Transcranial magnetic stimulation (TMS)-induced Blindsight of Orientation is Degraded Conscious Vision

Mika Koivisto, * Kalle Leino Aino Pekkarinen, Jaakko Karttunen, Henry Railo and Mikko Hurme

Department of Psychology, University of Turku, 20014 Turku, Finland

Abstract—Patients with blindsight are blind due to an early visual cortical lesion, but they can discriminate stimuli presented to the blind visual field better than chance. Studies using transcranial magnetic stimulation (TMS) of early visual cortex have tried to induce blindsight-like behaviour in neurologically healthy individuals, but the studies have yielded varied results. We hypothesized that previous demonstrations of TMS-induced blindsight may result from degraded awareness of the stimuli due to the use of dichotomous visibility scales in measuring awareness. In the present study, TMS was applied to early visual cortex during an orientation discrimination task and the subjective scale measuring awareness was manipulated: The participants reported their conscious perception either using a dichotomous scale or a 4-point Perceptual Awareness Scale. Although the results with the dichotomous scale replicated previous reports of blindsight-like behaviour, there was no evidence of TMS-induced blindsight for orientation when the participants used the lowest rating of the 4-point graded scale to indicate that they were not aware of the presence of the stimulus. Moreover, signal detection analyses indicated that across participants, the individual’s sensitivity to consciously discriminate orientation predicted behaviour on reportedly unconscious trials. These results suggest that blindsight-like discrimination of orientation in neurologically healthy individuals does not occur for completely invisible stimuli, that is, when the observers do not report any kind of consciousness of the stimulus. TMS-induced blindsight for orientation is likely degraded conscious vision.

© 2021 The Author(s). Published by Elsevier Ltd on behalf of IBRO. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Key words: awareness, blindsight, consciousness, TMS, vision.

INTRODUCTION

Blindsight refers to the phenomenon in which patients who have a blind visual area due to lesion in the primary visual cortex (V1) can still guide their behavior based on stimuli presented in the blind area, although they deny seeing the stimuli (Pöppel et al., 1973; Weiskrantz et al., 1974). Blindsight patients can discriminate features of the stimuli they report not having seen with surprisingly high accuracy (Stoerig and Cowey, 1989, 1992; Cowey, 2010). Blindsight has been explained by assuming that unconscious visual stimuli have a capacity to guide behavioural responses via subcortical pathways that bypass V1 on the way to cortex. Blindsight might be explained by functional connections from the superiorior collicus (SC) to the extrastriate cortex (Leh et al., 2006) or from lateral geniculate nucleus (LGN) to V5 (Ajina et al., 2015). However, it is not clear whether the subcortical tracts supporting blindsight are functional also in normal brain, because after V1 lesion, existing connections can change their functions and connectivity (Payne and Lomber, 2001; Leh et al., 2006; Mikellidou et al., 2019). Alternative explanations of blindsight argue that it is not strictly a form of unconscious vision, but that it represents near-threshold, degraded vision which is observed because the tasks used to measure (“objective”) behavioral performance have higher sensitivity than measures of subjective, conscious vision (Campion et al., 1983; Phillips, 2021a). The graded vision account of blindsight patients’ behavior was challenged already by Azzopardi and Cowey (1997) who showed that G.Y.’s (a famous blindsight patient) vision is unlike normal, near-threshold vision. They argued that blindsighted patients process visual stimuli in an unusual way. This debate still continues (Michel and Lau, 2021; Phillips, 2021b).

Studies using transcranial magnetic stimulation (TMS) have tried to simulate blindsight in the normal, neurologically healthy brain. TMS over early visual cortex (EVC) can disrupt neural processing and suppress visual awareness of stimuli presented to the contralateral visual field most strongly when applied about 60–140 ms after the onset of visual stimulus (Amassian et al., 1989; de Graaf et al., 2014). In a typical procedure to examine TMS-induced blindsight, TMS is applied over the EVC to suppress awareness while the participant is performing a forced-choice visual task in
which a discrimination about a specific feature of the stimulus (e.g., orientation of a line) is chosen from a set of alternative responses (e.g., vertical or horizontal). In addition to the discrimination task, in each trial the participant rates his/her awareness of the stimulus (for review of measures of awareness, see Timmermans and Cleeremans, 2015). If accuracy in the discrimination task exceeds the chance-level when no awareness is reported, or the unseen stimulus otherwise influences responding in other related paradigms (e.g., priming-like effects), the results are interpreted as revealing a blindsight-like dissociation.

Several studies claim to have provided evidence for TMS-induced blindsight (Ro et al., 2004; Boyer et al., 2005; Jolij and Lamme, 2005, 2008; Christensen et al., 2008; Railo and Koivisto, 2012; Koenig and Ro, 2019). However, this conclusion can be challenged on several grounds. First, when unconscious effects have been compared with a corresponding unconscious effects in a control condition, TMS of EVC typically reveals that also unconsciously guided performance depends on the activity of EVC: either the unconscious effects have been reduced but still exist (Railo et al., 2012; Koivisto et al., 2014) or they have been completely eliminated at some stimulus-TMS onset-asynchronies (SOAs) (Koivisto et al., 2010, 2012; Persuh and Ro, 2013; Railo et al., 2014; Hurme et al., 2017, 2019, 2020). Such findings suggest that in the neurologically healthy brain, EVC and the geniculo-striate pathway play a causal role in unconscious visual processing.

Second problem is related to the criterion content, that is, which feature of the visual stimulus the participants use when they report the contents of their perception (Kahneman, 1968). It is not clear if TMS-induced blindsight occurs when no awareness of the presence of the stimulus is reported, that is, when the stimulus does not give raise to any kind of visual qualia or change in the content of visual awareness. Many of the studies supporting the existence of TMS-induced blindsight have operationalized awareness in such way that awareness of the presence of the stimulus cannot be excluded. For example, Boyer et al. (2005) measured awareness by asking the participant “Did you see the orientation of the bar?”. A negative response to the question does not necessarily imply a complete absence of awareness of the stimulus as the question is only about awareness of the task-relevant feature (i.e., orientation). Similarly, in a study on TMS-induced affective blindsight (Jolij and Lamme, 2005) the participants were not aware of the location of an emotional face stimulus among other face stimuli, although they were likely aware of the presence of all the stimuli in the array. Note that while two types of blindsight has been distinguished in studies on patients, neither of these types involves any awareness of visual features: in type-1 blindsight the patient does not have any kind of awareness of the stimulus, and in type-2 blindsight the patient may have non-visual “feelings” or sensations induced by the stimulus, but not visual experiences (Weiskrantz, 1997). In addition, when high intensity or moving stimuli are presented, patients with visual cortical lesions may report awareness of the visual stimuli (Ffytche and Zeki, 2011).

