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Spatiotemporal dynamics of brightness coding in human visual cortex revealed by the temporal context effect

Hao Zhou [a,b,c,d,*], Matthew Davidson [e], Peter Kok [f,g], Li Yan McCurdy [e,h], Floris P. de Lange [f], Hakwan Lau [e,i,j,k,l], Kristian Sandberg [a,m,**]

[a] Center of Functionally Integrative Neuroscience, Aarhus University, Aarhus, 8000, Denmark
[b] Sino-Danish College, University of Chinese Academy of Sciences, Beijing, 100049, China
[c] Sino-Danish Center for Education and Research, Beijing, 100190, China
[d] State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, Beijing, 100101, China
[e] Department of Psychology, Columbia University, New York, NY, 10027, USA
[f] Donders Institute for Brain, Cognition, and Behaviour, Radboud University, Kapittelweg 29, 6525, EN Nijmegen, the Netherlands
[g] Wellcome Centre for Human Neuroimaging, University College London, London, WC1N 3BG, UK
[h] Interdepartmental Neuroscience Program, Yale University, New Haven, CT, 06520, USA
[i] Department of Psychology, University of California, Los Angeles, Los Angeles, 90095, USA
[j] Brain Research Institute, University of California, Los Angeles, Los Angeles, 90095, USA
[k] Department of Psychology, The University of Hong Kong, Pokfulam Road, Hong Kong
[l] State Key Laboratory of Brain and Cognitive Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong
[m] Hammel Neurorehabilitation and Research Centre, Aarhus University Hospital, 8450, Hammel, Denmark

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ABSTRACT

Human visual perception is modulated by both temporal and spatial contexts. One type of modulation is apparent in the temporal context effect (TCE): In the presence of a constant luminance patch (a long flash), the perceived brightness of a short flash increases monotonically with onset asynchrony. The aim of the current study was to delineate the neural correlates of this illusory effect, particularly focusing on its dynamic neural representation among visual cortical areas. We reconstructed sources of magnetoencephalographic (MEG) data recorded from observers (6 male and 9 female human adults) experiencing the TCE. Together with retinotopic mapping, signals from different occipital lobe areas were extracted to investigate whether different visual areas have differential representation of the onset vs. offset synchronized short flashes. From the data, TCE related responses were observed in LO and V4 in the time window of 200–250 m s, while neuronal responses to physical luminances were observed in the early time window at around 100 m s across early visual cortex, such as V1 and V2, also in V4 and VO. Based on these findings, we suggest that two distinct processes might be involved in brightness coding: one bottom-up process which is stimulus energy driven and responds fast, and another process which may be broadly characterized as top-down or lateral, is context driven, and responds slower. For both processes, we found that V4 might play a critical role in dynamically integrating luminances into brightness perception, a finding that is consistent with the view of V4 as a bottom-up and top-down integration complex.

1. Introduction

The human perceptual system employs a number of strategies for optimizing outputs when sensing and interpreting the physical world. It is widely observed that not only the physical properties of a stimulus, but also its embedded context, are essential to generate final percepts. Visual perception of a target, including brightness, orientation, size, or location (Gibson, 1937; Holway and Boring, 1941; Adelson, 1993; Cavanagh and Anstis, 2013), depends strongly on its context in a scene both spatially and temporally (Schwartz et al., 2007). For instance, in the presence of a patch of constant luminance (a long flash), the brightness of a short flash increases monotonically with onset asynchrony, a phenomenon referred to as the Temporal Context Effect (TCE) (Eagleman et al., 2004).

Brightness is the perceived absolute intensity of light in observer's

* Corresponding author., 15 Datun Road, Chaoyang District, Beijing, China.
** Corresponding author., Palle Juul-Jensens Boulevard 82. building NBG/10G, 10G-4-06, 8200, Aarhus N, Denmark.
E-mail addresses: haozhou@clin.au.dk (H. Zhou), kristian.sandberg@clin.au.dk (K. Sandberg).

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eye (Gilchrist, 2007). Previous studies (Georgeson, 1987; Rieiro et al., 2012) have shown that the perceived brightness of a static flash depends not only on its luminance intensity, but also on its duration. As flash duration increases, subjective brightness reaches a plateau after 100–200 m s. This indicates that before generating a brightness percept, luminance information is collected and integrated across a time window. Beyond this integration time window, brightness of a visual object is assigned and kept. The neural activation pattern is characterized by an early, strong transient response of around 200 m s followed by a sustained response that decreases with adaptation (Kinoshita and Komatsu, 2001). In spite of a decrease in neural activation during continuous presentation, the perceived brightness is generally reported as stable although decreases in luminance are more frequently detected than increases (Eagleman et al., 2004). Thus, the long flash stimulus changes the overall state of the spiking pool over time (high overall spiking rate during the transient response, lower afterwards), and it could be hypothesized that the visual system computes differently the brightness of identical short flashes with increasing onset asynchrony through comparison with or thresholding to the overall spike pool. As a result, it is likely that relative timing changes the perceived brightness of the short flash at the stage of integration.

