.

As in Experiment 1, sensitivity (d') and criterion (c) were calculated from saccadic reactions (i.e., the participant made a saccade to either target location when the stimulus was presented), when the target was reported not seen. We analyzed whether participants were able to unconsciously distinguish and react to the stimuli by calculating whether the d' differs from zero.

The result showed that the participants were not statistically significantly able to discriminate unconscious stimuli from catch trials (M = 0.37, SD = 0.79), $t(12) = 1.71$, $p = .113$, $d = 0.47$. Moreover, the participants criterion for making a saccadic response were more liberal when compared to Experiment 1 (M = -0.34, SD = 0.79).

We calculated the participants' sensitivity and criterion for *reporting conscious perception* of stimuli and examined whether they predicted saccadic reactions to unconscious stimuli across participants. Overall, sensitivity for to *report conscious perception* of the target was high, (M = 1.30, SD = 0.76), and response criterion was relatively low (M = -0.21, SD = 0.60). As the reactions towards either direction correlated strongly with reactions to correct direction each, only correlations with correct answers are analyzed.

The participants' sensitivity to report conscious perception of the target showed weak correlation with the proportion of reactions towards the correct direction when participants reported not seeing the target, $r = .35$, 95% CI [-.52, .57] (Fig. 7A). Criterion to report conscious detection of the target showed virtually no correlation with the proportion of reactions towards the correct direction, $r = .03$, 95% CI [-.53, .57] (see Fig. 7B).

The sensitivity of making saccadic reactions when the stimulus was presented but reported unseen, showed virtually no correlation with the sensitivity of consciously perceiving the stimulus, $r = .05$, 95% CI [-.51, .59] (see Fig. 7C). In addition, response bias (i.e., c) on whether stimulus was seen vs. not showed a very weak correlation with response bias measure of making saccadic reactions, $r = .15$, 95% CI [-.43, .65] (see Fig. 7D).