Third, the studies demonstrating TMS-induced blindsight have often measured awareness with dichotomous rating scales (e.g., seen vs. unseen) (Ro et al., 2004, 2008; Boyer et al., 2005; Koenig and Ro, 2019), which is known to be associated with the criterion problem: the participants may use a conservative response criterion and report unawareness of the stimulus or of its feature, although they have a weak visual experience of the stimulus or some of its feature (Erkenes, 1960). The dichotomous scale does not acknowledge the graduality of perceptual representations. It is now known that the contents of visual awareness can evolve in graded manner through different intermediate levels (Ramsøy and Overgaard, 2004; Overgaard et al., 2006; Sandberg et al., 2010; Pretorius et al., 2016), although access to these contents can be interpreted to be all-or-none (Sergent and Dehaene, 2004; Koulider et al., 2010) or gradual (Overgaard et al., 2006), depending on the theoretical perspective. Graded aware perception, measured with graded scales, correlates strongly with objective forced-choice performance (Sandberg et al., 2010) and electrophysiological measures (Tagliaube et al., 2016). Also, the conservative bias in response criterion can be reduced when the observers are allowed to use graded subjective scales such as Perceptual Awareness Scale (PAS) (Overgaard et al., 2006; Overgaard, 2011). PAS consists of four alternatives: “no experience,” “brief glimpse of something,” “almost clear experience,” and “clear experience”, which observers report to be easy to use and to correspond well to their subjective experiences (Ramsøy and Overgaard, 2004). In experiments on vision, the category “no experience” refers to no conscious visual perception of the presence of the stimulus (the whole stimulus was unconscious), whereas “brief glimpse of something” means that the observer saw something appearing, but was not aware of its task-relevant feature. Thus, it is possible that the “unseen” ratings given with dichotomous scales would correspond to either of the two lowest alternatives in PAS, and hence include trials where “a brief glimpse” of the stimulus was noticed. This implies that neurologically healthy participants who report that the stimulus (or its feature) was “unseen” do not necessarily show a genuine unconscious blindsight capacity. The interpretation that the reported “TMS-induced blindsight” in Boyer et al. (2005) was merely degraded conscious vision is supported by their observation that participants’ confidence ratings strongly predicted objective discrimination performance on trials where the participants reported unawareness of the orientation (Boyer et al., 2005): when participants reported low confidence, objective discrimination of orientation was at chance level, but with high confidence performance was nearly perfect.

Because a direct comparison of how visibility report scales influence the results in studies examining TMS-induced blindsight has been lacking, we studied whether the subjective scale used to measure (un)awareness influences the outcomes in TMS-induced blindsight
During an orientation discrimination task, TMS was applied at a short SOA (60, 75 or 90 ms) or a long SOA (155 ms) over the contralateral EVC, whereas in the control condition the ipsilateral EVC was stimulated at the short and long SOAs. The short SOA was expected to suppress awareness in relation to the control condition (Amassian et al., 1989; de Graaf et al., 2014). The participants rated their awareness using either the dichotomous scale or the 4-point PAS. We expected to replicate the previous results (Boyer et al., 2005; Koenig and Ro, 2019) showing above chance discrimination when unawareness is defined on basis of the dichotomous awareness scale and the content criterion is orientation. Stronger support for genuine TMS-induced blindsight would be obtained if above chance discrimination performance would occur when unawareness of the stimulus is defined as the lowest alternative of PAS, where “nothing seen” rating indicates no awareness of the stimulus.

It could be argued that above chance accuracy in discriminating a task-relevant visual feature (e.g., line orientation) counts as blindsight, when no awareness of orientation is reported. However, this interpretation is not necessarily valid because a degraded conscious perception of some feature may help perform the discrimination task although it does not necessarily meet the criterion for reporting it (e.g., participant may report no awareness of a line, but nevertheless be able to guess that the stimulus was horizontal because he sees a horizontally spread blur). Because we included also catch trials, it was possible to compute the bias-free signal detection measure of discrimination (d') and the response criterion (c) for awareness of orientation and orientation discrimination performance. This allowed us to test whether discrimination of orientation in trials without reported awareness of orientation actually depends on partial awareness of orientation when the conservative response criterion is controlled for. The signal detection theory-based comparison of awareness and discrimination also made it possible to study whether TMS suppresses awareness more strongly than discrimination performance, a pattern which should be observed if discrimination occurs relatively independently of consciousness (Lloyd et al., 2013).

EXPERIMENTAL PROCEDURES

Participants

Fifty-three adult participants were recruited from the undergraduate students at the University of Turku. Thirty-six of them (age: 20–29, 9 male) were able to pass the pretests and localization phase (see Pretests and localization below) and thus completed the experiment. They had normal or corrected-to-normal vision. They gave a written informed consent prior to participating. The participants were randomized into two visibility report scale groups (dichotomous scale vs. PAS). TMS was administered following all safety guidelines (Rossi et al., 2009). The study was conducted according to the Declaration of Helsinki and it was approved by the Ethics Committee of the Hospital District of Southwest Finland.

Apparatus and stimuli

The stimuli were presented on 24” VIEWPixx Lite monitor, set at a 120 Hz vertical synchronization rate. E-prime 2 (Psychology Software Tools, Inc.) was used for controlling the presentation of visual stimuli and TMS triggers, and for collecting responses.

The visual stimuli consisted of horizontal or vertical lines, either 0.3° × 0.05° (horizontal lines) or 0.05° × 0.3° (vertical lines) of visual angle. They were centered 0.25° to the right of the fixation square (0.25° × 0.25°). Thus, the stimulus size and location were identical to those in Koenig and Ro (2019) and almost identical to those in Boyer et al. (2005), both studies reporting TMS-induced blindsight for orientation, which we tried to partly replicate with dichotomous scale (“seen” vs. “unseen”) as a measure of visual awareness. The stimuli were dark gray (17.3, 18.6, or 19.5 cd/m²), presented on a light gray background (24.6 cd/m²), so that the Weber contrast of the visual stimuli was −0.30, −0.24, or −0.21.

Single TMS pulses were delivered with MagPro X100 stimulator (MagVenture). The coil was circular MCF-75 (MagVenture) with 65 mm outer winding diameter and 10 mm inner diameter.

We used a circular coil because they have been employed most often in studies which report TMS-induced blindsight (Ro et al., 2004; Boyer et al., 2005; Ro, 2008; Koenig and Ro, 2019).