But where does this integration happen in the human brain? Though disentangling the relationship between the physical luminance and perceptual brightness is one of the fundamental questions in visual neuroscience, it remains poorly understood, especially with respect to the underlying neural mechanisms. Neuronal responses to luminance take place along early visual processing pathway from retina, LGN, and striate cortex (Rossi and Paradiso, 1999; Kinoshita and Komatsu, 2001). Of these areas, only early visual cortex neuronal responses correlate with brightness perception (Rossi et al., 1996; Rossi and Paradiso, 1999; Kinoshita and Komatsu, 2001; Haynes et al., 2004; Roe et al., 2005; Boyaci et al., 2007; Pereverzeva and Murray, 2008; Ruff et al., 2018). Other studies show that higher visual cortex areas such as LO, IPS, and V4 might be specifically involved in brightness coding (Perna et al., 2005; Bushnell et al., 2011; Ruff et al., 2018), rather than early visual cortex (Cornelissen et al., 2006). Yet the locus of brightness perception remains controversial.

Using high-temporal resolution magnetoencephalography (MEG), we recorded neuronal responses directly from human observers who were experiencing the TCE. Sources were reconstructed to multiple regions of the visual cortex with a beamformer algorithm based on whole brain signals. Beamformer methods are becoming more and more prevalent in MEG signal source reconstruction because of their high spatial resolution, and because no prior selection of expected sources is required in this algorithm. Guided by fMRI retinotopic mapping data, signals from different occipital lobe areas were extracted to investigate whether different visual areas had differential representation of luminances under different temporal contexts.

2. Material and methods

2.1. Participants

23 healthy adult humans (9 male) with normal or corrected-to-normal vision gave written informed consent to participate in the behavioral experiment, and 15 of them (6 male) completed both MEG recording and MRI scanning sessions. The ages of the participants were between 23 and 33 years (mean = 26.53, SD = 2.70). The study was approved by the local ethics committee (Commisie Mensgebonden Onderzoek (CMO) Arnhem-Nijmegen, The Netherlands) under the general ethics approval (Imaging Human Cognition, CMO, 2014/288), and the experiment was conducted in accordance with these guidelines.

2.2. MEG procedure

MEG data was recorded in a magnetically shielded room with a 275 channel CTF Omega whole-head gradiometer system (VSM MedTech, Coquitlam, BC, Canada) with a 1200Hz sampling rate. Head localization was monitored continuously during the experiment using coils that were placed at the cardinal points of the head (nasion and left and right ear canals). An electro-oculogram (EOG) was recorded from the supraorbital and infraorbital ridge of the left eye, and an electrocardiogram (ECG) was recorded, both using 10-mm-diameter Ag–AgCl surface electrodes.

Stimuli were small bright discs on a black background. Stimulus size was 5 degrees of visual angle. The trial procedure is presented in Fig. 1. On each trial, a red fixation cross appeared for between 1217 and 2217 m s. This was followed by a short (50 m s) and a long (283 m s) flash, which were presented either with synchronized onset (Fig. 1A) or offset (Fig. 1B). During flash presentations, the fixation cross was white. Each flash could appear in each of the four quadrants of the screen (with a distance of 3 degrees of visual angle from the centre), but on any given trial the two flashes were always presented in opposite quadrants (i.e. if the long flash was in the lower right part of the screen, the short flash would be in the upper left). Finally, at flash offset the fixation cross turned red again, which indicated to participants that they should make a judgment regarding the relative brightness of the two flashes and report their confidence in this judgment. This was done using one of four response buttons: The left hand was used for report if the leftmost flash appeared brighter, and a response with the middle finger indicated high confidence whereas a report with the index finger indicated low confidence. The right hand was used for report if the rightmost flash appeared brighter, and a response with the middle finger again indicated high confidence whereas a report with the index finger again indicated low confidence. Reports of confidence were not used for analyses.

The short flash was presented at five different luminances (Fig. S1) for each hemifield: 0, 0.5, 5.8, 11.4, and 16.7 cd/m^2 respectively for the right hemifield, and 0, 0.5, 7.8, 11.4, and 16.7 cd/m^2 respectively for the left hemifield. The luminance of the long flash was kept constant during the entire experiment at 7.8 cd/m^2 for 17 participants and 5.8 cd/m^2 for the remaining 7. These individual and hemifield-specific calibrations of luminance were performed so that as many participants as possible experienced the brightest short flash as brighter than the long flash both at onset and offset, and so that all participants experienced the darkest short flash as darker than the long flash both at onset and offset.