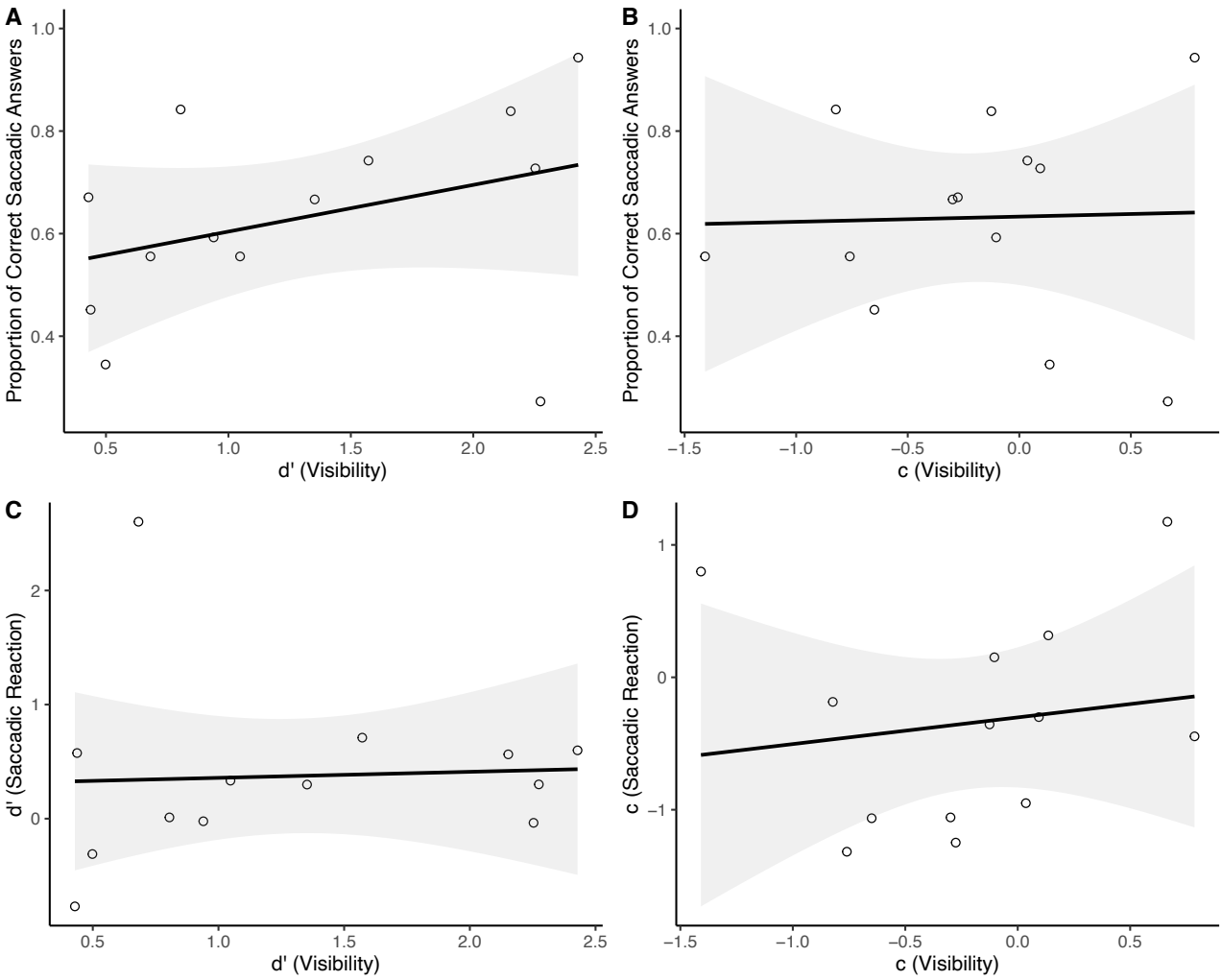

Figure 7. Saccadic responses to unconscious targets as a function of subjectively detecting the stimulus (d') and criterion of making saccadic reaction (c). A) Correlation between the sensitivity of subjectively detecting the stimulus and proportion correct saccadic answers (of the saccades made) in subliminal trials. B) Correlation between criterion for reporting conscious perception and proportion correct saccadic answers (of the saccades made) in subliminal trials. C) Correlation between sensitivity of reporting conscious vision, and sensitivity of reacting for the stimulus. D) Correlation between criterion for reporting conscious perception and criterion of making saccadic reaction. The grey area represents 95% CI.

Precision Saccadic Reactions and Saccadic Reaction Times

Descriptive statistics for the precision and reaction time of the saccadic reactions are presented in Table 6. The model on *saccade accuracy towards stimulus location* (see Table 7), showed that the higher the visibility rating, the closer the saccades were to the stimulus location (Fig 8A). Moreover, the model on *saccadic reaction times towards stimulus location* (see Table 8),

showed that saccadic reactions times became faster as visibility rating of the stimulus increased (see Fig. 8B).

Table 6
Descriptive statistics of the saccade accuracy and saccadic reaction times

	Distance from stimulus location		RT (ms)	
Visibility	*M*	*SD*	*M*	*SD*
Unseen	0.52	0.99	403	108
Seen	0.44	0.33	353	93

Note. Distance from stimulus location is reported as visual degrees.

Table 7
Model for distance of the end point of the saccadic answer from the stimulus location

Random Effects	*n*	*Variance*	*SD*
Participant (Intercept)	13	0.05	0.21
Residual		0.39	0.62
Fixed Effects	*Estimates*	*95% CI*	*T*
Intercept	-0.96	-1.08 – -0.84	**15.89**
Visibility (Seen vs. Unseen)	-0.06	-0.08 – -0.03	**-4.40**

Note. $t > |1.96|$ are bolded. N of observations = 2729.