Procedure

Each trial began with the fixation square for 2000 ms (Fig. 1A). It was followed by a line, randomly either horizontal or vertical, appearing on the screen for 8.3 ms, centered 0.25° to the right of the fixation (or in catch trials no line was presented). In every trial, a single TMS pulse was delivered randomly at a short or a long SOA. The long SOA was always 155 ms, whereas the short SOA was selected from 60, 75, or 90 ms SOAs on basis of the individual localization procedure (see below) to be the one that produces the strongest visual suppression. The stimulus contrast was also individually determined (see below). After each trial, the participant made a subjective rating of visibility and reported the line orientation as horizontal or vertical in a forced-choice task. They were instructed to guess if they did not know the orientation. In half of the stimulus blocks, the objective forced-choice task was made first, followed by the subjective rating; in the other half of the stimulus blocks, the subjective rating was the first task. The order was reversed after the third stimulus block. The order of the subjective task and the objective forced-choice task was counterbalanced so that half of the participants performed the objective task first in the beginning, whereas the other half began with the subjective task. In the beginning of the first block and the fourth block, a practice block was performed to familiarize the participants with the order of the tasks.
The forced-choice responses and subjective ratings were reported with a game pad (Logitech Gamepad F310). The participants were randomized into two subjective rating scale groups (dichotomous vs. PAS). The subjective rating scale was manipulated between participants so that the subjective response criteria would not transfer from one subjective task to the other task. For half of the participants, the subjective rating involved a dichotomous task: the participants reported whether or not they saw the orientation of the line (Boyer et al., 2005; Koenig and Ro, 2019). Half of the participants used a four-point PAS (Ramsøy and Overgaard, 2004) for reporting their subjective awareness of the line: (1) “I saw no stimulus” (“nothing”), (2) “I saw a glimpse of something” (“something”), (3) “I saw the orientation of the line almost clearly” (“almost clear”), and (4) “I saw the orientation of the line clearly” (“clear”). The instructions stressed that rating “nothing” should be used when they were not aware of the presence of any stimulus and rating “something” should be used when there was no perception of the orientation of the line, although they were aware of the presence of the stimulus. The distinction between not seeing and seeing the orientation was further clarified by stressing that when there was no perception of the orientation of the line, either “nothing” or “something” should be used, depending on whether they did not see any stimulus or saw something that they could not identify. It was also emphasized that the rating should be about the stimulus, not about any other changes appearing in the visual field (e.g., phosphenes, so that participants should not report seeing “something” when they experience a phosphen but do not see any stimulus).

Each participant performed six blocks of 32 stimulus-present and 6 catch trials (16/SOA + 3 catch trials/SOA). The first, third, fourth, and sixth blocks were the critical TMS blocks in which the coil was positioned over the suppression area. The second and the fifth block were control trials in which the coil was positioned 1–2 cm to the right and 0–3 cm up from the inion, that is over the ipsilateral right hemisphere. The vertical distance of the coil from the inion over the right hemisphere was never the same as in the contralateral left suppression area in order to avoid stimulating the same retinotopic area as in the critical TMS trials. Thus, each participant was given 64 critical TMS trials at the short SOA and 64 at the long SOA, and 32 ipsilateral control trials at the short and long SOAs.

**Pretests and localization**

The location which was stimulated by TMS was determined by searching a location that produced reliable suppression, as similar method was used in studies that are sometimes interpreted to demonstrate unconscious TMS-induced blindsight (Boyer et al., 2005; Koenig and Ro, 2019). Because TMS was not localized based on MRIs, the exact location of stimulation is not any specific cortical area, but varies across participants. Before the localization of TMS stimulation area, pretest blocks of 20 stimulus-present trials were run to ensure that each participant is able to discriminate the line orientation with an accuracy of 80–100% correct without TMS. The vertical and horizontal lines were presented in identical way as during the experimental blocks. The Weber contrast in the first block was $-0.24$. If the participant scored less than 80% correct, the contrast for the next block was increased to $-0.30$; if the participant scored 80–100% correct, the next block was run with the contrast of $-0.21$. This procedure was continued until we found the lowest contrast level that was performed with accuracy level of 80–100%. Such contrast level was used for the stimuli in the localization procedure (square) and in the TMS experiment (line).

To determine the optimal stimulation site, intensity, and stimulus-TMS SOA, the base of the TMS coil was first placed 2 cm above and 1 cm left of the inion (see Fig. 1B, C). First, single pulses without any visual tasks were administered to determine the stimulation intensity, starting with low TMS intensities and gradually increasing the intensity until we reached a maximal intensity that the participant considered as comfortable and with which the participant thought to be able to...
perform the tasks. The selected TMS intensity varied between 65% and 100% (mean = 91%).

To search for an efficient stimulation location, a square identical to the fixation square appeared for 8.3 ms, 0.25° to the right of the fixation square. It was followed by a TMS pulse randomly either 60, 75, or 90 ms after the visual stimulus onset. Participants reported after each trial whether or not they saw the square. Each localization block included 15 stimulus-present trials (5 trials/SOA) and 6 catch trials (2 trials/ SOA). The coil was positioned 2 cm above and 1 cm to left from the inion in the first block. The position of the coil was moved between the blocks slightly up or down or to the left or right from the initial position until we found a position from which the participant reported not seeing the stimulus on at least two out of five stimulus-present trials in one or more of the SOAs. The position and SOA that elicited the strongest suppression was selected for the stimulation position and short SOA in the actual experiment. In the case that two or more SOAs produced equally strong suppression, the shortest SOA was selected. The selected position was on average 1.3 cm left (ranging from 0 to 3 cm) and 1.5 cm up (ranging from 0 to 3 cm) from the inion. The SOA was 60 ms for 17 participants, 75 ms for 9 participants, and 90 ms for 10 participants. For the control position, we selected a position such that it was at least 1 cm above or below the stimulation position and at least 2 cm to the right from it over the ipsilateral hemisphere. Because we used a circular coil, which is less focal than the figure-of-8 coil, it is likely that the ring-shaped field falls below 0).

MPE was higher than 95% as statistically reliable (i.e. more than 95% of posterior effects either exceeds 0 or falls below 0).

Data and analysis scripts are available at (https://osf.io/rph2k/?view_only=622beaf6407543c993dd15d0ffdec23c).

RESULTS

Awareness

First, we confirmed that TMS of early visual cortex suppressed awareness in relation to the ipsilateral control stimulation, especially at the short SOA, as expected based on previous research (de Graaf et al., 2014). Because the dichotomous scale had two levels (seen vs. unseen) and the graded PAS scale involved four levels, we made the scales comparable by dichotomizing the PAS scale. PAS levels “nothing” and “something” were scored as “unseen” (instructions stressed that these ratings should be used when there was no perception of the orientation of the line) and “al-

| Variable                      | Median | MAD  | CI_lower | CI_higher | MPE     |
|-------------------------------|--------|------|----------|-----------|---------|
| R²                            | 0.12   | 0.01 | 0.11     | 0.15      | NA      |
| (Intercept)                   | 0.20   | 0.19 | -0.10    | 0.52      | NA      |
| TMSControl                    | 0.64   | 0.11 | 0.46     | 0.82      | >99.99  |
| SOALong                       | 0.87   | 0.09 | 0.82     | 0.81      | 99.98   |
| ScalePAS                      | -0.39  | 0.27 | -0.80    | 0.08      | 22.22   |
| TMSControl:SOALong            | -0.36  | 0.16 | -0.63    | -0.11     | 99.02   |
| TMSControl:ScalePAS           | 0.15   | 0.15 | -0.09    | 0.41      | 84.03   |
| SOALong:ScalePAS              | -0.15  | 0.12 | -0.37    | 0.05      | 89.38   |
| TMSControl:SOALong:ScalePAS   | -0.08  | 0.22 | -0.42    | 0.30      | 64.38   |

Table 1. The results of the model predicting reported awareness with TMS, SOA, and Scale. Baseline = Tms, short SOA, dichotomous scale
most clear" and "clear" were scored as "seen". The analysis predicted awareness reports with TMS (Tms vs. Control), SOA (short vs. long), Scale (dichotomous vs. PAS), and their interactions, as fixed effects, and the random intercept for participant as a random effect. We fitted a Markov Chain Monte Carlo binomial model on single stimulus-present trials to predict awareness (note that the effects are expressed in terms of log odds) (Table 1, Fig. 2).