The experiment was divided into blocks of 160 trials, and each participant completed 4-5 blocks (i.e. a total of 640–800 trials). Participants were allowed to take a break between blocks. As short flashes could be presented in each of four quadrants, have one of five luminances, and appear with either onset or offset synchronized with the long flash, the experiment contained a total of 40 conditions. Each of these conditions was presented four times in each block in pseudo-randomized order. The onset/offset stimuli were pseudo-randomly presented in same blocks.

Stimuli were generated using Psychtoolbox 3 for Matlab (http://www.psychtoolbox.org/) and were projected onto a 47.0 × 35.3 cm screen (resolution: 1024 × 768 pixels; refresh rate: 60Hz). The viewing distance was approximately 79 cm.

2.3. MRI procedure

MRI data were acquired with a Siemens Avanto 1.5T MRI scanner (SIEMENS Heathineers Global) at the Donders Centre for Cognitive Neuroimaging, using a 12-channel receive head coil. A gradient echo planar imaging sequence was used to acquire functional images (3.5 mm isotropic voxels, 32 axial slices of 3.5 mm thickness, 128 × 128 matrix with 3.5 mm in-plane resolution, TR/TE = 2280/40 m s, flip angle = 80°). A high-resolution anatomical volume was obtained with a T1 MPRAGE sequence (1 mm isotropic voxels, 176 sagittal slices at 1 mm thickness, 256 × 256 matrix with 1 mm in-plane resolution, TR/TE = 2290/2.95 m s, flip angle = 15°).

One EPI scan of 288 volumes was collected for typical phase encoding retinotopic mapping. A wedge stimulus (10 degrees of visual angle in radius and 90° in polar, respectively), with checkerboard patterns

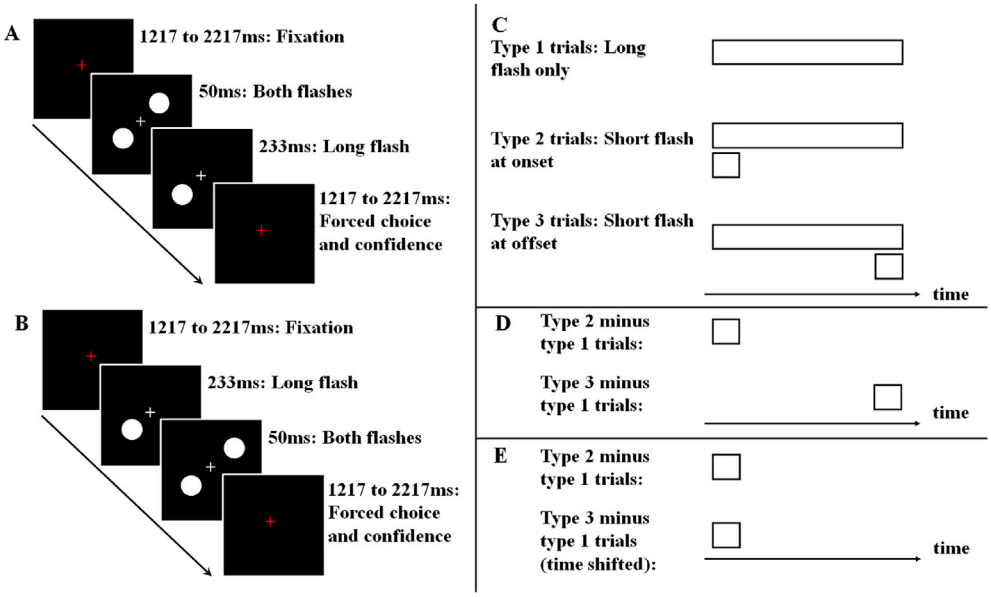

Fig. 1. Experimental paradigm. On each trial, participants were presented with a short (50 m s) and a long (283 m s) flash. Either onset (A) or offset (B) of the two flashes were synchronized. The physical luminance of the short flash was different from trial to trial. The task was to judge which of the two flashes appeared brighter and report confidence in that judgment. When onset is synchronized, the long flash is typically perceived as brighter if the two flashes have the same physical luminance (the Broca-Sulzer effect), but when offset is synchronized the short flash is typically perceived as brighter (the Temporal Context Effect, TCE). In order to compare MEG activity related to the perception of the short flash at onset and offset of the long flash without the activity related to the perception of the long flash as a confound, the long flash was presented alone on some trials (C). Activity on such trials was then subtracted from the other conditions (D), and finally the trials with the short flash at offset were shifted 233 m s in order to align the onset of the short flash to the onset on trials for which the short flash was presented synchronized to the onset of the long flash (E).

reversing at 5 Hz, was centered on a fixation point, cycling 15° per TR across the full visual field within 27.48 s clockwise in the first half scan and counter-clockwise in another half scan. In each direction, the wedge rotated 12 cycles in total.