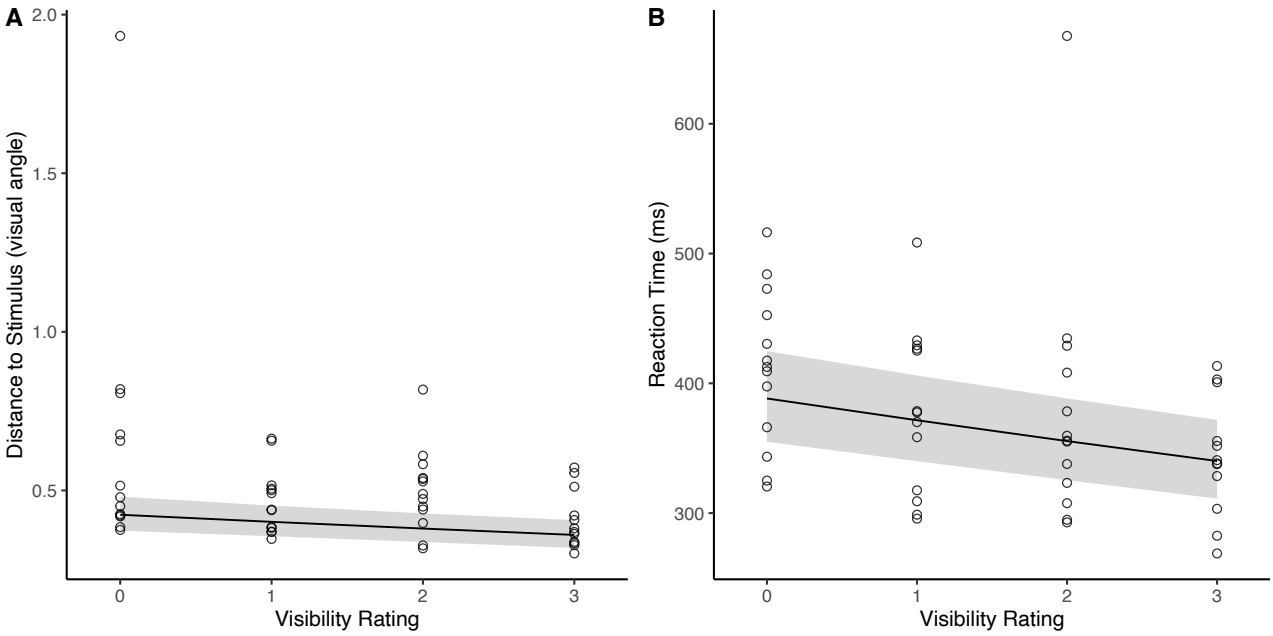

Figure 8. A) Model estimates for effect of visibility to saccade accuracy. Figure values are back transformed from log values. B) Model estimates for saccadic reaction times. For illustration purposes, the model estimates are back transformed from log-values. In both panels, shaded area represents 95% CI. Circles represent observed means for each participant.

Table 8
Model for saccadic reaction times.

Random Effects	*n*	*Variance*	*SD*
Participant (Intercept)	13	0.03	0.16
Residual		0.04	0.21
Fixed Effects	*Estimates*	*95% CI*	*t*
Intercept	5.88	5.80 – 5.98	**130.19**
Visibility	-0.05	-0.06 – -0.04	**-10.35**

Note. $t > |1.96|$ are bolded. N of observations = 2673.

Discussion

Experiment 2 largely replicated the results of Experiment 1 where V1 TMS was used to suppress visibility: Participants were able to initiate saccades towards the stimulus even though they reported not seeing the stimulus. Unlike in the TMS experiment, participants' sensitivity to consciously detect the stimulus did not predict how well participants shifted gaze towards the stimuli they reported not seeing. As in Experiment 1, lower stimulus visibility was associated with slower and more imprecise gaze shifts.

General Discussion

We tested neurologically healthy participants' ability to orient their gaze towards visual stimuli they reported not consciously seeing. Participants could, on average, initiate saccades towards stimuli they reported not seeing. Because this was true not only in the metacontrast masking experiment (Exp 2), but also in the TMS experiment (Exp 1), the results suggest that the capacity to guide saccades based on unconscious perception may not depend on the V1, corroborating findings on blindsight patients (Barbur et al., 1988; Perenin & Jeannerod, 1978; Weiskrantz et al., 1974; Zihl, 1980) and monkeys (Isa & Yoshida, 2021; Kato et al., 2011; Yoshida et al., 2008). While lending support for the conclusion that saccades can be guided based on unconscious visual information, our results also show that saccades initiated based on unconscious stimuli were also associated with a shortcoming: Saccades were initiated only roughly on 8% of trials when participants reported not

consciously seeing the stimulus (Experiment 1). In addition, decreased conscious stimulus visibility was associated with slower, and less precise saccadic eye movements.