The model had an explanatory power ($R^2$) of about 12.31% (MAD = 0.0064, 90% CI [0.11, 0.13]). The intercept (i.e., Tms condition, short SOA, dichotomous scale) was at 0.20 (MAD = 0.19, 90% CI [-0.10, 0.52]) which corresponds to 55% aware. At the short SOA, awareness ratings were higher in the Control condition than in the Tms condition (TMSControl), and at the longer SOA awareness ratings were higher than at the shorter SOA in the Tms condition (SOALong). The influence of TMS was smaller at the long SOA than at the shorter SOA (TMSControl:SOALong), as expected. None of the effects or interactions involving Scale were probable (MPEs < 95%). These results suggest that TMS suppressed awareness (of orientation) especially at the short SOA, and that the two subjective scales produced similar results.

**Signal detection analyses of awareness and discrimination**

Analysis of subjective ratings in stimulus-present trials, reported above, did not take into consideration the false alarm rates (i.e., responding "seen" to catch trials). To account for this, we calculated the signal detection discrimination index $d'$ and criterion index $c$ for subjective ratings. "Seen" responses in the dichotomous scale and "almost clear" and "clear" responses in PAS in response to stimulus-present trials were scored as hits, and in response to catch trials as false alarms. The signal detection indexes were calculated also for the objective discrimination task (hits: vertical responses to vertical lines; false alarms: vertical responses to horizontal lines). This allowed us to test whether TMS suppresses awareness (subjective task) more than orientation discrimination (objective task), or suppresses only awareness without influencing discrimination performance, a pattern of results that is predicted by the hypothesis of relative TMS-induced blindsight.

We predicted $d'$ with two different models, the first one involving TMS, Task (subjective vs. objective), SOA, and Scale with their interactions as fixed effect in Markov Chain Monte Carlo gaussian (link = identity) models. The second model was otherwise the same, with the exception that it did not include Scale as a fixed effect. Comparison of the models with leave-one-out cross-validation suggested that the model with TMS, Task, and SOA as fixed effects had the highest expected log predictive density (ELPD) and thus fitted better the data (Table 2, Fig. 3A). The model had an explanatory power ($R^2$) of about 42.30% (MAD = 0.038, 90% CI [0.37, 0.49], adj. $R^2 = 0.32$). The intercept was at 1.52 (MAD = 0.12, 90% CI [1.33, 1.72]).

The results showed that while performance was higher in the objective task than in the subjective task (TaskObjective), TMS impaired performance similarly in subjective and objective tasks, especially at the short SOA (TMSControl, SOALong, TMSControl:SOALong).

The analysis of the response criterion $c$ was performed in the same way as that of $d'$. As with the model examining $d'$, also for $c$ the model with TMS, Task, and SOA with their interactions as fixed effects...
Table 2. The results of the model predicting $d'$ with TMS, SOA, and task. Baseline = Tms, short SOA, subjective task

| Variable                       | Median | MAD  | CI_lower | CI_higher | MPE  |
|--------------------------------|--------|------|----------|-----------|------|
| $\beta^2$                      | 0.43   | 0.04 | 0.37     | 0.49      | NA   |
| (Intercept)                    | 1.52   | 0.12 | 1.33     | 1.72      | NA   |
| TMSControl                     | 0.29   | 0.13 | 0.08     | 0.50      | **98.83** |
| TaskObjective                  | 0.33   | 0.13 | 0.12     | 0.54      | **99.38** |
| SOALong                        | 0.27   | 0.13 | 0.07     | 0.49      | **97.95** |
| TMSControl:TaskObjective       | −0.01  | 0.18 | −0.33    | 0.26      | 52.75 |
| TMSControl:SOALong             | −0.33  | 0.18 | −0.63    | −0.03     | **96.50** |
| TaskObjective:SOALong          | −0.05  | 0.18 | −0.35    | 0.25      | 59.98 |
| TMSControl:TaskObjective:SOALong| 0.13   | 0.25 | −0.30    | 0.54      | 69.67 |

Fig. 3. (A) The boxplots show (A) the discrimination index $d'$ and (B) the response criterion $c$ as a function of TMS and SOA in subjective and objective tasks. The circles indicate individual participants’ data points and the black circle represents the group means. The modelled results for (C) $d'$ and (D) $c$. The Scale was not included as an effect in the models, because the comparison of models suggested that it did not have any effects. Error bars indicate 90% credibly intervals.
had the highest expected log predictive density (ELPD) and thus it fitted the data better than the model with Scale factor. The model (Table 3, Fig. 3B) had an explanatory power ($R^2$) of about 59.80% (MAD = 0.027, 90% CI [0.56, 0.64], adj. $R^2 = 0.54$). The intercept was at 0.78 (MAD = 0.05, 90% CI [0.69, 0.87]). The results showed that TMS elevated response criterion in the subjective tasks as compared with the Control condition (TMSControl). In the objective task, the criterion was neutral (TaskObjective, TMSControl: TaskObjective), as could be expected because there would not be any clear reason why the observers would prefer to respond "vertical" rather than "horizontal", or vice versa.

Discrimination with and without reported awareness

So far, we have demonstrated that TMS suppressed both awareness of orientation and discrimination of orientation especially at the short SOA, as expected, and the comparison with Control condition suggest that the suppression was due to neural effects of TMS. Next, we examined discrimination accuracy as a function of reported awareness with dichotomous scale in the short SOA Tms condition (Fig. 4A) in which TMS suppressed awareness most strongly. There were on average 29 (SD = 14) "unseen" and 35 (SD = 14) "seen" trials per participant in the short SOA condition. We fitted a Markov Chain Monte Carlo binomial (link = logit) model on trials with dichotomous scale and PAS by fitting a Markov Chain Monte Carlo binomial (link = logit) model on trials with dichotomous scale condition but not in the PAS condition. We compared discrimination accuracy directly between scales (above) suggested that subjectively unconscious discrimination succeeded better than expected by chance in the dichotomous scale condition but not in the PAS condition. We compared discrimination accuracy directly between dichotomous scale and PAS by fitting a Markov Chain Monte Carlo binomial (link = logit) model on trials with no reported awareness ("unseen" in dichotomous scale, "nothing" in PAS) in the short SOA Tms condition. The model had an explanatory power ($R^2$) of about 20.96% (MAD = 0.022, 90% CI [0.17, 0.24]). The intercept was at 0.63 (MAD = 0.13, 90% CI [0.41, 0.86]), which means that correct responses were more probable than incorrect ones (log odds ratio of 0 corresponds to chance level). In terms of percent correct, the intercept corresponds here to 65% correct. Thus, when no awareness of orientation was reported ("unseen"), performance exceeded the chance level. The effect of Awareness had a probability of >99.99% of being positive, Median = 2.97, MAD = 0.26, 90% CI [2.58, 3.42], indicating that in awareness trials ("seen") performance was substantially higher than in unaware ("unseen") trials.

