CORTEX 205 (2026) 24–41

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Registered Report

The role of extra-striate areas in conscious motor behavior: A registered report with fast-optical imaging

Elisabetta Colombari, Giorgia Parisi, Sonia Mele, Chiara Mazzi * *and Silvia Savazzi*

Perception and Awareness (PandA) Laboratory, Department of Neuroscience, Biomedicine and Movement Sciences, University of Verona, Verona, Italy

ARTICLE INFO

Article history:
Received 17 August 2026
Revised 3 September 2026
Accepted 3 September 2026
Action editor Anoushiravan Zahedi
Published online 8 September 2026

Keywords:
Visual awareness
Fast Optical Imaging
No-Report paradigm

ABSTRACT

Disclosing the brain areas responsible for the emergence of visual awareness and their timing of activation represents one of the major challenges in consciousness research. In particular, isolating the neural processes strictly related to consciousness from concurrent neural dynamics, either related to prerequisites or post-perceptual processing, has long engaged consciousness research. In this framework, the present study aims at unraveling the spatio-temporal dynamics underlying conscious vision by adopting a distinctive experimental design in which both awareness and motor response are manipulated, allowing the segregation of neural activity strictly related to awareness from response-related mechanisms. The study included 32 participants. We employed a GO/NOGO detection task, in which participants responded or withheld responding according to the experimental condition. Critically, during the performance of the task, participants' brain activity was recorded by means of Event-Related Optical Signal (EROS) technique, which provides accurate information about brain functions both from the temporal and spatial point of view within the covered regions, simultaneously. The combination of this experimental design with EROS recording enabled us to pinpoint the neural correlates underlying conscious vision and to disentangle them from processes related to the response. Extra-striate areas, specifically the Lateral Occipital Complex (LOC), showed greater awareness-related activity independently of motor response. Our findings support the view that LOC plays a key role as a proper correlate of visual awareness, rather than post-perceptual or response-related processes. They also show that awareness modulates motor activity only when a response is executed, clarifying how conscious perception influences downstream motor processing.

© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

* *Corresponding author*. Perception and Awareness (PandA) Laboratory, Department of Neuroscience, Biomedicine and Movement Sciences, University of Verona, Verona, Italy.
E-mail address: chiara.mazzi@univr.it (C. Mazzi).

https://doi.org/10.1016/j.cortex.2026.09.001

0010-9452/© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Consciousness, namely the set of subjective experiences we have when we are awake, is one of the most intriguing topics debated in neuroscience research. In particular, the search for its neural correlates (NCC) has permeated the literature in recent decades. In broad strokes, one of the most widely used approaches to assess such NCCs involves contrasting brain activity occurring when a visual stimulus enters consciousness with brain activity occurring when the same stimulus does not reach awareness. This renowned paradigm is known as *contrastive analysis* (Aru et al., 2012) and has been frequently combined with electrophysiological recording or functional neuroimaging, leading to numerous and dissimilar results (Förster et al., 2020). Indeed, the interpretations of spatio-temporal dynamics underlying conscious vision are among the most disparate. ERP studies propose two possible electrophysiological markers as correlates of visual awareness: an earlier occipito-temporal negative deflection (i.e., Visual Awareness Negativity—VAN) detectable 200 msec after the presentation of the stimulus, and a later positivity (i.e., Late Positivity—LP) widespread over centro-parietal regions, peaking 300–500 msec after the stimulus onset (Koivisto & Revonsuo, 2010). However, the electrophysiological signature/s characterizing conscious vision has still to be elucidated. This may be attributed to one of the main limitations of the contrastive analysis, which is represented by its ineffectiveness in dissociating the true NCC (i.e., the set of neural correlates necessary and sufficient to enable consciousness) from concurrent neural dynamics either related to prerequisites or post-perceptual processing (Aru et al., 2012). In most prior studies aiming at identifying such NCCs, participants were asked to make judgments about their experience. However, such an operation could lead to confounding neural processes related to the task, not strictly to awareness per se.

For this reason, in an effort to disentangle the proper correlates of consciousness from neural activity related to the response, no-report paradigms have been employed. In this framework, no-report paradigms, where participants are not requested to perform any tasks or to provide any judgments about their perceptual experience, represent an advantageous tool to dissociate the neural processes strictly related to consciousness from subsequent processes related to the required response (Hatamimajoumerd et al., 2022; Tsuchiya et al., 2015). Studies employing this kind of paradigm with different techniques such as EEG and fMRI concluded that LP is highly modulated by several different cognitive processes occurring at later stages of processing (Dembski et al., 2021; Kronemer et al., 2022; Mazzi et al., 2020; Schlossmacher et al., 2020), as well as by the task relevance of the stimulus (Dellert et al., 2021; Hense et al., 2024; Makeig & Jung, 2000; Pitts et al., 2014; Schelonka et al., 2017; Shafto & Pitts, 2015). By contrast, the role of response requirements, as well as that of attention, on the VAN are still debated as different studies have reported both positive (e.g., Bola & Doradzińska, 2021; Dellert et al., 2021; Doradzińska & Bola, 2024) and negative (e.g., Ciupińska et al., 2024; Cohen et al., 2020; Dellert et al., 2022; Koivisto et al., 2006) results. Interestingly, in a study published in 2016 by Koivisto and colleagues (Koivisto et al., 2016), authors successfully dissociated ERP correlates of visual awareness from those related to post-perceptual mechanisms, disclosing that VAN was not modulated by response requirements. The authors adopted a particular partial-report paradigm in which participants were sometimes asked to provide a report by pressing a response button when they were aware of the stimulus and sometimes to withhold responding in case of awareness. They found that, while the amplitude of LP was modulated by the response (i.e., it was greater in trials where participants were asked to respond in case of awareness, compared to the Aware condition where they were asked to withhold responding), VAN did not change depending on task requirements. This allowed Koivisto and colleagues to advocate for an early onset of visual awareness: the phenomenal content of a visual experience, indeed, takes place before LP, more specifically in the temporal window of VAN.

Several pieces of evidence are consistent in considering VAN as the electrophysiological signature of phenomenal consciousness (Koivisto et al., 2008; Railo et al., 2015), while the localization of its neural generator still remains open. In this regard, previous MEG source localization studies (Liu et al., 2012; Vanni et al., 1996) identified the Lateral Occipital Complex (LOC), an extra-striate visual areas traditionally associated with object recognition, as the generator of VAN. Moreover, previous no-report studies using both EEG and fMRI (Dellert et al., 2021; Kronemer et al., 2022) have also found awareness effects in LOC and linked it to VAN. The same result was achieved in a recent work aimed at unravelling the spatio-temporal dynamics underlying conscious vision (Colombari et al., 2024). In such study, participants were asked to perform a discrimination task on the orientation of a tilted Gabor patch while their brain activity was recorded first with EEG and then with Fast Optical Imaging. This allowed authors to identify the exact temporal window of VAN and LP and then, by taking advantage of the peculiarity of Fast Optical Imaging of achieving both temporal and spatial accurate information (Baniqued et al., 2013; Gratton & Corballis, 1995; Gratton & Fabiani, 2010), to investigate the spatio-temporal unfolding of brain activity occurring in these predetermined time windows. Authors contrasted activity of Aware trials (i.e., trials in which participants reported to perceive the orientation of the stimulus) with activity of Unaware ones and observed a sustained activation of LOC in the VAN temporal window, consistently with the above-mentioned MEG studies. More interestingly, they observed that, only when the stimulus crossed the threshold of consciousness, activity in extra-striate visual areas triggered subsequent activation of motor areas, although motor response was required in both Aware and Unaware conditions. Authors tried to interpret this unexpected finding by ascribing it to the selection of the correct response, that could be provided in the Aware trials only where participants consciously perceived the stimulus. Indeed, in Aware trials participants had to press a specific button on the response box (to provide the correct answer about the orientation of the Gabor patch), while when the stimulus was unseen (i.e., Unaware trials) they had to respond randomly, by pressing indifferently one of the two response buttons. However, the employed experimental paradigm did

not allow the authors to thoroughly investigate this issue. Thus, in order to clarify the interplay between extra-striate areas and motor regions in awareness, in the present study we adopted a go/no-go detection task (similar to that adopted by Koivisto et al., 2016), while recording participants' brain activity by means of Fast Optical Imaging. Specifically, Event-Related Optical Signal (EROS) technique was employed. This technique, by shedding near-infrared light through the brain tissues, is able to detect changes in the light scattering properties that are known to be directly related to neural activity, thus providing simultaneous spatial resolution at the sub-centimeter level and temporal resolution below 100 msec within the cortical regions accessible to near-infrared light, that is, cortical structures no deeper than approximately 3 cm from the scalp surface (Gratton et al., 1997; Gratton & Fabiani, 1998, 2001). The main limitations of the technique are its restricted depth of penetration, which precludes imaging of deep cortical structures and subcortical regions, and its relatively low signal-to-noise ratio, which requires a large number of trials per condition (Gratton & Fabiani, 2010). Accordingly, the montage employed here was designed to provide dense coverage of the occipital, temporal, and parietal cortices relevant to the pre-specified ROIs, and does not extend to prefrontal cortex (see Fig. 2 and Section 2.6). Critically, the study adopted a distinctive paradigm manipulating both awareness and response. The latter, indeed, was provided sometimes in the Aware condition (condition Aware-GO/Unaware-NOGO) and sometimes in the Unaware one (condition Aware-NOGO/Unaware-GO). This double manipulation enabled us to unravel the spatio-temporal unfolding of awareness-related activity, by disentangling neural activity related to awareness from response-related mechanisms. Indeed, in the present study, we could investigate the NCCs both when the motor response was required and when no task was performed, thus allowing to isolate consciousness effects from the effects related to the task. Importantly, the experimental paradigm adopted enabled us to elucidate the interplay between extra-striate visual areas and motor areas. Indeed, in addition to conventional EROS analyses, we performed Granger Causality analysis, in order to disclose the relationship existing among the investigated areas. In broad strokes, Granger analysis allows to move beyond the classical identification of cortical activation provided by EROS analysis by disclosing functional circuits underpinning the investigated brain function (Seth et al., 2015). When coupled with EROS, Granger Causality analysis represents a powerful tool to highlight predictive relationships between activations in the investigated regions of interest (ROI) at different time-points (Parisi et al., 2020).

Based on previous literature suggesting that VAN is independent from subjective report (Koivisto et al., 2016; Ye et al., 2024) and LOC represents the cortical generator of VAN (Colombari et al., 2024; Liu et al., 2012), we expected Aware trials to elicit early greater activation of LOC, independently of the response requirement. Moreover, by combining EROS conventional analysis with Granger Causality analysis, and manipulating both awareness and motor response, we aimed to highlight potential interplay between consciousness-related extra-striate areas and response-related motor areas both when the motor response was required and when it had to be inhibited.