In Experiment 1, we wanted to specifically target V1 using TMS to conceptually replicate the phenomenon of blindsight where V1 is lesioned. The aim was to compare conditions where TMS was applied to contralateral vs ipsilateral V1 location. The stimulated V1 locations in the left and right hemispheres were determined based on retinotopic mapping. The ipsilateral TMS condition was originally included as a control condition; we aimed to always stimulate the same area, while varying stimulus laterality. However, the results revealed surprisingly small differences between the ipsilateral and contralateral conditions. This is likely because the V1 representation of the stimulus location was close to the interhemispheric fissure in the majority of participants, meaning that stimulation could not be targeted specifically to either the contralateral or ipsilateral hemisphere. This means that even in the ipsilateral condition, the contralateral V1 was likely stimulated. While this means that our evidence for the role of (retinotopically defined) V1 is not as strong as we aimed for, because the pulses were targeted based on retinotopic mapping, we have good reasons to assume that V1 was nevertheless stimulated. Because the V2 and V3 areas are often close to the V1 (due to cortical folding, the V1 may lie deeper in the brain than V2/V3; Salminen-Vaparanta et al., 2012; Thielscher et al., 2010), it is possible that V2 and V3 were also stimulated in the present study.

Because we applied TMS pulses 100ms after stimulus onset, it is likely that the fastest "feedforward" stimulus-evoked responses in V1 were not affected by TMS. This makes direct comparison to blindsight patients difficult (as lesions both feedforward, and later feedback activity). Theories of (un)conscious vision suggest that the feedforward activity period may enable unconsciously guided behaviors (Dehaene et al., 2006; Lamme & Roelfsema, 2000; Vanrullen, 2007; VanRullen & Koch, 2003). Consistent with this, Hurme et al. (2017) previously showed that unconscious, blindsight-like behavior is eliminated when TMS pulses are applied after a delay that coincides with the timing of feedforward activity in V1 (around 60ms after stimulus onset). This

means that in the present study the saccades guided by unconscious stimuli may have been triggered by the transient feedforward activity passing through V1. Similarly, metacontrast masking, employed in Experiment 2, is assumed to leave feedforward activity largely intact (Breitmeyer & Ogmen, 2010; Macknik & Livingstone, 1998; Railo & Koivisto, 2012).

The present results replicate previous TMS-blindsight studies that have demonstrated that when the task is to simply detect the presence or localize a visual stimulus, blindsight-like behavior is observed (Christensen et al., 2008; Hurme et al., 2017; Railo & Koivisto, 2012; Ro, 2008, reviewed in, Railo & Hurme, 2021). The present study is the first report that neurologically healthy participants can initiate saccades towards stimuli they report not seeing, and that this process may not depend on the V1. Previously, Crouzet et al. (2014, 2017) studied whether saccades can be initiated towards a stimulus participants report not seeing. They observed that while participants could make accurate fast saccades to visual targets whose visibility was disturbed by visual masking, these responses were accompanied conscious perception of the stimulus. It should be noted that in the studies by Crouzet et al., the participants were asked to search for a target among distractor stimuli. The simpler task we employed in the present study may have been crucial to observe unconsciously guided saccades.

Although our results suggest that saccades can be initiate towards stimuli humans are unconscious of, it is very difficult to verify that participants indeed did not have any phenomenological experience related to the presented stimulus, even though they report not seeing a stimulus (Campion et al., 1983; Phillips, 2021). We used a graded visibility rating scale and defined unconscious stimuli as the lowest rating on a four-step scale, because earlier reports of unconscious, blindsight-like capacity may have been confounded by the use of dichotomous rating scales (Koivisto et al., 2021; Mazzi et al., 2016; Overgaard, 2011). Despite the use of a graded rating scale, our analysis suggests that in Experiment 1 reportedly unconscious saccades were nevertheless based on weakly conscious perception: Participants who showed higher sensitivity to *consciously* detect stimuli also showed the highest "reportedly unconscious" capacity. This suggests that stimuli that participants

report as “absolutely not seen”, nevertheless may be associated with weak degraded visual experience. This is consistent with research on “unconscious” saccadic reactions in monkeys (Isa & Yoshida, 2021; Yoshida & Isa, 2015). Similar correlation with conscious perceptual sensitivity and alleged “unconscious” perception have also been reported previously (Koivisto et al., 2021; Railo et al., 2021). Interestingly, similar pattern was not observed in Experiment 2. This could be because TMS to V1 induces suboptimal introspection (Peters et al., 2017), or because participants made more false-alarm responses in Experiment 2 when compared to Experiment 1.