Stimuli were presented by an MRI safe projector onto a 38.0×28.5 cm screen (resolution: 1024×768 pixels; refresh rate: 60Hz). The viewing distance was approximately 80 cm.

2.4. MEG data preprocessing

Using the MNE-Python package (Gramfort et al., 2013), data were band-pass filtered at 0.1–40 Hz. Trials were epoched as data ranging between 200 m s before stimulus onset and 600 m s after stimulus onset. MEG time courses of these trials were visually inspected, and trials with signals exceeding standard threshold (Magnetometer $> 5 \times 10^{-12}$ T) were rejected. Minimum 597 trials were retained among all the participants. The epoched data were downsampled to 500 Hz and were baseline-corrected between −200 and 0 m s.

2.5. Source reconstruction

Source-space activity time courses of each experimental condition were reconstructed with a unit-noise-gain linear constrained minimum variance (LCMV) beamformer (VanVeen et al., 1997; Sekihara and Nagarajan, 2008). This method creates a spatial filter, which provides an estimate of source response at a given location while suppressing influence coming from other sources. No a priori selection of expected activated sources is required, making it a well-suited method for multi-region brain source response reconstruction. Head model and forward computation grid of 2 mm isotropic were calculated based on individual T1 weighted MRI data. Head position coils and biological landmarks in the nasion and auricular points allowed for alignment of the MEG and MRI data. Freesurfer (Fischl, 2012) and the MNE software package were co-utilized in anatomical segmentation and co-registration.

A common data shrunk-covariance matrix (Engemann and Gramfort, 2015) was estimated for all experimental conditions from the sensor space epoched data in the time interval of 0–600 m s after stimulus onset, and noise covariance matrix was estimated from the baseline period of −200 m s–0 m s before stimulus onset. Apart from the bandpass filtering during preprocessing, the data were not additionally filtered before beamforming. The covariance matrices were regularized with the factor of 0.05. A common filter with same potential leakage was used for each experimental condition or contrast in order to reconstruct time courses of evoked data by taking norm power of the three orientations.

The evoked data were derived from either long-flash-only or short flash trials. The short flashes were contrasts of short flash subtracting long-flash-only trials before source reconstruction. Four non-zero levels of luminance as well as onset and offset synchronized short flashes were reconstructed separately.

2.6. Retinotopic mapping

MRI data were analyzed with AFNI software package (Cox, 1996), Freesurfer, and customized Python code. Functional images were corrected for motion distortion. The high-resolution T1 volume was co-registered to the mean volume of the corrected functional images. A cross-correlation method embedded in AFNI @RetinoProc was used to find the preferred polar angle position for each voxel. In addition to fMRI retinotopic mapping, a T1 anatomical based retinotopic mapping (Benson et al., 2012, 2014) was reconstructed as a reference. ROIs in the visual cortex (V1, V2, V3, V3ab, V4, VO, MT, and LO) were defined according to the functional and anatomical retinotopic maps on individual subject's inflated gray matter surface.

2.7. Statistical analysis

The differences between onset and offset synchronized short flashes of different luminances in behavioral and MEG experiments were tested using two-tailed paired T-tests across subjects provided by Scipy package (Oliphant, 2007). Statistical effects of the MEG data were further corrected for multiple comparison with cluster-based permutation test (Maris and Oostenveld, 2007) across the time course and different visual areas.

3. Results

3.1. Behavioral results

For each participant, the mean proportion of trials for which the short

flash was reported to be brighter than the long flash was calculated across luminances and temporal position of the short flash (whether it was presented synchronized to the onset or offset of the long flash). The group means are plotted in Fig. 2. A mean across all above-zero luminances was also calculated for the onset and offset conditions for all participants, and as expected the short flash at offset was more frequently reported as brighter than the long flash (67.0%, 95% CI: 58.1–75.9%) compared to the short flash at onset (53.0%, 95% CI: 42.0–64.0%). A *t*-test confirmed that this difference of 14.0% (95% CI: 6.5–21.6%) was statistically significant ($t(22) = 3.84$, $p < 0.001$).

3.2. Source analysis of the long and short flash representations

MEG sources were reconstructed respectively from individual-participant averages for the three analysis conditions mentioned in Materials and Method: long flash only (Figure S2A), onset synchronized short flash minus long flash only (Figure S2B), and offset synchronized short flash minus long flash only (Figure S2C). Before source reconstruction on short flash conditions, we subtracted long flash contributions in sensor space (Fig. 1C, D). This on one hand minimized irrelevant signal contaminations, and on the other hand avoided potential multiple source correlation in time (a leading constraint in adaptive spatial filtering method) (VanVeen et al., 1997). Time courses of the offset synchronized short flashes were shifted backward by 233 m s, so that both short flash conditions were temporally aligned (Fig. 1E). As shown in Fig. S3, cortical responses to onset and offset synchronized short flashes at different luminance levels were plotted separately in different visual cortical areas.