To study discrimination as a function of reported awareness with PAS in the short SOA Tms condition, we fitted a Markov Chain Monte Carlo binomial (link = logit) model on single trials to predict accuracy. PAS was scored as ordered factor, so the intercept is between ratings "something" and "almost clear". There were on average 15 (SD = 11) "nothing", 20 (SD = 7) "something", 15 (SD = 8) "almost clear", and 17 (SD = 12) "clear" trials per participant in the short SOA Tms condition. The model (Fig. 4B) had an explanatory power ($R^2$) of about 22.93% (MAD = 0.022, 90% CI [0.19, 0.26]). The intercept was at 2.01 (MAD = 0.22, 90% CI [1.63, 2.40]), which corresponds to 88% correct in the halfway between ratings "something" and "almost clear". Within this model, the best predictor of accuracy was a linear trend which had a probability of >99.99 of being positive (Median = 2.83, MAD = 0.28, 90% CI [2.38, 3.29]. In other words, accuracy increased as a function of awareness. As can be seen in Fig. 4B, the CIs indicate that the performance level was higher than chance level when "something" was reported, but at chance level when no awareness ("nothing") of the stimulus was reported (for statistical analysis of "nothing" trials, see the next paragraph).

The separate analyses of scales (above) suggested that subjectively unconscious discrimination succeeded better than expected by chance in the dichotomous scale condition but not in the PAS condition. We compared discrimination accuracy directly between dichotomous scale and PAS by fitting a Markov Chain Monte Carlo binomial (link = logit) model on trials with no reported awareness ("unseen" in dichotomous scale, "nothing" in PAS) in the short SOA Tms condition. The model had an explanatory power ($R^2$) of about 4.15% (MAD = 0.017, 90% CI [0.013, 0.068]). The intercept was at 0.61 (MAD = 0.13, 90% CI [0.40, 0.84]), showing that the log odds ratio of intercept was higher than 0, which reflects the above-chance level performance (65% correct) with dichotomous scale. Accuracy in PAS condition had a probability of 99.22% of being smaller than that in the dichotomous scale condition (Median = −0.52, MAD = 0.21, 90% CI [−0.89, −0.19]). With the PAS condition as the intercept in the model (intercept = 0.096, MAD = 0.17, 90% CI [−0.18, 0.37]), discrimination accuracy did not differ from the 50% chance-level (log odds ratio of 0 corresponds to the 50% chance level) when "nothing" was reported to be seen. In summary, the analyses of accuracy without reported awareness showed above.

| Variable | Median | MAD | CI_lower | CI_higher | MPE |
|----------|--------|-----|----------|-----------|-----|
| R²       | 0.60   | 0.03| 0.56     | 0.64      | NA  |
| (Intercept) | 0.78   | 0.05| 0.69     | 0.87      | NA  |
| TMSControl | −0.28  | 0.07| −0.40    | −0.17     | >99.99 |
| TaskObjective | −0.82  | 0.07| −0.94    | −0.71     | >99.99 |
| SOALong | −0.06  | 0.07| −0.17    | 0.07      | 79.00 |
| TMSControl:TaskObjective | 0.30   | 0.10| 0.14     | 0.48      | 99.80 |
| TMSControl:SOALong | 0.08   | 0.10| −0.09    | 0.24      | 77.48 |
| TaskObjective:SOALong | 0.02   | 0.10| −0.14    | 0.19      | 58.73 |
| TMSControl:TaskObjective:SOALong | −0.13  | 0.15| −0.36    | 0.10      | 82.47 |

Table 3. The results of the model predicting criterion (c) with TMS, SOA, and task. Baseline = Tms, short SOA, subjective task.
chance performance when awareness was reported with the dichotomous scale, but chance-level performance when awareness was reported with PAS.

Discrimination as a function of awareness ($d'$)

Finally, we studied in the Tms conditions whether the ability to consciously discriminate signal from noise, operationalized as $d'$ (calculated based on the subjective visibility ratings), predicts discrimination of orientation in the trials without reported awareness of orientation. PAS was dichotomized to allow analysis of data from both scales together (“nothing” and “something” = no awareness of orientation); note that we already showed that “nothing” seen ratings predict chance level performance). Sensitivity ($d'$), SOA, and Scale with their interactions were fixed effects in Markov Chain Monte Carlo gaussian (link = identity) model (Fig. 5A, Table 4). The model had an explanatory power ($R^2$) of about 44.92% (MAD = 0.12, 90% CI [0.23, 0.62], adj. $R^2 = 0.046$) (Table 5, Fig. 5B). The intercept was at 0.67 (MAD = 0.033, 90% CI [0.61, 0.72]). Within this model, suppression explained performance in the trials in which the observers reported that they did not see the orientation: the stronger TMS suppressed awareness, the less correctly the discrimination of orientation without reported awareness succeeded. This effect was stronger at the short than long SOA (Suppression: SOALong). In conclusion, the ability to discriminate orientation in trials without reported awareness of orientation depended on how strongly TMS suppressed awareness.

**DISCUSSION**

The existence of TMS-induced blindsight was studied in different ways in the present study: by measuring (un)awareness with a graded scale that measures awareness more exhaustively than dichotomous scales (Sandberg et al., 2010), by comparing the influence of TMS on subjective measures of awareness and objective forced-choice measures (Lloyd et al., 2013), and by examining whether or not discrimination accuracy in trials where observers reported no awareness of orientation correlated with signal detection measure ($d'$) of awareness or with the amount of TMS-induced suppression of subjective awareness.

The results replicated the previous finding that during suppression of neural activity in occipital cortex, the discrimination of orientation succeeded better than expected by chance when awareness was measured with dichotomous seen/unseen scale and the criterion content was orientation (Boyer et al., 2005; Koenig and Ro, 2019). However, when the observers reported with a graded scale that they did not see that any stimulus was present, discrimination accuracy was at chance level. Thus, TMS-induced blindsight did not occur for completely unaware stimuli. This pattern is similar to that observed in cases of hemianoptic patients who would
be inferred as showing blindsight with a dichotomous scale, but who did not show any blindsight when they reported no visual awareness of the presence of the stimulus with graded PAS (Overgaard et al., 2008; Mazzi et al., 2016).