2. Methods

This manuscript corresponds to Stage 2 of a Registered Report. The Stage 1 protocol has been peer-reviewed and is available at https://osf.io/8ya2t.

2.1. Ethics information

The study was approved by the local Ethics Committee (Prog.171CESC) and it was conducted in accordance with the principles laid down in the 2013 Declaration of Helsinki. Participants were recruited from the University of Verona community, by means of printed flyers displayed on notice boards at different University of Verona sites and through advertisements on social media. Each participant was fully informed about the modalities of the study before taking part in the experiment and written informed consent was signed. In addition, participants received compensation for their participation and were debriefed after the conclusion of the experiment.

2.2. Participants

We recruited healthy adults, right-handed (as assessed by means of the standard handedness inventory *Edinburgh Handedness Questionnaire*; Oldfield, 1971) and aged between 18 and 50 years old. All of them had to report normal or corrected-to-normal vision, no history of neurological or psychiatric disorders and no contraindications to MRI. The study was conducted at the PandA lab of the University of Verona (Italy).

2.2.1. Sample size estimation

The estimate of the sample size for the current study is based on our previous EROS study (Colombari et al., 2024), in which a similar paradigm was adopted, and similar analyses on similar ROIs were performed. Specifically, EROS data from the ROI of LOC were extracted, and significant time-points were averaged within participants so to have one value for each of them. Then, a one-sample t-test was performed [$t\ (23) = 2.99$, $p = .006$, Cohen's $d = .611$], and the resulting Cohen's d was employed to compute the sample size estimation for the current study. Specifically, the estimated sample size for research questions Q1 (i.e., "Can we replicate Colombari et al., 2024 findings showing that LOC is an NCC?") and Q2 (i.e., "Is the activity in LOC independent from the response?") was calculated with G-Power software (v. 3.1.9.7), with a power of 90% and a level of significance of 2%. The estimated sample size resulted in 32 participants (critical $t = 2.143$; actual power = .900). Considering that the estimated sample size for this study ($n = 32$) is more than double the typical sample size of EROS studies present in literature, the same estimated sample size seems to be also adequate to answer research questions Q3 (i.e., "Does consciousness modulate the

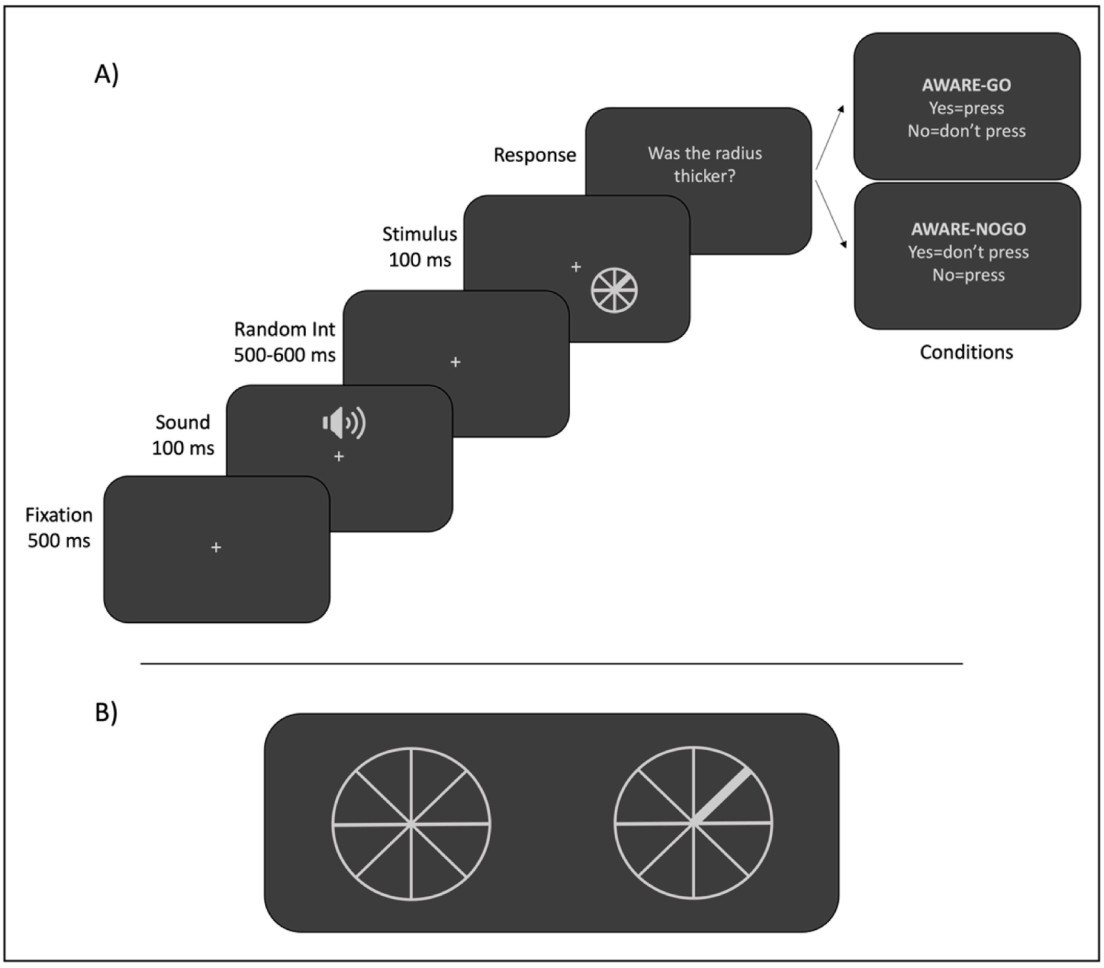

Fig. 1 – Trial procedure and stimuli: A) Experimental procedure: the trial began with a fixation cross persisting at the center of the screen for 500 msec. After that, an acoustic tone lasting 100 msec was presented, followed by a random interval ranging from 500 to 600 msec. Then, the stimulus was presented for 100 msec and participants were asked to respond according to the experimental condition (i.e., Aware GO or Aware-NOGO). B) Example of stimuli: on the left is shown the catch stimulus, with all the radii equally thick; on the right is depicted the critical stimulus, with the first radius, clockwise, thicker than the others.

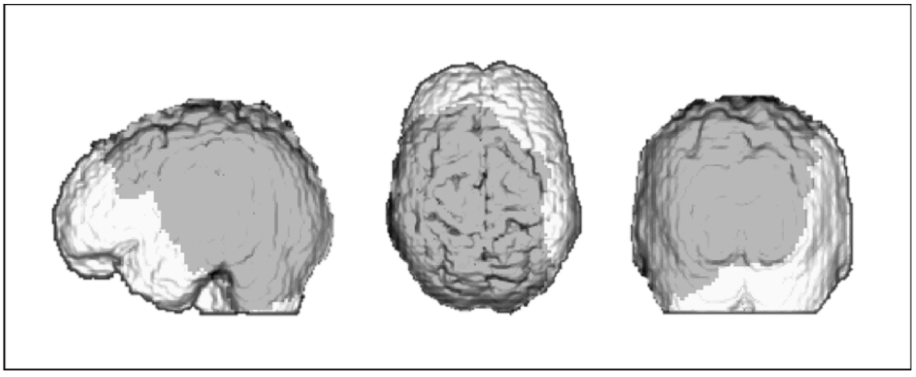

Fig. 2 – Covered area. The gray area represents the area covered by the EROS montages (combined together) from the sagittal, axial and coronal point of view.

activation of motor areas in a detection task?") and Q4 (i.e., "Does consciousness modulate the activation of motor areas in ABSENCE of motor response?"). For a review of the existing EROS literature, see Supplementary Table S1 in Supplementary Materials) from which emerges that, on average, EROS studies employ experimental samples composed of about 13 participants (mean 12.944; SD 7.008).

2.2.2. *Exclusion criteria*

As better specified in section 2.4, before getting involved in the study, participants underwent a perceptual threshold assessment, in order to identify the proper stimulus to be employed in the main experiment. To be enrolled in the study, participants had to successfully complete this session. The criterion used was that one of the stimuli presented during the threshold assessment had to be acknowledged as perceived by a minimum of 25%, a maximum of 75%, or closest to the 50% of the times (i.e., at perceptual threshold level). If no stimulus resulted at the threshold level, the participant was not enrolled in the study.

In addition, participants who did not complete all the experimental sessions, as well as participants reporting a level of Awareness superior to 75% or inferior to 25% at the end of the experiment were excluded from analyses. This was to maintain comparable the number of trials in the two experimental conditions (i.e., Aware and Unaware) and to ensure a reliable EROS activity (because of its relatively low signal-to-noise ratio, EROS needs a high number of trials per condition, in order to compute statistics). Moreover, participants whose behavioral performance was affected by biases related to the behavioral response (as assessed by catch trial analysis, explained more in detail below) were excluded from the analyses (see below –*Section 2.8.1 Behavioral data* for more detailed information on the analysis of catch trials). Finally, participants whose EROS signal could not be detected properly during the experiment (for example because of too dark hair or technical issues) were also not included in the analyses as well. In particular, the opacity value (i.e., the product of the scattering and absorption coefficients) was estimated for each participant. Based on this value, it was possible to judge the quality of the signal for each participant, independently from the experimental condition. Opacity values of all participants were averaged together providing the absorption coefficient to be used when running statistical analysis. Participants whose opacity value was equal to 0 or exceeded three standard deviations of the mean were excluded from statistical analyses.

Importantly, each participant who was excluded due to the previously mentioned exclusion criteria, was replaced with the recruitment of another participant. Thus, the number of participants to be recruited was increased to reach a total of 32 analyzed subjects, as specified in section 2.2.1.

2.3. *Stimuli*

Stimuli were created by means of a custom-made Matlab script (version R2022b; the MathWorks, Inc., Natick, MA) and resized by means of Photoshop (Adobe Photoshop CC, v2014.0.0). As shown in Fig. 1, they were gray circles (.85 .85 .85 RGB), presented on a black background, with 8 radii equally distanced from one another. One radius (the first one, clockwise) could be slightly thicker than the others (critical trials) or not (catch trials). The thickness of the radius for critical stimuli was individually assessed for each participant on the basis of a subjective perceptual threshold assessment that was held before the main experiment.