Source activity from the onset and offset synchronized short flash conditions was compared to delineate the neural correlates of the illusory effect. As shown in Fig. 3, significantly larger source activities from onset synchronized short flashes were observed compared to those from offset synchronized short flashes in LO and V4, peaking at 200 and 204 m s respectively ($t(14) = 4.24$, $p = 0.00081$; $t(14) = 3.69$, $p = 0.0024$). A later significant difference was observed only in V4, peaking at 250 m s ($t(14) = 3.05$; $p = 0.0086$), with activity being stronger for onset than for offset synchronized short flashes. Somewhat surprisingly, compared to perceptually dimmer onset synchronized short flashes, smaller responses in LO or V4 corresponding to perceptually brighter offset synchronized short flashes were evident throughout the late time window of

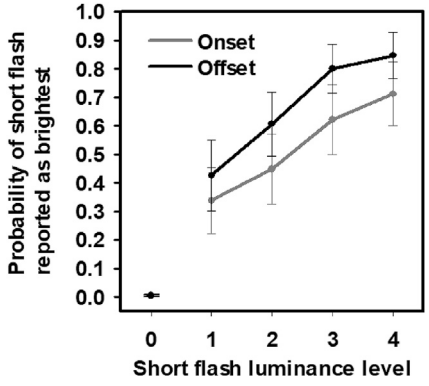

Fig. 2. Temporal Context Effect (TCE), behavioral data. The probability of reporting the short flash as brighter than the long flash is plotted across participants as a function of short flash luminance. The short flash has five luminance levels: 0, 0 cd/m^2, 1, 0.5 cd/m^2; 2, 5.8 or 7.8 cd/m^2; 3, 11.4 cd/m^2; 4, 16.7 cd/m^2. The short flash luminance level of zero corresponds to no short flash presented. Data are plotted separately for short flashes presented synchronized to the onset (gray line) and offset (black line) of the long flash. Note that for all non-zero luminances, the short flash at offset is reported as brightest more often than the short flash at onset, thus replicating the TCE. Error bars represent the 95% confidence interval of the group mean estimated from individual mean probabilities for each condition.

200–250 m s (see also in Supplemental Fig. S4, hemisphere-specific analysis). This finding nevertheless appears in line with some previous literature as we address in the Discussion.

We further compared differential brightness representations induced by physical luminances in visual cortical areas. As shown in Fig. S1, the physical luminances were divided into two groups: lower luminances consist of 0.5 cd/m^2 and 5.8 cd/m^2 (or 7.8 cd/m^2) luminance short flashes; and higher luminances consist of 11.4 cd/m^2 and 16.7 cd/m^2 luminance short flashes. From behavioral tests in Fig. 2, we observed that the higher luminances were reported more frequently brighter than the long flash compared to the lower luminances, indicating that the increase of luminance intensity was a linear factor of subjective brightness enhancement within the spectrum of luminance levels in this study. Source activity from the two groups of luminances were compared to further examine the dynamic neuronal response differences driven by differential physical input. As shown in Fig. 4, significantly stronger source responses to higher luminance was observed in V1, V2, V4, and VO peaking at 98, 98, 104, and 104 m s respectively ($t(14) = 8.26$, $p = 0.00000094$; $t(14) = 6.15$, $p = 0.000025$; $t(14) = 5.41$, $p = 0.000091$; $t(14) = 7.32$, $p = 0.0000037$). Further linear regression was conducted in the time window of 100 m s, showing a strong correlation between the change of luminance intensities and MEG responses in V1, V3, V4, and VO (see in Supplemental Fig. S6).

Taken together, only V4 activity was statistically significantly different for changes in perceived brightness induced by both illusion and physical luminance change (with differences in latency in the two cases). We discuss how this finding might be interpreted and its significance below.

4. Discussion

We investigated how the human visual system differentially processes luminance depending on temporal context, specifically how bright a short flash is perceived in the presence of a long flash, depending on whether the short flash is onset or offset synchronized with the long flash. Our behavioral data replicated the Temporal Context Effect (TCE) (Eagleman et al., 2004) across different luminance levels, showing that the offset synchronized short flashes are more frequently rated as brighter than a long flash compared to equiluminant onset synchronized ones.

Source reconstructed MEG brain activity related to onset and offset synchronized short flashes were compared to delineate the neural correlates of the illusory effect across selected occipital lobe areas. We observed strong TCE related responses in LO and V4 peaking at around 200 m s and 250 m s. No statistically significant differences were observed in other visual areas after correction for multiple comparisons. It is likely that during the early period of processing, neuronal responses to luminance are propagating from lower to higher visual areas. Since the two short flashes were physically identical in luminance and duration, no differences in terms of neuronal responses should be expected – at least in an early time window – in early retinotopic areas of the visual hierarchy. Integration of the propagated information is likely to be finished later in LO and V4, where the TCE related differences were detected, showing that the context dependent integration happens in a rather late stage of visual processing both spatially and temporally. This is consistent with previous findings showing that spatially higher visual areas are involved in illusory brightness representation (Perna et al., 2005; Bushnell et al., 2011; Ruff et al., 2018), but not the early visual cortex (Cornelissen et al., 2006).