The results showed both with the dichotomous scale and with PAS rating “something [but not the orientation] seen” that the discrimination of orientation succeeded better than expected by chance when the observers reported not having seen the orientation. These findings could be interpreted to support TMS-induced blindsight for orientation (Boyer et al., 2005; Koenig and Ro, 2019). This interpretation should be considered with caution for several reasons. First, even if the observers report that they do not see the line (or its orientation), they may see a degraded or blurred stimulus which gives cues about the orientation. For example, in the case of horizontal line, they may see a visual blur that is wider than it is higher, giving a clear cue for the orientation response. The cue may guide their discrimination responses, even if the participant is not aware of its relevance or does not interpret it as line. The situation is similar to what may occur in visual masking, where the participants may not see the target stimulus but the mask may inherit some features of the target (Herzog et al., 2012). Perception of the inherited features may guide the discrimination responses. In both cases, the participant does not see the target stimulus, but one cannot argue that their discrimination responses were guided by unconscious percep-

![Fig. 5. (A) Accuracy in trials without awareness of orientation as a function of awareness and SOA. (B) Accuracy in trials without awareness of orientation as a function of TMS-induced suppression (Control $d'$ - TMS $d'$) and SOA.](image)

**Table 4.** The results of the model predicting accuracy in trials without awareness of orientation with $d'$, SOA, and Scale. Baseline = short SOA, dichotomous scale

| Variable                  | Median | MAD  | CI_lower | CI_higher | MPE  |
|---------------------------|--------|------|----------|-----------|------|
| $R^2$                     | 0.41   | 0.13 | 0.20     | 0.59      | NA   |
| (Intercept)               | 0.52   | 0.07 | 0.41     | 0.64      | NA   |
| $d'$                      | 0.08   | 0.04 | 0.02     | 0.14      | 97.52|
| SOALong                   | -0.02  | 0.12 | -0.20    | 0.18      | 56.25|
| ScalePAS                  | 0.10   | 0.09 | -0.05    | 0.25      | 88.47|
| $d'$:SOALong              | -0.01  | 0.06 | -0.12    | 0.08      | 59.85|
| $d'$:ScalePAS             | -0.04  | 0.05 | -0.13    | 0.06      | 74.78|
| SOALong:ScalePAS          | -0.02  | 0.14 | -0.24    | 0.23      | 55.38|
| $d'$:SOALong:ScalePAS     | 0.05   | 0.08 | -0.09    | 0.17      | 72.70|

**Table 5.** The results of the model predicting accuracy in trials without awareness of orientation with TMS-induced suppression (Control $d'$ - TMS $d'$), SOA, and Scale. Baseline = short SOA, dichotomous scale

| Variable                  | Median | MAD  | CI_lower | CI_higher | MPE  |
|---------------------------|--------|------|----------|-----------|------|
| $R^2$                     | 0.45   | 0.12 | 0.23     | 0.62      | NA   |
| (Intercept)               | 0.67   | 0.03 | 0.61     | 0.72      | NA   |
| **Suppression**           | -0.07  | 0.04 | -0.13    | -0.01     | 96.83|
| SOALong                   | -0.04  | 0.04 | -0.10    | 0.03      | 84.65|
| ScalePAS                  | 0.02   | 0.05 | -0.06    | 0.10      | 67.53|
| **Suppression:SOALong**   | 0.12   | 0.06 | -0.02    | 0.22      | 96.83|
| Suppression:ScalePAS      | 0.02   | 0.07 | -0.08    | 0.15      | 66.75|
| SOALong:ScalePAS          | 0.05   | 0.06 | -0.02    | 0.14      | 82.65|
| **Suppression:SOALong:ScalePAS** | -0.11 | 0.11 | -0.29    | 0.05      | 85.95|
tion. Of course, it remains possible that when reporting not being conscious of orientation, the participant really is not conscious of the orientation or task-relevant cues of orientation, but sees something completely task-irrelevant, and thus in this sense, shows blindsight-like behaviour. Although this kind of dissociations in consciousness of the features may arguably be present in patients with blindsight due to variation in their lesions and neural plasticity (Morland et al. 1999), it is not at all clear whether they occur in normal brain due to TMS of early visual cortex. These examples highlight the importance of defining unawareness in TMS studies in such way that the observers do not report being aware of anything visual, task-relevant or -irrelevant, presented on the screen. Below we present other reasons for interpreting with caution our findings as support for TMS-induced blindsight for orientation.

In contrast to the previous studies supporting TMS-induced blindsight for orientation (Boyer et al., 2005; Koenig and Ro, 2019), we included catch trials (without any stimulus) and a control condition in which TMS was applied to the ipsilateral hemisphere. Therefore, it was possible to apply signal detection measures to test whether TMS impaired more the subjective measure of awareness than the objective discrimination of orientation. Here the criterion content was orientation for both scales (“seen” for dichotomous scale and “almost clear [perception of orientation]” for PAS). If TMS would have influenced subjective awareness without affecting discrimination performance, the results would have supported the concept of “relative blindsight”. According to the relative blindsight framework (Lau and Passingham, 2006), if masking or TMS affects the subjective measure but not the objective one, it would follow that the objective performance is at least partially unconsciously guided. The modelling on $d'$ (as a measure of subjective awareness of orientation and as a measure of discrimination performance) did not show any evidence that subjective awareness was only or predominantly suppressed by TMS, a pattern that would have supported TMS-induced relative blindsight. Neither did TMS suppress subjective awareness more strongly than that of objective discrimination. Similar results have been reported also by Lloyd et al. (2013). Thus, also these findings speak against the existence of TMS-induced blindsight for orientation.

Analyses concerning response criterion c showed that the subjective reports of awareness were conservative in all conditions and TMS even increased conservative reporting: when TMS was applied (to the contralateral hemisphere relative to the hemifield of stimulus), the observers had an increased bias to report that they were not aware of stimulus' orientation rather than that they were aware of it. This is interesting, because subjective reports of awareness, in general, are conservative, and TMS seems to further increase the conservative bias. Thus, the results are in line with the hypothesis that TMS-induced blindsight for orientation does not exist in normal brain, but it may be an artifact resulting from participants’ tendency to report no awareness of orientation, although some limited awareness was in fact present. Lloyd et al. (2013) speculated that participants may try to avoid responding to the TMS-induced phosphenes (i.e., flashes of light in the visual field), which might explain why TMS increases conservative responding. Alternatively, Peters et al. (2017) suggest that TMS results in suboptimal metacognitive judgements, hence reducing visibility ratings. In the context of the current discussion on predictive coding and hallucinatory percepts (Powers et al., 2017; Aru et al., 2018; Vetik et al., 2020), one might also wonder whether the increased conservative bias due to TMS reflects higher number of hallucinatory perceptions (i.e., false alarms) in the ipsilateral control condition than in the critical stimulation condition. However, the results do not support this view, because false alarms were not reliably more common in the control conditions as compared with TMS conditions (the effect of TMS had a probability of 86.78%, Median = −0.011, 90% CI [−0.029, 0.0054]). Anyway, this is not a critical issue for the criterion problem argument, because awareness reports were conservative in all conditions. Finally, we wish to refer the reader to a recent proposal that two different criteria may be at play in blindsight-like behavior: perceptual and non-perceptual (Michel and Lau, 2021). To what extent multiple criteria are needed, and to what extent such view helps to understand blindsight-like behavior has, however, been questioned (Phillips, 2021b). We note here that the present discussion is based on the classical interpretation of a single criterion, and we feel that it is a more parsimonious interpretation and sufficient to explain the present findings.