Both in the perceptual threshold assessment and in the main experiment, the stimulus was presented in the lower right quadrant of the screen, specifically at an eccentricity of 3.5° from the fixation cross along the vertical meridian and of 2° along the horizontal one. This was to allow a left-lateralized EROS montage, as a full-head montage is not achievable in our lab due to technical constraints (i.e., insufficient probes). Moreover, since EROS technique is sensitive to depth, a right-lateralized stimulus ensures that it elicits activity in the left portion of the primary visual cortex, which is known to be anatomically closer to the skull compared to the right one (Zhao et al., 2022), thus ensuring a better penetration of near-infrared light through brain tissues.

2.4. *Perceptual threshold assessment*

Before starting the experiment, participants underwent a perceptual threshold assessment, with the aim of identifying, for each participant, the level of thickness of the critical radius so that it resulted to be perceived as thicker 50% of the times. To this aim, stimuli with different levels of radius thickness were randomly presented and the subjective perceptual threshold was measured using the method of constant stimuli. Specifically, 9 levels of radius thickness were presented. The range of stimuli to be used in the perceptual threshold assessment was selected based on the results of a pilot experiment in which participants were asked to perform the same task employed in the perceptual threshold assessment while presented with a wider range of radius thickness. This allowed us to identify a smaller range of optimal stimuli to be presented thus excluding a range of stimuli whose thickness was almost never or always reported by participants. Each level of radius thickness was presented 5 times per block, for a total of 8 blocks. Thus, all the stimuli, as well as the catch stimulus, were presented 40 times each. Participants were asked to press the spacebar as soon as they detected the stimulus with a thicker radius. The stimulus identified as perceived a minimum of 25%, a maximum of 75%, and closest to 50% of the times at the end of the subjective perceptual threshold assessment was used in the experimental task, together with the catch. The perceptual threshold assessment, as well as the main experiment, was conducted in a dimly illuminated room and participants were sitting in front of a 17 in. LCD monitor (resolution 1920 × 1080, refresh rate of 144 Hz) placed at a viewing distance of 57 cm. Their head was held in place by means of an adaptable chin rest so that eyes were aligned with the center of the screen. Both the perceptual threshold assessment and the main experiment were programmed and administered using E-Prime 3.0 software (E-Prime Psychology Software Tools Inc., Pittsburgh, PA, USA). Before starting the perceptual threshold assessment, participants underwent a fixation training (Leung et al., 2009), in order to ensure they could maintain their gaze on the central fixation cross correctly.

2.5. Experimental procedure

The experiment was composed of two identical sessions lasting approximately 3 h each performed on different days. The first session was preceded by the assessment of the subjective perceptual threshold, which, in turn, lasted around 20 min. The two experimental sessions were identical except for the EROS montages, specifically devised to obtain better coverage of the brain areas of interest. The order of the montages was counterbalanced across participants, as well as the order of conditions (see below and Table 2 for more detailed information).

The task was a two-conditions go/no-go detection task, similar to that adopted by Koivisto et al., 2016, in which participants have to respond in different ways according to the experimental condition (Table 1). In condition "Aware-GO", they were asked to press the spacebar on the keyboard as soon as they perceived the thicker radius, and withhold responding when they did not perceive any difference among radii. On the contrary, in condition "Aware-NOGO", participants were asked to withhold responding when they perceived a thicker radius, and press the response button when they did not perceive any difference. Each trial began with the presentation of a central fixation cross, followed 500 msec later by a sound (1000 Hz) presented for 100 msec, notifying participants of the subsequent onset of the stimulus. After a random interval ranging from 500 to 600 msec, the stimulus was presented for 100 msec in the lower right quadrant of the screen. After that, participants were asked to respond according to the experimental condition. Each experimental session was composed of 24 blocks: 12 blocks for condition Aware-GO/Unaware-NOGO and 12 blocks for condition Aware-NOGO/Unaware-GO, counterbalanced across participants according to the order depicted in Table 1. Each block consisted of 50 critical trials and 15 catch trials. The whole experiment was composed of 48 blocks per participant, for a total of 2400 critical trials and 720 catch trials per participant. In order to test the experimental paradigm, we pilot-tested the task (see the Supplementary Materials section—Pilot Study).

2.6. Optical recording

Three synchronized Imagent frequency domain systems (ISS, Inc., Champaign, IL) were used to record continuous fast optical data throughout experimental sessions. Each system was equipped with 4 photo-multiplier tubes detectors, for a total of 12 detectors. Near-infrared light (830 nm) was delivered from 48 laser diodes on participants' scalp and it was modulated at 110 MHz. Each of 12 detectors received light from sets of 16 light emitters, multiplexed every 25.6 msec, resulting in a sampling rate of 39.0625 Hz.

To avoid cross-talk between channels, the array of source–detector pairs (i.e., the montage) was created by means of a specific program (NOMAD, Near-Infrared Optode Montage Automated Design) implemented in Matlab, useful to place sources and detectors at optimal distances. In this experiment, we set the minimal distance to 17.5 mm and the maximum distance to 50 mm, in order to ensure an extensive coverage of the brain regions of interest both from the spatial and the depth point of view. The distance between the source and the detector of a channel, in fact, determines the depth of the light pathway (Gratton et al., 2000), thus corresponding to the depth of the investigation: namely, longer channels can investigate deeper layers and shorter channels can examine shallower regions.

Both light emitters and detectors were placed on participants head using a custom-built helmet. To minimize interferences, before placing the optical fibers on the head, hairs were carefully moved with cotton buds, so that the fibers could reach the scalp directly. In order to better adhere to the head of the participant, we employed two helmets of different sizes: one 55–56 cm large, and one 57–58 cm large. For each helmet, we developed two different montages, so that to provide a dense coverage of the regions of interest (i.e., the left occipital, temporal and parietal cortices, see Fig. 2). Each montage consisted of the combination of 12 detectors and 48 light emitters, resulting in a total of 192 channels per montage. As mentioned before, each montage was recorded in a separate session, and the order was counterbalanced across participants.

At the end of each EROS session, the scalp location of each source and detector was digitized in relation to four fiducial points (i.e., nasion, inion and pre-auricular points) with a neuro-navigation software (SofTaxic, E.M.S., Bologna, Italy) combined with a 3D optical digitizer (Polaris Vicra, NDI, Waterloo, Canada). Afterwards, the digitized scalp locations were co-registered with each participant's individual MRI, using a

Table 1 – Experimental conditions. Both Awareness and Response were manipulated: Awareness was experimentally manipulated by employing a threshold stimulus, so that sometimes it was consciously perceived (Aware) and sometimes not (Unaware). Response was manipulated by the task: in condition GO participants were asked to respond by pressing a key, while in condition NOGO they were asked to withhold responding. The combination of these two manipulations gives rise to the 4 experimental conditions depicted in the table.

		Awareness	
	Yes		No
Response	No	Aware-NOGO	Unaware-NOGO
	Yes	Aware-GO	Unaware-GO

Table 2 – Counterbalancing of montages and task conditions across participants. Both EROS montages and task conditions (G = Aware-GO/Unaware-NOGO; N = Aware-NOGO/Unaware-GO) were counterbalanced across participants. In the column "Task", each letter represents 6 blocks of task. Thus, each day, participants performed 12 blocks per condition, for a total of 24 blocks of task per day.

	Day 1		Day 2	
Participants	EROS montage 1	Task	EROS montage 2	Task
1	A	GNNG	B	NGGN
2	B	GNNG	A	NGGN
3	A	NGGN	B	GNNG
4	B	NGGN	A	GNNG

dedicated software package (OCP, Optimized Co-registration Package, Matlab code developed by Chiarelli and colleagues (Chiarelli et al., 2015).

For this reason, participants underwent a structural MRI at the Azienda Ospedaliera Universitaria Integrata of Verona (AOUI).

2.7. MRI acquisition

Participants' individual structural MRI was acquired by means of a 3 T Philips Elition S scanner with a 32-channel head RF receive coils. A whole brain high-resolution 3D T1-weighted image (T1w) Turbo-field echo image (1 mm-isotropic TE/TR = 3.8/8.4 msec, TI = 1050 msec) was acquired.

The T1w field of view (240 × 240 × 180 mm) was large enough to allow for the ears and the entire scalp to be fully included in the image to facilitate later and accurate co-registration with functional data.

2.8. Data analysis

2.8.1. Behavioral data

Raw data were processed by means of custom scripts created on Matlab (the MathWorks, Inc., Natick, MA). Data were divided into the 4 experimental conditions (i.e., Aware-GO, Unaware-NOGO, Aware-NOGO, Unaware-GO). For each participant, trials with reaction times lower than 150 msec and higher than 3 standard deviations from the mean were excluded from the analysis. Data were successively analyzed using Jamovi (version 2.3.28): first, the percentage of Aware and Unaware trials was calculated, in order to assess that a sufficient amount of trials was present for each condition. Participants presenting more than 75% or less than 25% of Awareness were discarded from the sample. This was because, in that case, the number of Unaware (or Aware) trials would be insufficient for statistical EROS analysis. EROS technique, indeed, although having a high localization power from both the spatial and temporal point of view, has a relatively low signal-to-noise ratio. For this reason, a high number of trials is required for statistical analysis. Subsequently, reaction times (RTs) were analyzed for the "GO" conditions, thus paired sample *t*-tests (two-tailed) were applied to compare the mean RTs between Aware-GO and Unaware-GO conditions. Finally, to verify that participants were performing the task accurately and that there were no biases related to the response, catch trials were analyzed. As mentioned above, catch trials were those trials in which all the radii of the stimulus were equally thick, thus no differences in the stimulus were present. In case of catch trials, the participants' task was different according to the condition: in the Aware-GO condition, they were expected to withhold responding, while in the Aware-NOGO condition, they were expected to respond. Thus, catch trials were analyzed separately for the two conditions (GO and NOGO) by means of a paired sample *t*-test (two-tailed), in order to ensure that the behavioral performance followed the above-mentioned trend. Paired sample *t*-tests (two-tailed) were indeed performed to test whether catch trials performance was significantly different from critical trials.

2.8.2. EROS data

Pre-processing of continuous phase delay (i.e., time-of-flight) data was computed by means of a dedicated in-house software, P-POD (Pre-Processing of Optical Data, run in Matlab, version R2013b). Thus, raw data were normalized (i.e., corrected for phase wrapping and de-trended to remove low-frequency drifts), demeaned and filtered by means of a 6th order Butterworth band-pass filter which allows frequencies between .5 Hz and 15 Hz. Pulse artifacts were removed by using a regression algorithm (GRATTON et al., 1995). After that, data were averaged separately for each subject, condition, and channel and segmented into epochs time-locked to the onset of the stimulus. Each epoch comprised a period from 486 msec before the stimulus onset to 998 msec following the stimulus onset, resulting in an epoch lasting 1484 msec. Subsequently, statistical analyses were computed with an in-house software package (Opt-3d; Gratton, 2000), which provides statistical spatial maps of fast optical data.