But does this neural integration mechanism overlap temporally or spatially with physical luminance processing? We observed neuronal responses to physical luminances were mainly localized at around 100 m s across early visual cortex, such as V1, V2, and also in V4, VO. No statistically significant differences were observed in LO and V4 in the late time window of 200–250 m s. This indicates that a separate sensory process might account for brightness coding driven by physical energies,

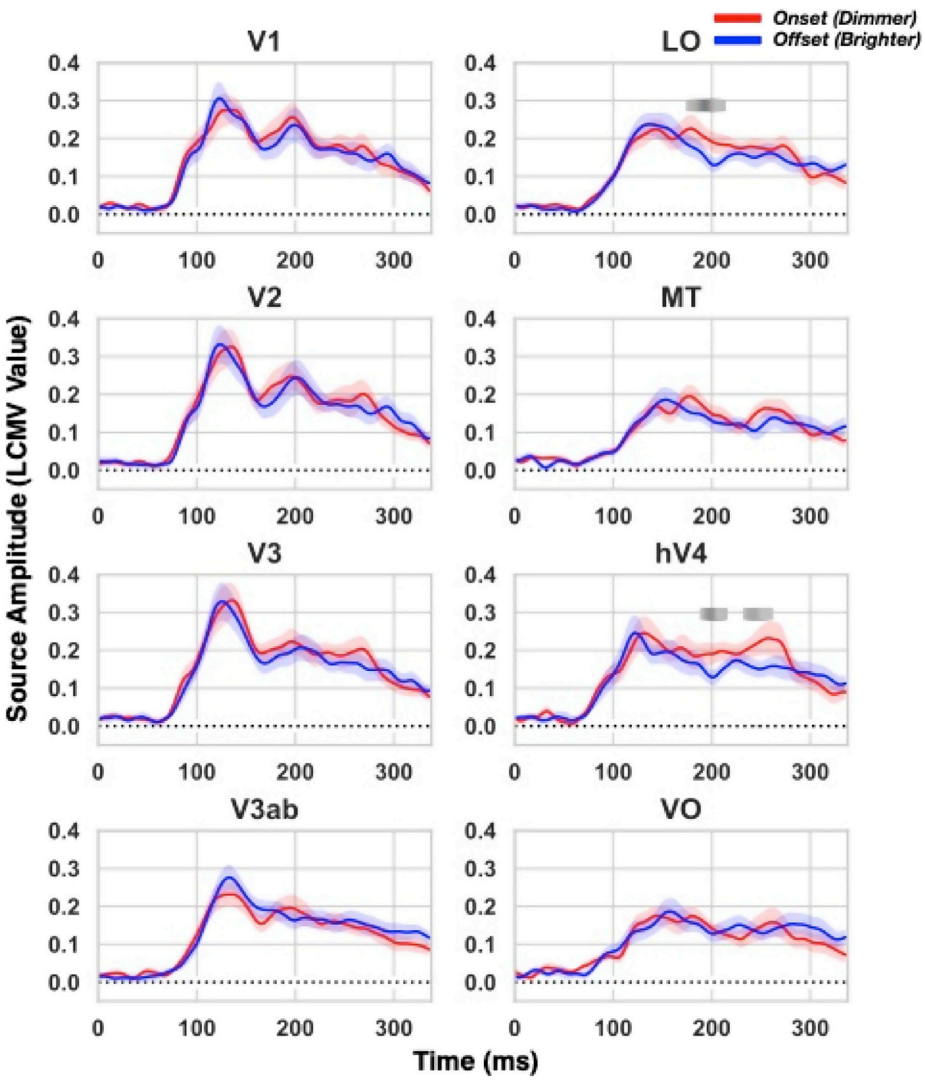

Fig. 3. Time aligned comparison between onset and offset synchronized short flashes. Sources derived from onset (red line) and offset (blue line) synchronized short flashes are plotted across difference visual areas, providing a direct comparison of the physically identical short flashes in different temporal context. Error bars represent one standard error of the group mean estimated from individual mean probabilities for each condition. The horizontal black bars represent time points at which source strength differed significantly ($p < 0.05$ after multiple comparison correction) between two types of experimental condition.