The modelling of discrimination in trials without reported awareness of orientation showed that discrimination depended on the participants’ awareness sensitivity to discriminate orientation (as measured by $d'$): the less aware sensitivity, the less discrimination without reported awareness was likely. Without any awareness of orientation, the discrimination performance was at chance level, irrespective of the scale measuring awareness (similar finding was reported by Raio et al., 2021, in a study without TMS). In addition, we showed that the more strongly TMS suppressed awareness of orientation, the less discrimination without reported awareness of orientation occurred. In this context, we must note that the amount of TMS-induced suppression in the present study was underestimated. This is due to using ipsilateral stimulation as the control condition, combined with the presentation of the visual stimulus near (0.25°) the fixation. With the circular coil, it is likely that some suppression occurred also in the control condition, reducing the difference between control and TMS conditions. We on purpose used this type of paradigm as it was used in studies that reported finding support for TMS-induced blindsight (e.g., Koenig and Ro, 2019). Moreover, the main purpose of the ipsilateral control condition here was not to estimate the absolute magnitude of suppression, but to show that suppression was due to neural effects of TMS on visual cortex rather than due to the non-neural effects of TMS (e.g., sound, tactile sensations). The ipsilateral control condition kept the non-neural effects of TMS similar to those in the critical TMS condition, which is not true in more typical
control conditions such as vertex stimulation or sham stimulation. Here, a limitation in our design must be mentioned: the order of TMS and control blocks was not completely counterbalanced due to the lower number of control blocks.

We manipulated the scale between participants to eliminate the possibility that performing the task with one of the scales has effects on the response criterion in using the other scale. A within-participants design would have been problematic as the response criterion might have been affected by carry-over effects between the scales. Counterbalancing the order of scales in a within-participant design would not have solved this issue, because it does not eliminate carry-over effects, but simply balances the effects between conditions. For example, if the criterion of reporting no awareness with the dichotomous scale would have spilled over to using “nothing” rating with PAS, potentially half of the participants (the ones using PAS after the dichotomous scale) might have shown above-chance discrimination performance. This, together with some of the other participants showing slightly above-chance performance due to random variation, might have produced reliably higher performance than expected by chance in “nothing” seen trials. In the between-participants design the carry-over effects are impossible. Our analyses, comparing directly awareness ratings and discrimination performance between the scales, after dichotomization of PAS, did not indicate any differences between the scales (i.e., between participant groups). One should also note that the participants came from a relatively homogenous population, and in involving 36 participants (18/scale) and 64 trials per SOA, our experiment was statistically more powerful when compared with the relevant previous studies (5 participants and unreported number of trials in Boyer et al., 2005; 16 participants and 24 trials per SOA in Koenig and Ro, 2019).

Our findings speak against the phenomenon of TMS-induced blindsight for orientation. Without any awareness of the presence of the stimulus, performance was at chance level. Importantly, even without subjectively reported awareness of orientation the discrimination performance depended on awareness. In addition, we showed with signal detection analysis that the more strongly TMS suppressed awareness of orientation, the less discrimination without reported awareness of orientation occurred. Neither was there any evidence for TMS-induced relative blindsight for orientation as TMS influenced similarly both awareness and discrimination of orientation. These results suggest that TMS-induced blindsight for orientation is due to graded but not eliminated awareness. In summary, at least when the task is to discriminate orientation, it seems that there does not exist genuine TMS-induced blindsight, in which the observer would not have any visual awareness of the stimulus. Neither did we find any convincing evidence for a weaker form of unconsciously guided behavior in which the observer would have a degraded awareness of the appearance of the stimulus, but not of the task-relevant feature. The most parsimonious explanation for TMS-induced blindsight-like behavior for orientation is that it relies on degraded visual awareness and hence on the same neural mechanisms as visual awareness. The results are in line with a recent review (Railo & Hurme, 2021) which did not find any convincing support for completely unconscious blindsight-like capacity in neurologically healthy individuals when the activity of early visual cortex is suppressed, with a possible exception of TMS-induced blindsight of stimulus presence or location.

DECLARATIONS OF INTEREST
None.

ACKNOWLEDGEMENTS
We thank Teemu Laine for technical help. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

REFERENCES
Ajina S, Pestilli F, Rokem A, Kennard C, Bridge H (2015) Human blindsight is mediated by an intact geniculo-extrastriate pathway. Elife 4, https://doi.org/10.7554/eLife.08935.
Amassian VE, Cracco RQ, Maccabee PJ, Cracco JB, Rudell A, Eberle L (1989) Suppression of visual perception by magnetic coil stimulation of human occipital cortex. Electroenceph Clin Neurophysiol 74:458–462.
Ani J, Tuliver K, Bachmann T (2018) It’s all in your head: Expectations create illusory perception in a dual-task setup. Cons Cogn 65:197–208.
Azzopardi P, Cowey A (1997) Is blindsight like normal, near-threshold vision? Proc Natl Acad Sci U S A 94:14190–14194.
Boyer JL, Harrison S, Ro T (2005) Unconscious processing of orientation and color without primary visual cortex. Proc Natl Acad Sci U S A 102(46):16875–16879. https://doi.org/10.1073/pnas.0506332102.
Campion J, Latto R, Smith YM (1983) Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? Behav Brain Sci 6(3):423–448. https://doi.org/10.1017/S0140525X0001681X.
Christensen MS, Kristiansen L, Rowe JB, Nielsen JB (2008) Action-blindsight in healthy subjects after transcranial magnetic stimulation. Proc Natl Acad Sci 105(4):1353–1357. https://doi.org/10.1073/pnas.0705858105.
Cowey A (2010) The blindsight saga. Exp Brain Res 200(1):3–24.
Galbraith J, Goodrich B (2017) rstanarm: Bayesian applied regression modeling via Stan. http://mc-stan.org/ Interfaces/rstanarm.html.
de Graaf TA, Koivisto M, Jacobs C, Sack AT (2014) The chronometry of visual perception: review of occipital TMS masking studies. Neurosci Biobehav Rev 45:295–304. https://doi.org/10.1016/j.neubiorev.2014.06.017.
Erken CW (1960) Discrimination and learning without awareness: A methodological survey and evaluation. Psychol Rev 67 (5):279–300.
Flytche DH, Zeki S (2011) The primary visual cortex, and feedback to it, are not necessary for conscious vision. Brain 134(1):247–257. https://doi.org/10.1093/brain/awq305.
Herzog MH, Otto TU, Ögmen H (2012) The fate of visible features of invisible elements. Front Psychol 3:119. https://doi.org/10.3389/fpsyg.2012.00119.
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.
Hurmé M, Koivisto M, Revonsuo A, Railo H (2019) V1 activity during feedforward and early feedback processing is necessary for both conscious and unconscious motion perception. Neuroimage 185:313–321.

Hurmé M, Koivisto M, Henriksson L, Railo H (2020) Neuronavigated TMS of early visual cortex eliminates unconscious processing of chromatic stimulation. Neuropsychologia 136:107266.