To perform statistics, data from channels whose diffusion paths intersect a given voxel were combined (Wolf et al., 2014). Phase delay data were spatially filtered with an 8-mm Gaussian kernel and baseline corrected using a 204 msec time-window preceding the stimulus onset. Within each ROI, t-Statistics were calculated at group level, converted into z-scores and corrected for multiple comparisons using random field theory (Kiebel et al., 1999; Worsley et al., 1995). Then, z-scores were weighted and orthogonally projected onto the surface of an MNI template brain, according to the physical homogenous model (Arridge & Schweiger, 1995; Gratton, 2000).

In order to investigate the neural dynamics related to conscious vision and to disentangle the role of the motor areas, the following contrasts between conditions were computed: 1) Aware-GO versus Unaware-GO and 2) Aware-NOGO versus Unaware-NOGO. These contrasts allowed to investigate the research questions the proposed study aimed at answering (see Section 3 for a detailed description of the planned analysis). Importantly, both frequentist and Bayesian statistics (with default priors) were computed, to test both positive and negative effects.

Moreover, Granger Causality analysis was computed. Granger Causality analysis allows to explore the predictive interactions between different brain areas at different time-points. Specifically, this approach requires a region of interest (ROI) to be used as a "seed" and investigating whether the activity of this seed predicts activity in the other ROIs at a later time-lag, by deriving statistical maps from t-statistics computation (then transformed into z scores) for each lag.

Statistical functional analysis was computed within specific predetermined regions of interest (ROIs) and time intervals. ROIs were defined by a 2-dimensional box-shaped structure, covering an area of 20 × 20 mm. Critical ROIs were selected on the basis of the results obtained in the above-mentioned experiment (Colombari et al., 2024) and they were located in the occipital and in the left parietal and temporal lobes, specifically over the primary visual cortex (V1, Brodmann Area 17), the left lateral occipital cortex (LOC, Brodmann Area 19), the left supplementary motor area (SMA, Brodmann Area 6), the left premotor area (PM, Brodmann Area

Table 3 – Study design.

Question	Hypothesis	Sampling plan	Analysis plan	Rationale for deciding the sensitivity of the test for confirming or disconfirming the hp	Interpretation given different outcomes	Observed outcomes
Q1: Can we replicate Colombari et al., 2024 findings showing that LOC is an NCC?	**H1:** We hypothesized to replicate Colombari et al., 2024 results: Greater activity in LOC in an early temporal window (i.e., 150 –350 msec post stimulus onset) is observed when contrasting aware and unaware trials in the condition in which the response is required (i.e., GO condition) **Expected outcome:** LOC aware-GO > LOC unaware-GO, as measured by EROS activity	Since the present research question aims at replicating the results of Colombari et al., 2024, sample size estimation is based on those EROS data. Sample size calculation was performed with G-power software (v. 3.1.9.7), with a power of 90% and a significance level of 2%, resulting in 32 participants.	**A1**: The goal is to replicate the results of Colombari et al., 2024, in which the manual response was required for both aware and unaware conditions. Here, in order to perform the same analysis, early LOC activity in Aware-GO and Unaware-GO trials was compared by using a paired-sample one-tailed *t*-test, computed with the EROS dedicated analysis software "Opt3d". In addition to frequentist statistics, Bayesian statistics (with default prior) was computed to test potential null effects. **Contrast to be computed:** AWARE GO *vs* UNAWARE GO **ROI to be tested:** LOC **Time interval of interest:** 150–350 msec after stimulus onset	Sample size estimation is based on previous EROS data (Colombari et al., 2024), on which similar analyses were performed.	**O1.1:** A significant *t*-test within the interval of interest is interpreted as a successful replication of previous findings, supporting the involvement of LOC in NCC. **O1.2:** The absence of this effect does not confirm the hypothesis, suggesting that LOC is not involved in the conscious detection of a stimulus property.	**OO1:** Our hypothesis was confirmed by our results, as the results from Colombari et al. was replicated. Indeed, when contrasting aware and unaware trials in the condition in which the response is required (i.e., GO condition), greater activity in LOC was observed 179 msec after the stimulus onset.

(*continued on next page*)

Table 3 – (*continued*)

Question	Hypothesis	Sampling plan	Analysis plan	Rationale for deciding the sensitivity of the test for confirming or disconfirming the hp	Interpretation given different outcomes	Observed outcomes
Q2: Is the activity in LOC independent from the response?	**H2:** We hypothesized that LOC activity is independent from response requirement: When contrasting activity elicited by Aware-NOGO trials with activity elicited by Unaware-NOGO trials, we expect to find the same activation of LOC found in the Aware-GO *vs* Unaware-GO contrast. **Expected outcome:** LOC aware-NOGO > LOC unaware-NOGO, as measured by EROS activity (LOC aware-GO > LOC unaware-GO)=(LOC aware-NOGO > LOC unaware-NOGO)	Since research question Q2 involves the same analyses of research question Q1 (but for the NOGO condition), the sampling plan for Q2 is the same as for Q1.	**A2.1:** A paired-sample one-tailed *t*-test was computed in order to compare early activity in LOC in the NOGO condition. Thus, activity in Aware-NOGO and Unaware-NOGO trials was contrasted. Both frequentist and Bayesian statistics (with default prior) was computed. **Contrast to be computed:** AWARE NOGO *vs* UNAWARE NOGO **ROI to be tested:** LOC **Time interval of interest:** 150–350 msec after stimulus onset **A2.2:** The interaction effect between awareness and motor response was tested by means of a paired-sample one-tailed *t*-test computed between contrast Aware-GO *vs* Unaware-GO and contrast Aware-NOGO *vs* Unaware-NOGO In addition to frequentist statistics, Bayesian statistics (with default prior) was computed to test potential null effects **Contrast to be computed:** (AWARE GO *vs* UNAWARE GO) - (AWARE NOGO *vs* UNAWARE NOGO) **ROI to be tested:** LOC **Time interval of interest:** 150–350 msec after stimulus onset	As above	**O2.1.1:** A significant *t*-test in the time window of interest suggests that LOC activity is independent from response, since its activity is observed even when no response is required (NOGO conditions). **O2.1.2:** If greater activity in LOC in the time window of interest is not observed, then it means that LOC activity is somehow related to the motor response. **O2.2.1:** Significant interaction effect suggests that activity in LOC depends from response requirement **O2.2.2:** The absence of a difference between the two effects suggests that motor response does not affect awareness-related activity in LOC	**OO2:** Our hypothesis was confirmed by our results, as greater activity in LOC was observed 204 msec after the presentation of the stimulus when contrasting activity elicited by Aware-NOGO trials with activity elicited by Unaware-NOGO trials, thus independently from response requirement.

Q3: Does consciousness modulate activation of motor areas in a detection task?	**H3:** When a motor response is required, consciousness modulates activation of motor areas (MA), as activity in motor areas is triggered by LOC (Colombari et al., 2024) **Expected outcome:** MA aware-GO > MA unaware-GO, as measured by EROS activity LOC activity predicts MA activity (investigated by means of Granger causality analysis)	Considering that the estimated sample size for this study ($n = 32$) is more than twice the typical sample size of EROS studies present in literature (see Supplementary Table S1, where a systematic review of existing EROS literature revealing that the typical sample size used is 13 participants is depicted), the same estimated sample size of Q1 and Q2 seems to be also adequate to answer research questions Q3 and Q4.	**A3.1** A paired-sample one-tailed *t*-test was computed in order to compare early activity in motor areas in the GO condition. Thus, activity in Aware-GO and Unaware-GO trials was contrasted. In addition to frequentist statistics, Bayesian statistics (with default prior) was computed to test potential null effects **Contrast to be computed:** AWARE GO *vs* UNAWARE GO **ROI to be tested:** Motor areas **Time interval of interest:** Based on mean RTs, with a time window of ±1.5 SD around the mean **A3.2**: In order to further investigate the flow of activity occurring in the investigated brain areas, Granger causality analysis was performed. In the present study, we performed Granger analysis on the "Aware-GO *vs* Unaware-GO" contrast, since we are interested in investigating whether activity in motor areas is predicted by previous activity in LOC, when a motor response is required (i.e., in the GO condition). Thus, LOC was used as seed ROI and later activity in motor areas was investigated. In addition to frequentist statistics, Bayesian statistics (with default prior) was computed to test potential null effects **Contrast to be computed:** AWARE GO *vs* UNAWARE GO **ROI to be tested:** LOC (as seed ROI) Motor areas as predicted areas **Time interval of interest:** LOC: 150–350 msec after the stimulus onset (within this interval, about ±4 time points around the peak value -according to the peak waveform- were selected) MA: Based on mean RTs, with a time window of ±1.5 SD around the mean	As above	**O3.1.1:** A statistically significant difference between the two conditions suggests that, even in a detection task, response related motor activity is stronger in the aware condition compared to the unaware one. In Colombari et al., 2024 this difference was observed. Importantly, in this previous study a *discrimination* task was employed and participants were asked to provide two different responses in case of awareness (intentional) or unawareness (random). Instead, in this study participants are asked to perform a *detection* task, in which the motor behavior made to provide the response, when required, is the same for both aware and unaware condition and thus no response selection is required. **O3.1.2:** If no difference between the tested conditions is observed, it will suggest that in a detection task there is no difference in the motor activity related to the response. **O3.2.1:** Significant predictive interactions between LOC and motor areas will suggest that, when the stimulus enters consciousness, awareness-related activity in LOC predicts subsequent activity in motor areas. This (expected) outcome will suggest that consciousness modulates subsequent response-related motor activity, by directly triggering activation of motor areas, as observed in Colombari et al., 2024 **O3.2.2:** If no significant interactions between LOC and MA will be highlighted, then it would mean that activity in motor areas is not predicted by LOC. Specifically, it could be surmised that in a *detection* task, consciousness does not modulate activation of motor areas, as observed in Colombari et al., 2024, where a *discrimination* task was employed. The difference in the two tasks, indeed, consists in the type of motor response required: In the case of the discrimination task, the participant is asked to press one button or another according to the response. Conversely, in a detection task, the participant has to press a key when the target stimulus is detected. Thus, no selection of the response is needed. This difference could play a role in the relationship between consciousness and motor areas.	**OO3:** Our hypothesis was partially supported by our results. Indeed, greater activity in M1 was observed when contrasting aware and unaware conditions, suggesting that response related motor activity is stronger in the aware condition compared to the unaware one However, Granger analysis revealed no significant predictive effects between extra-striate and motor areas.