We used small visual stimuli (about 0.20 visual degrees) in the present study to maximize the chances of complete visual suppression by TMS, but nevertheless the analysis in Experiment 1 (*M* = 74 suppressed trials/participant, range = 9–145) and Experiment 2 were (*M* = 61 suppressed trials/participant, range = 13–114)) based on a small amount of data. It is possible that larger, or more meaningful (e.g., emotional) visual stimuli could have enabled better ability to initiate saccades towards unconscious stimuli. Although saccadic reaction times were relatively fast in the present study (300–400ms), they were not *reflexively* fast: Express saccades can have onset latencies as fast as 100ms (Kingstone & Klein, 1993; Marino et al., 2015; Schiller et al., 2004), and likely the stimuli used in the present study were too small to trigger express saccades. Furthermore, in our study, decreased conscious visibility was associated with slower saccadic reactions, suggesting that saccades towards target whose visibility was suppressed was not based on reflex-like circuits.

Conclusions

In conclusion, our results show that neurologically healthy humans can sometimes orient their gaze towards stimuli they subsequently report not consciously perceiving. However, such actions were less precise, slower, and clearly less frequent when compared to stimuli that were consciously perceived. Our results suggest that the ability to saccade towards unconscious stimuli may be at least partly independent of V1. The present results are important because previous reports of ability to

launch saccades towards unconscious stimuli has been based on patients and non-human primates with permanent V1 lesions. That similar capacity may be present even in neurologically healthy individuals suggests that it is not due to neural reorganization that often accompanies lesions, but a property of neurologically intact human brain.

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References

Amassian, V. E., Cracco, R. Q., Maccabee, P. J., Cracco, J. B., Rudell, A., & Eberle, L. (1989). Suppression of visual perception by magnetic coil stimulation of human occipital cortex. *Electroencephalography and Clinical Neurophysiology/ Evoked Potentials* Section, *74*(6), 458–462. https://doi.org/10.1016/0168-5597(89)90036-1

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language, 59*(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Baldwin, M. K. L., Balaram, P., & Kaas, J. H. (2017). The evolution and functions of nuclei of the visual pulvinar in primates. *Journal of Comparative Neurology, 525*(15), 3207–3226. https://doi.org/10.1002/cne.24272

Barbur, J. L., Forsyth, P. M., & Findlay, J. M. (1988). Human saccadic eye movements in the absence of the geniculocalcarine projection. *Brain*, *111*(1), 63–82. https://doi.org/10.1093/BRAIN/111.1.63

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*. https://doi.org/10.1016/j.jml.2012.11.001

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Breitmeyer, B., & Ogmen, H. (2010). *Visual Masking: Time Slices Through Conscious and Unconscious Vision*. Oxford University Press: New York. https://doi.org/10.1093/ACPROF:OSO/9780198530671.001.0001

Bridge, H., Thomas, O., Jbabdi, S., & Cowey, A. (2008). Changes in connectivity after visual cortical brain damage underlie altered visual function. *Brain*, *131*(6), 1433–1444. https://doi.org/10.1093/brain/awn063

Campion, J., Latto, R., & Smith, Y. M. (1983). Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? *Behavioral and Brain Sciences, 6,* 423–448. https://doi.org/10.1017/S0140525X00016861

Christensen, M. S., Kristiansen, L., Rowe, J. B., & Nielsen, J. B. (2008). Action-blindsight in healthy subjects after transcranial magnetic stimulation. *Proceedings of the National Academy of Sciences*, *105*(4), 1353–1357. https://doi.org/10.1073/pnas.0705858105

Cowey, A. (2010). The blindsight saga. *Experimental Brain Research*, *200*, 3–24. https://doi.org/10.1007/s00221-009-1914-2

Crouzet, S. M., Kovalenko, L. Y., del Pin, S. H., Overgaard, M., & Busch, N. A. (2017). Early visual processing allows for selective behavior, shifts of attention, and conscious visual experience in spite of masking. *Consciousness and Cognition, 54,* 89–100. https://doi.org/10.1016/j.concog.2017.01.021