Jolij J, Lamme VAF (2005) Repression of unconscious information by conscious processing: evidence from affective blindsight induced by transcranial magnetic stimulation. Proc Natl Acad Sci 102 (30):10747–10751. https://doi.org/10.1073/pnas.0500834102.

Kahnerman D (1968) Method, findings, and theory in studies of visual masking. Psychol Bull 70(6, Pt.1):404–425. https://doi.org/10.1037/h0028731.

Koenig L, Ro T (2019) Dissociations of conscious and unconscious perception in TMS-induced blindsight. Neuropsychologia 128:215–222. https://doi.org/10.1016/j.neuropsychologia.2018.03.028.

Koivisto M, Henriksson L, Revonsuo A, Railo H (2012) Unconscious response priming by shape depends on geniculostral visual projection. Eur J Neurosci 35(3–4):623–633. https://doi.org/10.1111/j.1460-9568.2011.07973.x.

Koivisto M, Lähteenmäki M, Kaasinen V, Parkkola R, Railo H (2014) Overlapping activity periods in early visual cortex and posterior intraparietal area in conscious visual shape perception: a TMS study. Neuroimage 84:765–774. https://doi.org/10.1016/j.neuroimage.2013.09.051.

Koivisto M, Mäntylä T, Silvanto J (2010) The role of early visual cortex (V1/V2) in conscious and unconscious visual perception. Neuroimage 51(2):828–834. https://doi.org/10.1016/j.neuroimage.2010.02.042.

Kouider S, de Gardelle V, Sackur J, Dupoux E (2010) How rich is consciousness? The partial awareness hypothesis. Trends Cogn Sci 14(7):301–307.

Lau HC, Passingham RE (2006) Relative blindsight in normal observers and the neural correlate of visual consciousness. Proc Natl Acad Sci U S A 103(49):18763–18768.

Leh SE, Johansen-Berg H, Pito 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/awl11.

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

Makowski D (2018) The psycho package: an efficient and publishing-oriented workflow for psychological science. J Open Source Softw 3(22):470. https://doi.org/10.21105/joss.00470.

Mazzi C, Bagattini C, Savazzi S (2016) Blind-sight vs. degraded-sight: Different measures tell a different story. Front Psychol 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). Psychol Rev 128(3):592–595. https://doi.org/10.1037/h0026731.

Mikeliou K, Arrighi R, Aghakhanyan G, Tinelli F, Frijia F, Crespi S, De Masi F, Montanaro D, et al. (2019) Plasticity of the human visual brain after an early cortical lesion. Neuropsychologia 128:215–222. https://doi.org/10.1016/j.neuropsychologia.2018.03.028.

Overgaard M, Rote J, Mouridsen K, Ramsey T (2006) Is conscious perception gradual or dichotomous? A comparison of report methodologies during a visual task. Cons Cogn 15:700–708.

Peters MAK, Fesi J, Amendi N, Knotts JD, Lau H, Ro T (2017) Transcranial magnetic stimulation to visual cortex induces suboptimal introspection. Cortex 93:119–132.

Phillips I (2021a) Blindsight is qualitatively degraded conscious vision. Psychol Rev 128(3):558–584. https://doi.org/10.1037/rev000254.

Phillips I (2021b) Bias and blindsight: A reply to Michel and Lau (2021). Psychol Rev 128(3):592–595. https://doi.org/10.1037/h0026731.

Peters M, Ro T (2013) Unconscious priming requires primary visual cortex at specific temporal phases of processing. J Cogn Neurosci 25:1493–1503.

Power AR, Mathys C, Corlett PR (2017) Pavlovian conditioning–induced hallucinations result from overweighting of perceptual priors. Science 357:596–600. https://doi.org/10.1126/science.aag458.

Pöppel E, Held R, Froit 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 (2018) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Railo H, Piccin R, Lukasik KM (2021) Subliminal perception is continuous with conscious vision and can be predicted from prestimulus electroencephalographic activity. Eur J Neurosci 54:4985–4999. https://doi.org/10.1111/ejn.15354.

Railo H, Humre M (2021) Is the primary visual cortex necessary for blindsight-like behavior? Review of transcranial magnetic stimulation studies in neurologically healthy individuals. Neurosci Biobehav Rev 127:353–364.

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 Stim 7:415–420.

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, Salminen-Varpanta N, Henriksson L, Revonsuo A, Koivisto M (2012) Unconscious and conscious processing of color rely on activity in early visual cortex: a TMS study. J Cogn Neurosci 24(4):819–829. https://doi.org/10.1162/jocn_a_00172.

Ramsey TZ, Overgaard M (2004) Intraocular and subliminal perception. Phenomenol Cogn Sci 3(1):1–23.

Ro T (2008) Unconscious vision in action. Neuropsychologia 46 (1):379–383. https://doi.org/10.1016/j.neuropsychologia.2007.09.005.

Ro T, Shelton D, Lee OL, Chang E (2004) Extrageniculate mediation of unconscious vision in transcranial magnetic stimulation-induced blindsight. Proc Natl Acad Sci 101(26):9933–9935. https://doi.org/10.1073/pnas.0403961101.

Rossi S, Hallet M, Rossini M P, Pascual-Leone A (2009) Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. Clin Neurophysiol: Off J. Inter Feder Clin Neurophys 120(12):2008–2039. https://doi.org/10.1016/j.clinph.2009.08.016.

Sandberg K, Timmermans B, Overgaard M, Cleeremans A (2010) Measuring consciousness: Is one measure better than the other? Cons Cogn 19(4):1089–1078. https://doi.org/10.1016/j.concog.2009.12.013.
Sergent C, Dehaene S (2004) Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. Psychol Sci 15:720–728.
Stoerig P, Cowey A (1989) Wavelength sensitivity in blindsight. Nature 342(6252):916–918. https://doi.org/10.1038/342916a0.
Stoerig P, Cowey A (1992) Wavelength discrimination in blindsight. Brain 115(2):425–444. https://doi.org/10.1093/brain/115.2.425.
Tagliabue CF, Mazzi C, Bagattini C, Savazzi S (2016) Early local activity in temporal areas reflects graded content of visual perception. Front Psychol 7:572. https://doi.org/10.3389/fpsyg.2016.00572.
Timmermans B, Cleeremans A (2015) How can we measure awareness? An overview of current methods. In: Overgaard M, editor. Behavioural Methods in Consciousness Research. Oxford: Oxford University Press. p. 21–46.
Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave one-out cross-validation and WAIC. Statist Comp 27(5):1413–1432. https://doi.org/10.1007/s11222016-9696-4.
Vetik S, Tulver K, Lints D, Bachmann T (2020) Among the to kinds of metacognitive evaluation, only one is predictive of illusory object perception. Percept 49(10):1043–1056. https://doi.org/10.1177/0301006620954322.
Weiskrantz L (1997) Consciousness lost and found. A neuropsychological exploration. Oxford: Oxford University Press.
Weiskrantz L, Warrington EK, Sanders MD, 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.

(Received 10 May 2021, Accepted 24 August 2021) (Available online 2 September 2021)