(*continued on next page*)

Table 3 – (*continued*)

Question	Hypothesis	Sampling plan	Analysis plan	Rationale for deciding the sensitivity of the test for confirming or disconfirming the hp	Interpretation given different outcomes	Observed outcomes
Q4: Does consciousness modulate activation of motor areas in ABSENCE of motor response?	**H4:** Consciousness modulates activation of motor areas, even if the motor response is not required **Expected outcome:** MA aware-NOGO > MA unaware-NOGO LOC predicts MA (investigated by means of Granger causality analysis)	As Q3	**A4.1:** A paired-sample one-tailed *t*-test was computed in order to compare activity in motor areas in the NOGO condition. Thus, activity in Aware-NOGO and Unaware-NOGO trials was contrasted. In addition to frequentist statistics, Bayesian statistics (with default prior) was computed to test potential null effects **Contrast to be computed:** AWARE NOGO *vs* UNAWARE NOGO **ROI to be tested:** Motor areas **Time interval of interest:** Based on mean RTs, with a time window of ±1.5 SD around the mean **A4.2:** With the aim of investigating the flow of activity occurring in the investigated brain areas also in the condition where no response is required, Granger analysis was performed on the "Aware-NOGO *vs* Unaware-NOGO" contrast. This allowed to investigate whether activity in motor areas is triggered by previous activity in LOC, even when a motor response is not required. Thus, LOC was used as seed ROI and later activity in motor areas was investigated. In addition to frequentist statistics, Bayesian statistics (with default prior) was computed to test potential null effects **Contrast to be computed:** AWARE NOGO *vs* UNAWARE NOGO **ROI to be tested:** LOC (as seed ROI) Motor areas as predicted areas **Time interval of interest:** LOC: 150–350 msec after the stimulus onset (within this interval, about ±4 time points around the peak value -according to the peak waveform- were selected) MA: Based on mean RTs, with a time window of ±1.5 SD around the mean	As above	**O4.1.1:** A statistically significant *t*-test suggests that, when a motor response is not provided, the inhibition required to withhold responding is stronger when the visual characteristic of the stimulus is consciously perceived, compared to when no difference is perceived. **O4.1.2:** If no difference between the tested conditions is observed, this suggests that ì) no inhibition is required to withhold responding, both in the aware and unaware condition, or ii) the inhibition is equally strong for the two conditions. **O4.2.1:** If significant predictive interactions between LOC and motor areas will be observed, then consciousness modulates subsequent activity in motor areas also in absence of a motor response. This could be due to inhibition of the response processes. **O4.2.2:** If no significant interactions between LOC and MA are highlighted, then LOC does not predict activity in motor areas in absence of motor response.	OO4: This hypothesis was not supported by our findings, as no significantly greater activation was observed in M1 when contrasting aware and unaware trials in the condition in which no motor response was required.

6) and the left primary motor cortex (M1, Brodmann Area 4). Statistical analysis was computed within specific temporal windows of interest selected on the basis of the results obtained by Colombari et al., 2024. This is to reduce the risk of false positives, as Opt3d does not offer the possibility to correct data for multiple comparisons in the temporal domain. The specific time windows tested for each hypothesis are listed in Table 3.

3. Results

3.1. Level of bias control

Level 6. No part of the data or evidence that was used to answer the research question was generated until after IPA.

3.2. Behavioral results

Raw data were processed using scripts created on Matlab (version R2017b; the MathWorks, Inc., Natick, MA). Trials were sorted into the four experimental conditions (i.e., Aware-GO, Unaware-NOGO, Aware-NOGO and Unaware-GO) based on the participants' responses. Aware trials were those trials in which the participant reported perceiving the thicker radius, while Unaware trials were those trials in which participants could not perceive that the radius was thicker.

As specified in Section 2.8 (Data Analysis), trials with RTs lower than 150 msec or higher than 3SD from the mean were removed. After removal, we had on average 801.4 trials for the Aware-GO condition, 372.7 for the Unaware-NOGO condition, 738.9 trials for the Aware-NOGO condition and 450.2 for the Unaware-GO. Thus, in the GO condition, Aware trials accounted for an average of 68.36% of the trials (SD = 9.64), while in the NOGO condition, Aware trials accounted for 62.13% of the trials (SD = 10.21). A two-tailed paired-samples *t*-test comparing the number of Aware trials in the GO and NOGO conditions revealed no statistically significant difference between conditions [t (31) = 2.01, p = .053, Cohen's d = −.355].

Subsequently, mean RTs for Aware and Unaware trials in the GO condition were calculated and contrasted by means of a paired-sample two-tailed *t*-test. Statistical analysis highlighted that mean RTs for the Aware condition (592.49 msec) and the Unaware condition (643.34 msec) were statistically different [t (31) = - 4.19, p < .001, Cohen's d = −.741].

Moreover, analysis of catch trials was performed as described in Section 2.8.1. As specified above, catch trials were those in which all the stimulus radii were equally thick. Hence, in those cases, participants should report not seeing the thicker radius. As expected, they correctly reported not seeing the thicker radius on average 95.72% of the time (SD = 5.41) in the Aware GO condition and 96.25% (SD = 5.10) in the Aware NOGO condition. Paired sample (two-tailed) *t*-test revealed no significant difference between the two conditions [t (31) = −.63, p = .533, Cohen's d = −.11]. Importantly, catch trials performance was significantly different from critical trials performance both in the GO condition [t (31) = −12.4, p < .001, Cohen's d = − 2.19] and in the NOGO condition [t (31) = −15.1, p < .001, Cohen's d = − 2.66].

3.3. EROS results

EROS data were pre-processed with a dedicated in-house software, P-POD (Pre-Processing of Optical Data, run in Matlab, version R2013b), as described in Section 2.8 and co-registered with each subject's structural MRI using the dedicated OCP software package. Subsequently, we computed statistical analyses on pre-processed data by means of the dedicated in-house software package Opt-3d. EROS results are shown in Fig. 3 and Supplementary Fig. S1.

In order to address the research question Q1 (i.e., "Can we replicate Colombari et al., 2024 findings showing that LOC is an NCC?"), we investigated awareness-related activity in LOC by comparing Aware and Unaware trials in the condition in which the motor response was required. To do so, Aware-GO and Unaware-GO conditions were contrasted, and activity in LOC was analyzed. EROS analyses showed a significantly increased activation at 179 msec after the stimulus onset (z = 2.80; z crit = 2.47).

In the same manner, with the aim of investigating whether the activity in LOC is independent from the response (i.e., research question Q2) we contrasted Aware and Unaware trials in the condition where the motor response was not required. Thus, the contrast between Aware-NOGO and Unaware-NOGO conditions was computed, revealing that even when a motor response was not required, Aware trials yielded greater activation in LOC 204 msec after stimulus onset (z = 3.37; z crit = 2.75).

Moreover, the interaction effect between awareness and motor response was tested by means of a paired-sample one-tailed *t*-test comparing the contrast Aware-GO versus Unaware-GO and Aware-NOGO versus Unaware-NOGO, and the interaction was not statistically significant. This null effect was further confirmed by Bayesian statistics computed with the default prior. Specifically, the Bayes factors indicated moderate support for the absence of an effect (BF_{10} = .19, error = 3.8%).

To address research questions Q3 and Q4, namely whether consciousness modulates activation of motor areas both in the presence and absence of motor response, we investigated activity in the motor areas while computing the above-mentioned contrasts. Indeed, the Aware-GO versus Unaware-GO contrast showed that activity reached statistical significance in motor areas 511 msec after stimulus onset (z = 2.73; z crit = 2.59), whereas the contrast between aware and unaware trials in the NOGO condition did not yield any significant results. To test this null effect, a Bayesian analysis using the default prior was computed, providing moderate evidence against the effect (BF_{10} = .20, error = 3.7%).

3.4. Granger causality analysis results

To further investigate the flow of activity in the investigated brain areas, Granger causality analysis was performed. Specifically, since in research question Q3 we were interested in investigating whether activity in motor areas was predicted by previous activity in LOC when a motor response is required (i.e., in the GO condition), we performed Granger analysis on the "Aware-GO versus Unaware-GO" contrast using LOC as seed ROI and investigating later activity in motor areas.

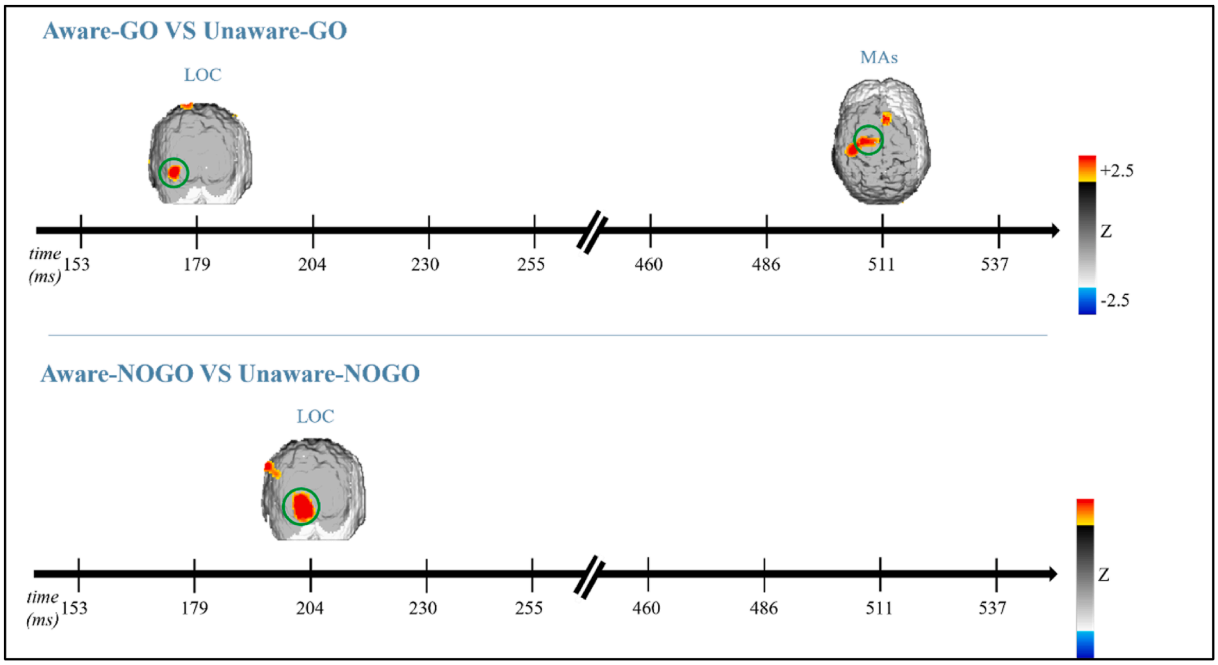

Fig. 3 – EROS results. The upper panel shows the statistical parametric maps of the z-score difference computed contrasting Aware and Unaware trials in the GO condition. The lower panel shows the statistical parametric maps of the z-score difference computed by contrasting Aware and Unaware trials in the NOGO condition. Each map represents a 25.6 msec interval.