Crouzet, S. M., Overgaard, M., & Busch, N. A. (2014). The fastest saccadic responses escape visual masking. *PLoS ONE, 9*(2), e87418 https://doi.org/10.1371/journal.pone.0087418

Danckert, J., & Rossetti, Y. (2005). Blindsight in action: what can the different sub-types of blindsight tell us about the control of visually guided actions? *Neuroscience and Biobehavioral Reviews*, *29*(7), 1035–1046. https://doi.org/10.1016/J.NEUBIOREV.2005.02.001

de Graaf, T. A., Koivisto, M., Jacobs, C., & Sack, A. T. (2014). The chronometry of visual perception: Review of occipital TMS masking studies. *Neuroscience and Biobehavioral Reviews, 45,* 295–304. https://doi.org/10.1016/j.neubiorev.2014.06.017

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences, 10*(5), 204–211. https://doi.org/10.1016/j.tics.2006.03.007

Ffytche, D. H., & Zeki, S. (2011). The primary visual cortex, and feedback to it, are not necessary for conscious vision. *Brain*. https://doi.org/10.1093/brain/awq305

Henriksson, L., Karvonen, J., Salminen-Vaparanta, N., Railo, H., & Vanni, S. (2012). Retinotopic maps, spatial tuning, and locations of human visual areas in surface coordinates characterized with multifocal and blocked fMRI designs. *PLoS ONE*, *7*(5), e36859. https://doi.org/10.1371/journal.pone.0036859

Hurme, M., Koivisto, M., Henriksson, L., & Railo, H. (2020). Neuronavigated TMS of early visual cortex eliminates unconscious processing of chromatic stimuli. *Neuropsychologia, 136,* 107266. https://doi.org/10.1016/j.neuropsychologia.2019.107266

Hurme, M., Koivisto, M., Revonsuo, A., & Railo, H. (2017). Early processing in primary visual cortex is necessary for conscious and unconscious vision while late processing is necessary only for conscious vision in neurologically healthy humans. *NeuroImage*, *150, 230 – 238.* https://doi.org/10.1016/j.neuroimage.2017.02.060

Isa, T., & Yoshida, M. (2021). Neural mechanism of blindsight in a macaque model. *Neuroscience*, *469*, 138–161. https://doi.org/10.1016/J.NEUROSCIENCE.2021.06.022

Kato, R., Takaura, K., Ikeda, T., Yoshida, M., & Isa, T. (2011). Contribution of the retino-tectal pathway to visually guided saccades after lesion of the primary visual cortex in monkeys. *European Journal of Neuroscience, 33*(11), 1952–1960. https://doi.org/10.1111/j.1460-9568.2011.07729.x

Kingstone, A., & Klein, R. M. (1993). What are human express saccades? *Perception & Psychophysics*, *54*(2), 260–273. https://doi.org/10.3758/BF03211762

Koivisto, M., Leino, K., Pekkarinen, A., Karttunen, J., Railo, H., & Hurme, M. (2021). Transcranial magnetic stimulation (TMS)-induced Blindsight of Orientation is Degraded Conscious Vision. *Neuroscience*, *475*, 206–219. https://doi.org/10.1016/J.NEUROSCIENCE.2021.08.025

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences, 23*(11), 571–579. https://doi.org/10.1016/S0166-2236(00)01657-X

Leh, S. E., Johansen-Berg, H., & Ptito, A. (2006). Unconscious vision: New insights into the neuronal correlate of blindsight using diffusion tractography. *Brain*, *129*(7), 1822–1832. https://doi.org/10.1093/brain/awl111

Leh, S. E., Mullen, K. T., & Ptito, A. (2006). Absence of S-cone input in human blindsight following hemispherectomy. *European Journal of Neuroscience, 24*(10), 2954–2960. https://doi.org/10.1111/j.1460-9568.2006.05178.x

Lloyd, D. A., Abrahamyan, A., & Harris, J. A. (2013). Brain-stimulation induced blindsight: Unconscious vision or response bias? *PLoS ONE*, *8*(12), e82828. https://doi.org/10.1371/journal.pone.0082828

Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neuroscience*, *1*(2), 144–149. https://doi.org/10.1038/393

Marino, R. A., Levy, R., & Munoz, D. P. (2015). Linking express saccade occurance to stimulus properties and sensorimotor integration in the superior colliculus. *Journal of Neurophysiology*,

114(2), 879–892. https://doi.org/10.1152/JN.00047.2015/ASSET/IMAGES/LARGE/Z9K0131531940008.JPEG

Mazzi, C., Bagattini, C., & Savazzi, S. (2016). Blind-sight vs. degraded-sight: Different measures tell a different story. *Frontiers in Psychology*, *7*, 901. https://doi.org/10.3389/fpsyg.2016.00901

Michel, M. & Lau, H. (2021). Is blindsight possible under signal detection theory? Comment on Phillips (2021), *Psychological Review, 128*, 585-591, https://doi.org/10.1037/REV0000266

Overgaard, M. (2011). Visual experience and blindsight: A methodological review. *Experimental Brain Research, 209,* 473–479. https://doi.org/10.1007/s00221-011-2578-2

Perenin, M. T., & Jeannerod, M. (1978). Visual function within the hemianopic field following early cerebral hemidecortication in man-I. Spatial localization. *Neuropsychologia, 16*(1), 1–13. https://doi.org/10.1016/0028-3932(78)90037-4

Peters, M. A. K., Fesi, J., Amendi, N., Knotts, J. D., Lau, H., & Ro, T. (2017). Transcranial magnetic stimulation to visual cortex induces suboptimal introspection. *Cortex, 93,* 119–132. https://doi.org/10.1016/j.cortex.2017.05.017

Phillips, I. (2021). Blindsight is qualitatively degraded conscious vision. *Psychological Review*, 128, 558–584. https://doi.org/10.1037/rev0000254

Pöppel, E., Held, R., & Frost, D. (1973). Residual visual function after Brain Wounds involving the central visual pathways in Man. *Nature*, *243*(5405), 295–296. https://doi.org/10.1038/243295a0

R Core Team (2021). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. Retrieved from: http://www.R-project.org/

Rafal, R., Smith, J., Krantz, A., Cohen, C. B. (1990). Extrageniculate vision in hemianopic humans: Saccade inhibition by signals in the blind field. *Science*, *250*, 118–121.

Railo, H., Andersson, E., Kaasinen, V., Laine, T., & Koivisto, M. (2014). Unlike in clinical blindsight patients, unconscious processing of chromatic information depends on early visual cortex in healthy humans. *Brain Stimulation, 7*, 415–420. https://doi.org/10.1016/j.brs.2014.01.060

Railo, H., & Hurme, M. (2021). Is the primary visual cortex necessary for blindsight-like behavior? Review of transcranial magnetic stimulation studies in neurologically healthy individuals. *Neuroscience and Biobehavioral Reviews*, *127*, 353–364. https://doi.org/10.1016/j.neubiorev.2021.04.038

Railo, H., & Koivisto, M. (2012). Two means of suppressing visual awareness: A direct comparison of visual masking and transcranial magnetic stimulation. *Cortex, 48*(3), 333 - 343. https://doi.org/10.1016/j.cortex.2010.12.001

Railo, H., Piccin, R., & Lukasik, K. M. (2021). Subliminal perception is continuous with conscious vision and can be predicted from prestimulus electroencephalographic activity. *European Journal of Neuroscience, 54,* 4985–4999. https://doi.org/10.1111/EJN.15354

Ramsøy, T. Z., & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences, 3*, 1–23. https://doi.org/10.1023/b:phen.0000041900.30172.e8

Ro, T. (2008). Unconscious vision in action. *Neuropsychologia*, *46*, 379–383.

Ro, T., Shelton, D., Lee, O. L., & Chang, E. (2004). Extrageniculate mediation of unconscious vision in transcranial magnetic stimulation-induced blindsight. *Proceedings of the National Academy of Sciences, 101*(26), 9933 –9935. https://doi.org/10.1073/pnas.0403061101

Roth, T., Sokolov, A. N., Messias, A., Roth, P., Weller, M., & Trauzettel-Klosinski, S. (2009). Comparing explorative saccade and flicker training in hemianopia: A randomized controlled study. *Neurology, 72*(4), 324–331. https://doi.org/10.1212/01.wnl.0000341276.65721.f2

Schad, D. J., Vasishth, S., Hohenstein, S., Kliegl, R. (2020). How to capitalize on a priori contrasts in linear (mixed) models: A tutorial. *Journal of Memory and Language, 110*, 104038. https://doi.org/10.1016/j.jml.2019.104038.