where early visual cortex as well as VO/V4 together compute luminance information into brightness percepts at an earlier stage of visual processing. These findings are broadly consistent with previous studies showing that brightness perception driven by physical luminance change correlates with neuronal responses in early visual cortex (Rossi et al., 1996; Rossi and Paradiso, 1999; Kinoshita and Komatsu, 2001; Haynes et al., 2004; Roe et al., 2005; Boyaci et al., 2007; Pereverzeva and Murray, 2008; Ruff et al., 2018). The current study uses subtraction logic to identify the neural correlate of the TCE brightness effect. One limitation of this subtraction method is that it ignores non-linear neuronal interactions. Future research can address this by including, for instance, a parametric manipulation of the lag between the short and long flash. Note that, in the current study, we report a significant correlation between participants' brightness reports and their MEG responses in the time window of 200–250 m s, suggesting that the MEG responses measured here did to some extent reflect brightness processing (See in Supplemental Fig. S5). Furthermore, linear regression was conducted in the representative time window of 100 m s, showing that a strong correlation of source amplitudes in V1, V3, V4, and VO (also noticeable in V2) with the increase of luminance levels.

The divergent findings for physical and illusory effects may be understood further in the context of theoretical work regarding V4 and in the context of the literature on M/EEG correlates of perceptual awareness, in particular the literature on Visual Awareness Negativity (VAN). According to Koivisto and Revonsuo (2010, p. 925), the VAN often starts shortly after 100 m s after stimulus onset, typically peaks at 200–250 m s, but can in some cases occur as late as 400 m s. A number of EEG and MEG studies have observed activity in this time window related to perceptual experience more than to physical stimulus characteristics (Koivisto and Revonsuo, 2010; Sandberg et al., 2013, 2014; Andersen et al., 2016). Particularly the MEG studies have shown clearly that the time window contains two peaks in the event related signal (e.g. both Sandberg et al. (2013) and Andersen et al. (2016) identified peaks at around 180–190 m s and 270–290 m s), but it is unclear what the role of each of those peaks are. It has also been difficult to establish whether one of the peaks is more consistently related to perceptual experience across paradigms than the other. For both peaks, however, it appears that activity in intermediate/higher stages of the visual processing hierarchy are the most predictive of perceptual experience at the single source level, yet lower stages of processing are equally predictive when multiple sources are combined in multivariate analyses (Sandberg et al., 2013). This last observation is consistent with our finding of V4 being related to the experience of brightness for both physical and illusion manipulations in the present study.

The stimulus driven differences in brightness perception coincide temporally with the earliest observations of the first VAN peak (often peaking 130–180 m s after stimulus onset) whereas the illusion driven differences coincide with the later part (often peaking 200–290 m s after onset). This is interesting when viewed in the context of recent theoretical work regarding the functional role of V4. Some recent evidences