This analysis revealed no significant predictive effects between extra-striate and motor areas. Importantly, Bayesian statistics computed with default priors confirmed the absence of an effect, as all confidence intervals included zero, further indicating that the estimated effects were not reliably different from the null hypothesis.

4. Discussion

The present study aimed to unravel the spatio-temporal dynamics underlying conscious vision by combining a go/no-go detection task with EROS recordings, thereby disentangling neural activity related to visual awareness from concurrent response-related mechanisms. Taken together, the results provide converging evidence for a central role of the LOC in conscious visual processing, while also shedding light on the relationship between awareness and motor activity.

As for research question Q1, the EROS data successfully replicated the main finding of Colombari et al. (2024), showing greater activation in LOC approximately 179 msec after stimulus onset when Aware-GO trials were contrasted with Unaware-GO trials. This early activation of LOC is consistent with the temporal window of the ERP component most commonly associated with visual awareness, the Visual Awareness Negativity (VAN; Koivisto & Revonsuo, 2010; Koivisto et al., 2016) and aligns with previous MEG source localization evidence pointing to the lateral occipito-temporal region as a key generator of awareness-related activity (Liu et al., 2012; Vanni et al., 1996). Source reconstruction analyses of ERP data have consistently placed the VAN generators in the lateral occipital and inferior occipito-temporal cortex (Ciupinska et al., 2025; Förster et al., 2020). These findings fit within a broader theoretical and empirical framework, suggesting that the extra-striate cortex, and in particular LOC, is a key area for the neural correlates of visual awareness (Rees et al., 2002). Recent literature using different approaches, such as single-neuron recordings from the human LOC across a variety of perceptual tasks (Quiroga et al., 2024) and a TMS-EROS paradigm bypassing V1 feedforward input (Knight et al., 2024), has likewise identified LOC as a critical site of early awareness-related activity, which is fully consistent with this picture. Importantly, the present result extends beyond the discrimination paradigm employed by Colombari and colleagues, demonstrating that the early involvement of LOC in conscious visual processing generalizes to a detection task in which no selection between motor responses is required.

Crucially, the results for research question Q2 demonstrate that LOC activation at 204 msec post-stimulus was equally present in the no-go condition, in which participants were asked to withhold responding. The absence of significant interaction between awareness and response requirement, further supported by Bayesian evidence in favor of the null hypothesis, confirms that the early LOC response is not modulated by response requirements and therefore cannot be attributed to preparation or execution of the motor response. This finding is consistent with the view put forward by Koivisto et al. (2016), who argued that subjective visual awareness emerges prior to P3 and independently of post-perceptual mechanisms. Along the same lines, Mazzi et al. (2020) demonstrated that the LP component—but not the VAN—is modulated by the response criterion adopted by

participants, providing direct electrophysiological evidence that early posterior activity reflects the conscious percept per se, whereas later components are contaminated by post-perceptual decision-related processes. Taken together, these findings strongly argue for considering LOC early activity as a genuine NCC rather than an epiphenomenon of response-related processes.

The finding that early LOC activation is independent of response requirement places the present results in direct dialogue with a body of EEG and fMRI research aimed at dissociating genuine NCCs from correlates of post-perceptual processing. No-report paradigms using EEG and fMRI have consistently shown that the late positivity (LP), but not early posterior activity, is strongly modulated by task demands, report requirements, and stimulus relevance (Dellert et al., 2021; Hense et al., 2024; Kronemer et al., 2022; Schlossmacher et al., 2020). Specifically, Dellert et al. (2021) demonstrated, using simultaneous EEG-fMRI, that awareness effects in LOC and in the early ERP component (VAN) persisted across report and no-report conditions, whereas frontal awareness effects were confined to the report condition. Likewise, Kronemer et al. (2022) identified awareness-related activity in LOC across a broad network using a no-report fMRI masking paradigm, and Hense et al. (2024) provided electrophysiological evidence for sustained conscious perception that similarly implicated posterior rather than frontal cortex. The present EROS data, showing response-independent LOC activation at approximately 200 msec, are fully consistent with this picture. Moreover, the role played by attention in modulating early posterior awareness effects remains debated. Several studies have reported that VAN amplitude is sensitive to both exogenous and endogenous attentional manipulations (Bola & Doradzińska, 2021; Doradzińska & Bola, 2024; Koivisto et al., 2006), and others have found that it can be dissociated from attentional effects (Ciupińska et al., 2024; Cohen et al., 2020; Dembski et al., 2021). The present paradigm was not designed to manipulate attention independently of awareness, and we therefore cannot rule out a contribution of differential attentional engagement across aware and unaware trials. Importantly, however, the response-independence of the LOC effect argues against the simplest confound, namely that LOC activation merely reflects response–preparation processes triggered only in the aware condition. With respect to the relevance of no-report paradigms more broadly, the findings from studies by Pitts et al. (2014), Shafto and Pitts (2015), Schelonka et al. (2017), and Dellert et al. (2022) collectively establish that late frontal and centro-parietal activity (including LP and P3) are particularly sensitive to task relevance, response criterion, and attentional blink dynamics, while early occipito-temporal effects show greater stability. This supports interpreting the early LOC effect reported here as more likely to reflect the conscious percept per se, rather than a post-perceptual consequence of detecting the stimulus and preparing a response.

Regarding research question Q3, the contrast between the aware and unaware conditions when a motor response was required showed a significant increase in motor area activation at approximately 511 msec after stimulus onset, within a time window consistent with the mean reaction times observed in the GO condition. This finding indicates that, even in a detection task in which the same motor response is performed regardless of whether the stimulus is consciously perceived, awareness modulates the magnitude of motor area activation. This result is consistent with Colombari et al. (2024), who reported a similar effect in a discrimination task in which aware and unaware trials required qualitatively different motor responses (i.e., a specific *vs* a random button press), thus, potentially introducing a response selection confound. By contrast, in the present detection task, the motor output was identical across awareness levels, making it less likely that the observed difference in motor area activity was driven by response selection demands alone, and suggesting that conscious perception can modulate motor-related processing even in simple detection contexts. However, another possible interpretation must be considered. Aware and Unaware trials differed not only in awareness but also in mean reaction times, reflecting a well-established advantage in processing speed for consciously perceived stimuli. In this respect, evidence accumulation frameworks propose that neural signals in motor and centroparietal regions track a decision variable that builds to a threshold, with its rate of rise scaling with the quality of sensory evidence (O'Connell et al., 2012; Kelly & O'Connell, 2013; Twomey et al., 2015; Tagliabue et al., 2019). On this account, the greater motor area activation at 511 msec in Aware-GO compared to Unaware-GO trials might reflect faster or steeper accumulation in the aware condition, rather than awareness per se. We consider this interpretation unlikely to fully account for the present result for two reasons. First, the motor activation effect emerged at 511 msec, which falls within, rather than clearly before, the range of mean RTs for both conditions; if the difference were driven by an earlier threshold crossing in the aware condition, one might expect the effect to appear at a shorter latency. Second, in the present paradigm the threshold stimulus was individually calibrated to produce approximately 50% detection: any difference in evidence quality between aware and unaware trials is thus inherent to the phenomenal state itself and cannot be independently manipulated without altering the experimental design. Nonetheless, without a parametric manipulation of stimulus strength or a model-based analysis of the RT distributions, we cannot definitively rule out the possibility that the motor area difference at 511 msec reflects, at least in part, a difference in the rate of decision accumulation between conditions. Future work combining EROS with computational modelling of accumulation-to-bound dynamics would help to disentangle these accounts. More generally, this interpretation is consistent with a broader literature emphasizing that motor areas are sensitive not only to the execution of movements, but also to the cognitive context in which they are embedded (Montani et al., 2026).

Addressing research question Q4, the analysis of the no-go condition revealed no significant difference in motor area activity between aware and unaware trials, a null result further supported by Bayesian evidence. This finding suggests that, when participants successfully withhold their motor response, consciousness does not produce detectable differences in motor area activation, or, alternatively, that any inhibitory activity elicited by conscious perception of the

stimulus is equally present across awareness levels and thus does not manifest as a difference in the contrast. This interpretation aligns with the well-established role of the pre_SMA in response conflict resolution and inhibitory motor control: meta-analytic evidence (Swick et al., 2008) consistently identifies the pre-SMA as a region recruited across simple and complex go/no-go tasks, playing a critical role in selecting appropriate behavior whether that entails executing or withholding a response. The absence of a consciousness-related modulation of motor areas in the no-go condition thus suggests that the inhibitory process required to withhold responding may operate at a level that is not differentially sensitive to awareness in a detection context.

The investigation of the directed flow of activity between LOC and motor areas, using Granger causality analyses, did not reveal significant predictive interactions between early LOC activation and subsequent motor area dynamics, neither in the GO nor in the NO-GO condition. Although this null result should be interpreted with caution, it was also supported by Bayesian evidence and, despite being unexpected in light of Colombari et al. (2024)'s findings in a discrimination task, remains informative and theoretically meaningful when considered alongside the pattern of results from the conventional EROS analyses. Indeed, while awareness modulated motor area activation in the GO condition, this modulation does not appear to be driven by a direct predictive influenceof LOC on motor areas. One possible interpretation is that the difference in task demands between the present detection paradigm and the discrimination paradigm of Colombari et al. (2024) may account for this discrepancy: in a discrimination task, the need to select among alternative responses may amplify the predictive influence of awareness-related occipito-temporal activity on motor areas, a dynamic that may be reduced or absent when only a single, stereotyped response is required. This interpretation is, again, consistent with evidence showing that pre-SMA and premotor areas are particularly recruited when response conflict or selection demands are high (Nachev et al., 2008; Rushworth et al., 2002), and with the broader finding that the relationship between visual awareness and motor control is flexible and contingent on the cognitive and biomechanical demands of the task (Montani et al., 2026). A further, non-mutually exclusive, interpretation concerns the nature of the information that LOC may need to convey to motor areas. In a discrimination task, LOC encodes specific perceptual content (i.e., the orientation of the Gabor patch) that is directly relevant for selecting which response to execute. On this account, the selection of the correct action to perform may depend on the transmission of content-specific information to motor areas, and it is precisely this content-specific process that the Granger causality analysis may have captured in Colombari et al. (2024). In a detection task, by contrast, the motor system may not need access to detailed perceptual content, but only to the presence of a target. This kind of signal can reach M1 through more generic sensorimotor circuits, without requiring LOC to directly drive motor activity. From this perspective, the predictive LOC–motor link may not reflect a general feature of awareness, but rather a process that becomes relevant when the perceptual content encoded in LOC is necessary to guide response selection. This interpretation is consistent with the present finding that LOC activation is equally present and equally strong across GO and NOGO conditions, but its downstream influence on motor circuits depends on whether that content is decision-relevant for the required action.