Salminen-Vaparanta, N., Noreika, V., Revonsuo, A., Koivisto, M., & Vanni, S. (2012). Is selective primary visual cortex stimulation achievable with TMS? *Human Brain Mapping, 33*(3), 652–665. https://doi.org/10.1002/hbm.21237

Sandberg, K., Timmermans, B., Overgaard, M., & Cleeremans, A. (2010). Measuring consciousness: Is one measure better than the other? *Consciousness and Cognition, 19*(4), 1069–1078. https://doi.org/10.1016/j.concog.2009.12.013

Savina, O., & Guitton, D. (2018). The primitive retino-tecto-reticular pathway is functional in hemidecorticate patients. *Current Biology, 28*(20), R1184–R1186. https://doi.org/10.1016/j.cub.2018.09.006

Schiller, P. H., Haushofer, J., & Kendall, G. (2004). An examination of the variables that affect express saccade generation. *Visual Neuroscience, 21*, 119–127. https://doi.org/10.1017/s0952523804042038.

Schneider, G. E. (1969). Two visual systems. *Science, 163*(3870), 895–902. https://doi.org/10.1126/science.163.3870.895

Tamietto, M., & De Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience, 11,* 697–709. https://doi.org/10.1038/nrn2889

Tamietto, M., Pullens, P., de Gelder, B., Weiskrantz, L., & Goebel, R. (2012). Subcortical connections to human amygdala and changes following destruction of the visual cortex. *Current Biology, 22*(15), 1449–1455. https://doi.org/10.1016/j.cub.2012.06.006

Thielscher, A., Reichenbach, A., Uurbil, K., & Uluda, K. (2010). The Cortical site of visual suppression by transcranial magnetic stimulation. *Cerebral Cortex, 20*(2), 328–338. https://doi.org/10.1093/CERCOR/BHP102

Vanni, S., Henriksson, L., & James, A. C. (2005). Multifocal fMRI mapping of visual cortical areas. *NeuroImage*, *27*(1), 95–105. https://doi.org/10.1016/J.NEUROIMAGE.2005.01.046

Vanrullen, R. (2007). The power of the feed-forward sweep. *Advances in Cognitive Psychology,3,* 167–176. https://doi.org/10.2478/v10053-008-0022-3

VanRullen, R., & Koch, C. (2003). Visual selective behavior can be triggered by a feed-forward process. *Journal of Cognitive Neuroscience, 15,* 209–217. https://doi.org/10.1162/089892903321208141

Weiskrantz, L. (2009). Is blindsight just degraded normal vision? *Experimental Brain Research, 192*, 413–416. https://doi.org/10.1007/s00221-008-1388-7

Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain*, *97*(4), 709–728. https://doi.org/10.1093/brain/97.4.709

Wurtz, R. H. (2010). Superior Colliculus. In *Encyclopedia of Neuroscience*. https://doi.org/10.1016/B978-008045046-9.01103-7

Yoshida, M., & Isa, T. (2015). Signal detection analysis of blindsight in monkeys. *Scientific Reports*. https://doi.org/10.1038/srep10755

Yoshida, M., Takaura, K., Kato, R., Ikeda, T., & Isa, T. (2008). Striate cortical lesions affect deliberate decision and control of saccade: Implication for blindsight. *Journal of Neuroscience*. https://doi.org/10.1523/jneurosci.1973-08.2008

Zihl, J. (1980). "Blindsight": Improvement of visually guided eye movements by systematic practice in patients with cerebral blindness. *Neuropsychologia, 18*(1), 71–78. https://doi.org/10.1016/0028-3932(80)90085-8

Zihl, J. (1995). Visual scanning behavior in patients with homonymous hemianopia. *Neuropsychologia*, *33*(3), 287–303. https://doi.org/10.1016/0028-3932(94)00119-a