From a broader theoretical standpoint, the present findings speak to an ongoing debate in consciousness research about the spatial and temporal locus of phenomenal awareness and its relationship to cognition and action. The convergent evidence reviewed here—namely, early and response-independent activation of LOC as a candidate NCC, the absence of a direct predictive link from LOC to motor areas in a detection context, and the selective modulation of motor activity only when a response is executed—seems to be better accommodated by a framework in which conscious visual experience emerges from early, localized activity in extrastriate cortex, rather than depending on late widespread activity. This interpretation is in line with converging report and no-report evidence suggesting that later widespread activity mainly reflects post-perceptual processes such as report, decision-making, and response selection, while the neural correlates of perceptual awareness arise at earlier processing stages (Koivisto et al., 2016; Mazzi et al., 2017, 2020; Tsuchiya et al., 2015). It is also consistent with the most recent large-scale adversarial test of the global neuronal workspace theory and integrated information theory, in which decoding of conscious content was strongest in posterior cortex and often unsuccessful in prefrontal areas (Cogitate et al., 2025). However, an important qualification is necessary: the EROS montage employed here covered occipital, temporal, and parietal cortices but did not extend to prefrontal cortex (see Fig. 2 and the limitations paragraph below). The present data are therefore silent on whether prefrontal activation accompanies the early LOC effect, and our conclusions should be read as characterizing the temporal and spatial profile of awareness-related activity within the covered territory, not as arbitrating the full frontal versus posterior NCC debate. Whether and when PFC activity constitutes a genuine NCC or a post-perceptual correlate of report in paradigms such as the present one remains an open question that EROS as currently configured cannot address.

Importantly, the comparison between the present study and Colombari et al. (2024) suggests that the critical factor determining whether LOC drives motor areas is not awareness per se, but the degree to which the specific perceptual content encoded in LOC is necessary to guide the required response. This distinction between awareness as a presence signal and awareness as discriminative content may prove a useful organizing principle for understanding when and how conscious perception propagates to motor and executive areas and invite future work to systematically characterize the conditions under which conscious perception shapes downstream processing.

The present findings should be interpreted in light of some limitations. First, although EROS provides a valuable combination of temporal and spatial information, the montage used in the present study did not provide full whole-brain coverage. In particular, major portions of the frontal cortex could not be investigated because of the relatively limited number of available optodes. Therefore, the present findings should not be interpreted as ruling out possible awareness-related

activity in frontal areas, which are considered crucial by some theories of consciousness (e.g., Dehaene & Changeux, 2011). Importantly, our conclusions are restricted to the preregistered regions covered by the EROS montage, namely posterior visual and motor-related areas.

Second, EROS has a relatively low signal-to-noise ratio compared with other neuroimaging techniques and therefore requires a high number of trials to obtain reliable estimates. Although all conditions retained a substantial number of trials after preprocessing, fewer trials were available in the Unaware than in the Aware conditions. While this imbalance was anticipated and accounted for in the preregistered exclusion criteria, this difference may have influenced signal quality to some extent and should be considered when interpreting the results. Nonetheless, trial counts per condition were well above the threshold for reliable EROS statistics, even for the less represented conditions.

Third, the in-house Opt-3d software implements correction for multiple comparisons in the spatial domain but does not directly provide correction across the temporal domain. For this reason, temporally extended effects should be interpreted with some caution. Importantly, however, this concern is mitigated by the fact that all analyses were restricted to preregistered ROIs and time windows. Future studies combining EROS with whole-brain EEG, MEG, or fMRI recordings may help clarify how early LOC activity relates to later frontal and parietal dynamics during conscious visual processing.

A further limitation concerns the interpretation of the motor-area effect observed at 511 msec in the Aware-GO versus Unaware-GO contrast. Aware and Unaware trials differed not only in phenomenal state but also in mean reaction time, with responses being faster in Aware trials than in Unaware trials (592 msec *vs* 643 msec, respectively). This difference is unlikely to reflect differences in stimulus quality, since the same threshold stimulus was used across all trials. Rather, it plausibly reflects the phenomenological difference between responding on the basis of a conscious percept and responding in its absence, with the latter condition introducing greater decisional uncertainty and a less direct mapping between sensory input and motor output. To this extent, the RT difference may itself be a consequence of the awareness manipulation rather than an independent confound. Future studies combining EROS with computational modelling of decision accumulation would help to fully characterize the relationship between conscious state, response speed, and motor-area activation in paradigms of this type.

In conclusion, the present registered report provides robust and pre-registered evidence that LOC represents a key extrastriate correlate of visual awareness, whose activity appears to be independent of motor response requirements. Moreover, by demonstrating that awareness selectively modulates motor area activation only when a response is executed, the study helps clarify the nature of the interplay between awareness-related extra-striate regions and response-related motor areas, thereby advancing our understanding of the neural architecture underlying the early genesis of phenomenal awareness and the conditions under which conscious perception shapes downstream motor activity.

Scientific transparency statement

DATA: All raw and processed data supporting this research are publicly available: https://osf.io/ebfu3/?view_only=9ec2e6bf32ba4a8bb8b858639ec40a59.

CODE: All analysis code supporting this research is publicly available: https://osf.io/ebfu3/overview?view_only=9ec2e6bf32ba4a8bb8b858639ec40a59.

MATERIALS: All study materials supporting this research are publicly available: https://osf.io/ebfu3/overview?view_only=9ec2e6bf32ba4a8bb8b858639ec40a59.

DESIGN: This article reports, for all studies, how the author(s) determined all sample sizes, all data exclusions, all data inclusion and exclusion criteria, and whether inclusion and exclusion criteria were established prior to data analysis.

PRE-REGISTRATION: At least part of the study procedures was pre-registered in a time-stamped, institutional registry prior to the research being conducted: https://osf.io/8ya2t At least part of the analysis plans was pre-registered in a time-stamped, institutional registry prior to the research being conducted: https://osf.io/8ya2t.

For full details, see the *Scientific Transparency Report* in the supplementary data to the online version of this article.

CRediT authorship contribution statement

Elisabetta Colombari: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Giorgia Parisi:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Sonia Mele:** Writing – review & editing, Methodology, Investigation. **Chiara Mazzi:** Writing – review & editing, Supervision, Software, Methodology, Data curation. **Silvia Savazzi:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Conflict of interest

The authors declare no competing interests.

Acknowledgments

The present project is supported by the Center for Open Science through the "Funding Consciousness Research with Registered Reports" grant program, the Ministero dell'università e della ricerca, PRIN 2022 (grant n. 2022TBKCM5) and Fondazione Cassa di Risparmio di Verona, Vicenza, Belluno e Ancona "Ricerca scientifica d'eccellenza 2018", "Emergence of Consciousness: From neural dynamics to complex conscious behaviour" grant no. 2018.0861; SS is supported by #NEXTGENERATIONEU (NGEU) and funded by the Ministry of University and Research (MUR), National Recovery and Resilience Plan (NRRP), project MNESYS (PE0000006)—"A Multiscale integrated approach to the study

of the nervous system in health and disease" (DN. 1553 11.10.2022), CM is supported by MIUR D.M. 737/2021—"Neural correlates of perceptual awareness: from neural architecture to the preservation of conscious vision in brain tumor patients", EC is supported by NGEU and funded by MUR, NRRP DM 637 30/04/2024—"SpeechDynamics: Neural dynamics of (un)conscious speech feedback control in health and disease".

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2026.09.001.

REFERENCES

Arridge, S. R., & Schweiger, M. (1995). Sensitivity to prior knowledge in optical tomographic reconstruction in chance, B. In R. R. Alfano (Ed.), *Optical tomography, photon migration, and spectroscopy of tissue and model media: Theory, human studies, and instrumentation. SPIE,* (pp. 378–388).

Aru, J., Bachmann, T., Singer, W., & Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neuroscience and Biobehavioral Reviews, 36*, 737–746.

Baniqued, P. L., Low, K. A., Fabiani, M., & Gratton, G. (2013). Frontoparietal traffic signals: A fast optical imaging study of preparatory dynamics in response mode switching. *Journal of Cognitive Neuroscience, 25*, 887–902.

Bola, M., & Doradzińska, Ł. (2021). Perceptual awareness negativity—does it reflect awareness or attention? *Frontiers in Human Neuroscience, 15*, 1–4.

Chiarelli, A. M., Maclin, E. L., Low, K. A., Fabiani, M., & Gratton, G. (2015). Comparison of procedures for co-registering scalp-recording locations to anatomical magnetic resonance images. *Journal of Biomedical Optics, 20*, Article 016009.

Ciupinska, K., Koculak, M., Bola, M., & Wierzchon, M. (2025). Early and late ERP correlates of consciousness – A direct comparison between visual and auditory modalities. *Psychophysiology, 62*, Article e70099.

Ciupińska, K., Orłowska, W., Zębrowski, A., Łępa, L., Koculak, M., Bola, M., & Wierzchon, M. (2024). The influence of spatial and temporal attention on visual awareness—a behavioral and ERP study. *Cerebral Cortex, 34*.

Cogitate, C., Ferrante, O., Gorska-Klimowska, U., Henin, S., Hirschhorn, R., Khalaf, A., … Melloni, L. (2025). Adversarial testing of global neuronal workspace and integrated information theories of consciousness. *Nature, 642*, 133–142.

Cohen, M. A., Ortego, K., Kyroudis, A., & Pitts, M. (2020). Distinguishing the neural correlates of perceptual awareness and postperceptual processing. *Journal of Neuroscience: the Official Journal of the Society for Neuroscience, 40*, 4925–4935.

Colombari, E., Parisi, G., Tafuro, A., Mele, S., Mazzi, C., & Savazzi, S. (2024). Beyond primary visual cortex: The leading role of lateral occipital complex in early conscious visual processing. *NeuroImage, 298*, Article 120805.

Dehaene, S., & Changeux, J. P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron, 70*, 200–227.

Dellert, T., Krebs, S., Bruchmann, M., Schindler, S., Peters, A., & Straube, T. (2022). Neural correlates of consciousness in an attentional blink paradigm with uncertain target relevance. *NeuroImage, 264*, Article 119679.

Dellert, T., Müller-Bardorff, M., Schlossmacher, I., Pitts, M., Hofmann, D., Bruchmann, M., & Straube, T. (2021). Dissociating the neural correlates of consciousness and task relevance in face perception using simultaneous EEG-fMRI. *Journal of Neuroscience: the Official Journal of the Society for Neuroscience, 41*, 7864–7875.

Dembski, C., Koch, C., & Pitts, M. (2021). Perceptual awareness negativity: A physiological correlate of sensory consciousness. *Trends in Cognitive Sciences, 25*, 660–670.

Doradzińska, Ł., & Bola, M. (2024). Early electrophysiological correlates of perceptual consciousness are affected by both exogenous and endogenous attention. *Journal of Cognitive Neuroscience, 36*, 1297–1324.

Förster, J., Koivisto, M., & Revonsuo, A. (2020). *ERP and MEG correlates of visual consciousness: The second decade* (Vol. 80). Conscious. Cogn.

Gratton, G. (2000). "Opt-cont" and "opt-3D": A software suite for the analysis and 3D reconstruction of the event-related optical signal (EROS). *Psychophysiology, 37*, Article S44.

Gratton, G., & Corballis, P. M. (1995). Removing the heart from the brain: Compensation for the pulse artifact in the photon migration signal. *Psychophysiology, 32*, 292–299.

Gratton, G., & Fabiani, M. (1998). Dynamic brain imaging: Event-related optical signal (EROS) measures of the time course and localization of cognitive-related activity. *Psychonomic Bulletin and Review, 5*, 535–563.

Gratton, G., & Fabiani, M. (2001). Shedding light on brain function: The event-related optical signal. *Trends in Cognitive Sciences, 5*, 357–363.

Gratton, G., & Fabiani, M. (2010). Fast optical imaging of human brain function. *Frontiers in Human Neuroscience, 4*, 1–9.

Gratton, G., Fabiani, M., Corballis, P. M., Hood, D. C., Goodman-Wood, M. R., Hirsch, J., Kim, K., Friedman, D., & Gratton, E. (1997). Fast and localized event-related optical signals(EROS) in the human occipital cortex: Comparisons with the visual evoked potential and fMRI. *NeuroImage, 6*, 168–180.

Gratton, G., Sarno, A., Maclin, E., Corballis, P. M., & Fabiani, M. (2000). Toward noninvasive 3-D imaging of the time course of cortical activity: Investigation of the depth of the event-related optical signal. *NeuroImage, 11*, 491–504.

Hatamimajoumerd, E., Ratan Murty, N. A., Pitts, M., & Cohen, M. A. (2022). Decoding perceptual awareness across the brain with a no-report fMRI masking paradigm. *Current Biology: CB, 32*, 4139–4149.e4.

Hense, A., Peters, A., Bruchmann, M., Dellert, T., & Straube, T. (2024). Electrophysiological correlates of sustained conscious perception. *Scientific Reports, 14*, 1–11.

Kelly, S. P., & O'Connell, R. G. (2013). Internal and external influences on the rate of sensory evidence accumulation in the human brain. *Journal of Neuroscience, 33*, 19434–19441.

Kiebel, S. J., Poline, J. B., Friston, K. J., Holmes, A. P., & Worsley, K. J. (1999). Robust smoothness estimation in statistical parametric maps using standardized residuals from the general linear model. *NeuroImage, 10*, 756–766.

Knight, R. S., Chen, T., Gratton, G., Fabiani, M., Savazzi, S., Mazzi, C., & Beck, D. M. (2024). Neuropsychologia bypassing input to V1 in visual awareness: A TMS-EROS investigation. *Neuropsychologia, 198*, Article 108864.

Koivisto, M., Lähteenmäki, M., Sørensen, T. A., Vangkilde, S., Overgaard, M., & Revonsuo, A. (2008). The earliest electrophysiological correlate of visual awareness? *Brain and Cognition, 66*, 91–103.

Koivisto, M., & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience and Biobehavioral Reviews, 34*, 922–934.

Koivisto, M., Revonsuo, A., & Lehtonen, M. (2006). Independence of visual awareness from the scope of attention: An electrophysiological study. *Cerebral Cortex, 16*, 415–424.

Koivisto, M., Salminen-Vaparanta, N., Grassini, S., & Revonsuo, A. (2016). Subjective visual awareness emerges prior to P3. *European Journal of Neuroscience, 43*, 1601–1611.

Kronemer, S. I., Aksen, M., Ding, J. Z., Ryu, J. H., Xin, Q., Ding, Z., Prince, J. S., Kwon, H., Khalaf, A., Forman, S., Jin, D. S., Wang, K., Chen, K., Hu, C., Agarwal, A., Saberski, E., Mohammad, S., Wafa, A., Morgan, O. P., … Pitts, M. (2022). *Human visual consciousness involves large scale cortical and subcortical networks independent of task report and eye movement activity*.

Leung, P., Franconeri, S., Grabowecky, M., & Suzuki, S. (2009). Rapid eye-fixation training without eyetracking. *Psychonomic Bulletin and Review, 16*, 491–496.

Liu, Y., Paradis, A. L., Yahia-Cherif, L., & Tallon-Baudry, C. (2012). Activity in the lateral occipital cortex between 200 and 300 ms distinguishes between physically identical seen and unseen stimuli. *Frontiers in Human Neuroscience, 6*, 1–9.

Makeig, S., & Jung, T. (2000). Independent component analysis of simulated ERP data. *Brain: a Journal of Neurology*, 1–24.

Mazzi, Mazzeo, & Savazzi. (2017). Markers of TMS-evoked visual conscious experience in a patient with altitudinal hemianopia. *Consciousness and Cognition, 54*, 143–154.

Mazzi, C., Mazzeo, G., & Savazzi, S. (2020). Late positivity does not meet the criteria to be considered a proper neural correlate of perceptual awareness. *Frontiers in Systems Neuroscience, 14*, 1–14.

Montani, V., Pascucci, F., Colombari, E., Savazzi, S., & Cesari, P. (2026). Visual awareness of stimulus features shapes motor control through action end-state comfort. *Scientific Reports, 16*, Article 10801.

Nachev, P., Kennard, C., & Husain, M. (2008). Functional role of the supplementary and pre-supplementary motor areas. *Nature Reviews. Neuroscience, 9*, 856–869.

O'connell, R. G., Dockree, P. M., & Kelly, S. P. (2012). A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nature Neuroscience, 15*, 1729–1735.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.

Parisi, G., Mazzi, C., Colombari, E., Chiarelli, A. M., Metzger, B. A., Marzi, C. A., & Savazzi, S. (2020). Spatiotemporal dynamics of attentional orienting and reorienting revealed by fast optical imaging in occipital and parietal cortices. *NeuroImage, 222*, Article 117244.

Pitts, M. A., Padwal, J., Fennelly, D., Martínez, A., & Hillyard, S. A. (2014). Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness. *NeuroImage, 101*, 337–350.

Quiroga, R. Q., Mormann, F., Kreiman, G., Koch, C., & Fried, I. (2024). Single-neuron correlates of visual consciousness in human lateral occipital complex. *Nature Neuroscience*.

Railo, H., Revonsuo, A., & Koivisto, M. (2015). Behavioral and electrophysiological evidence for fast emergence of visual consciousness. *Neuroscience Consciousness, 2015*, 1–12.

Rees, G., Kreiman, G., & Koch, C. (2002 Apr). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience, 3*(4), 261–270. https://doi.org/10.1038/nrn783. PMID:11967556.

Rushworth, M. F. S., Hadland, K. A., Paus, T., & Sipila, P. K. (2002). Role of the human medial frontal cortex in task switching: A combined fMRI and TMS study. *Journal of Neurophysiology, 87*, 2577–2592.

Schelonka, K., Graulty, C., Canseco-gonzalez, E., & Pitts, M. A. (2017). ERP signatures of conscious and unconscious word and letter perception in an inattentional blindness paradigm. *Consciousness and Cognition, 54*, 56–71.

Schlossmacher, I., Dellert, T., Pitts, M., Bruchmann, M., & Straube, T. (2020). Differential effects of awareness and task relevance on early and late ERPs in a no-report visual oddball paradigm. *Journal of Neuroscience: the Official Journal of the Society for Neuroscience, 40*, 2906–2913.

Seth, A. K., Barrett, A. B., & Barnett, L. (2015). Granger causality analysis in neuroscience and neuroimaging. *Journal of Neuroscience: the Official Journal of the Society for Neuroscience, 35*, 3293–3297.

Shafto, J. P., & Pitts, M. A. (2015). Neural signatures of conscious face perception in an inattentional blindness paradigm. *Journal of Neuroscience: the Official Journal of the Society for Neuroscience, 35*, 10940–10948.

Swick, D., Ashley, V., & Turken, A. U. (2008). Left inferior frontal gyrus is critical for response inhibition. *BMC Neuroscience, 9*, Article 102.

Tagliabue, C. F., Veniero, D., Benwell, C. S., Cecere, R., Savazzi, S., & Thut, G. (2019). The EEG signature of sensory evidence accumulation during decision formation closely tracks subjective perceptual experience. *Scientific Reports, 9*, Article 4949.

Tsuchiya, N., Wilke, M., Frässle, S., & Lamme, V. A. F. (2015). No-Report paradigms: Extracting the true neural correlates of consciousness. *Trends in Cognitive Sciences, 19*, 757–770.

Twomey, D. M., Murphy, P. R., Kelly, S. P., & O'Connell, R. G. (2015). The classic P300 encodes a build-to-threshold decision variable. *European Journal of Neuroscience, 42*, 1636–1643.

Vanni, S., Revonsuo, A., Saarinen, J., & Hari, R. (1996). Visual awareness of objects correlates with activity of right occipital cortex. *NeuroReport, 8*, 183–186.

Wolf, U., Wolf, M., Toronov, V., Michalos, A., Paunescu, L. A., & Gratton, E. (2014). Detecting cerebral functional slow and fast signals by frequency-domain near-infrared spectroscopy using two different sensors. In *Biomedical optical spectroscopy and diagnostics (2000)*. The Optical Society, Article TuF10. *Paper TuF10*.

Worsley, K. J., Poline, J. B., Vandal, A. C., & Friston, K. J. (1995). Tests for distributed, nonfocal brain activations. *NeuroImage, 2*, 183–194.

Ye, M., Wang, A., Liang, H., & Liu, X. (2024). Late positivity correlates with subjective reports: Evidence from the low-frequency and high-frequency reporting tasks. *Neuroscience, 546*, 143–156.

Zhao, L., Matloff, W., Shi, Y., Cabeen, R. P., & Toga, A. W. (2022). Mapping complex brain torque components and their genetic architecture and phenomic associations in 24 , 112 individuals. *Biological Psychiatry, 91*, 753–768.