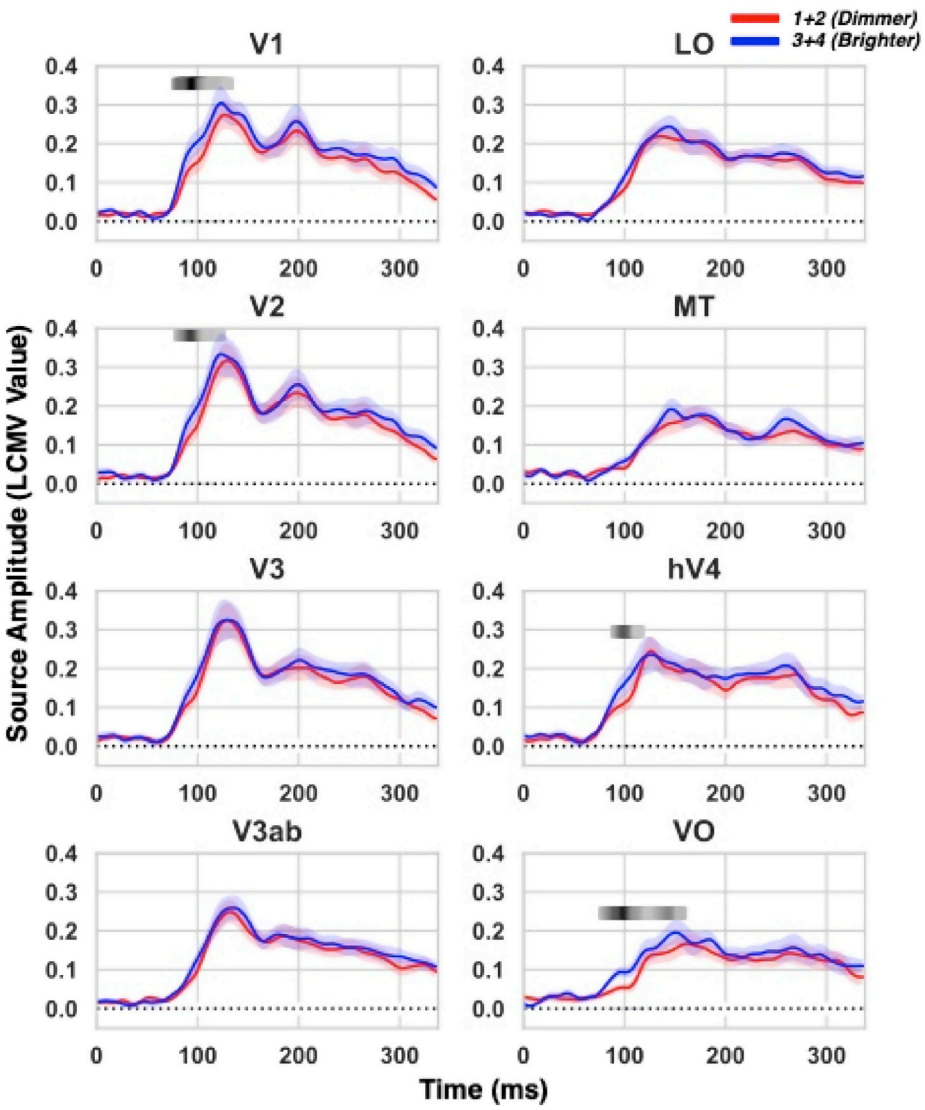

Fig. 4. Time aligned differences between lower and higher physical luminances across the visual cortex. Sources derived from lower (red line) and higher (blue line) luminance short flashes are plotted across different visual areas, providing a direct comparison of cortical representations of the physical luminances. Error bars represent one standard error of the group mean estimated from individual mean probabilities for each condition. The horizontal black bars represent time points at which source strength differed significantly ($p < 0.05$ after multiple comparison correction) between two types of experimental condition.

indicate that V4 plays a role in brightness coding (Bushnell et al., 2011; Ruff et al., 2018), but also in integrating various visual information, such as color, shape, depth, motion (Roe et al., 2012). Roe et al. (2012) emphasize that V4 is an area of importance in mediating bottom-up and top-down effects, and propose that feature representation in V4 is tightly linked anatomically/functionally to feature-specific networks, thus becoming a modulator of domain networks and enabler of selective feature extraction. When viewed in this context, they point out, there may be surprisingly little difference between object-induced effects and what they refer to as attentionally induced effects. The "surprisingly little difference" in our stimulus driven and illusion driven brightness enhancements could be thought of as the difference in timing: In the first case, the brightness modulation is established already in the part of the transient signal that is dominated by feedforward and local feedback signals whereas in the latter case, the brightness modulation is established slightly later when feedback from more distant areas are integrated.

That the temporally extended response correlates negatively with perceived brightness was surprising and contrary to our initial prediction. This result, however, is consistent with a previous electrophysiological study (Ruff et al., 2018) showing that V4 activity may, on average over an extended period, respond to subjectively brighter objects in a way that is opposite to early visual areas and opposite to the perceived brightness. One interpretation is that for more certain information, less energy/activity is required to encode at higher processing stages.

Given this surprising finding, we cannot rule out that ultimately brightness perception under the TCE may depend also on even higher-up areas, such as those in the temporal, parietal, and prefrontal cortices. Indeed, one of the features of the TCE was that the effect does not seem to be retinotopically specific; Eagleman et al. (2004) reported that the effect remained similar regardless whether the long and short flashes are spatially in the same quadrant or not. It should be noted that in order to get detailed information on distinct occipital areas, our MEG source reconstruction was guided by an fMRI localizer. This localizer we used is suitable for distinguishing occipital areas only, and our method thus limits us to examine these areas only, and not later, e.g. parietal/temporal, areas in the visual processing stream, or frontal areas. In order to examine areas higher up the stream, different localizers would have to be employed (Silver and Kastner, 2009). For this reason, we cannot conclude on the role of later areas such as the intraparietal sulcus (Perna et al., 2005), which might also be involved in brightness perception. Future studies may benefit from different experimental designs targeted for these higher regions.

Furthermore, it should be noted that, as always, the non-significance of the results in some of the examined occipital areas should not be interpreted as evidence of no involvement. It may indeed be that multiple areas are involved, but without significant results, our conclusions regarding V4 cannot be extended to these areas, and neither do we

conclude that V4 is the only relevant area.

It may also be noted that the TCE and other effects like it are at least to some extent contrast effects rather than (purely) brightness effects as a similar, but smaller, effect is observed in the other direction when the luminance of stimulus and background are reversed (Claessens et al., 2015).

Finally, the influence on the results of a number of processes that might differ between conditions should be considered. Binding and attention might differ between conditions, but since the stimuli are presented above the threshold of awareness in all conditions, it would be reasonable to expect that these processes do not differ substantially across conditions. Working memory is another candidate given the small, but consistent difference of 200 m s between percept and report. In the terminology of Aru et al. (2012), we might thus identify an NCC-co (a consequence of consciousness). This would, nevertheless, be a somewhat surprising explanation, as the time window we examine is often discussed in terms of whether it is an NCC or an NCC-pr (i.e. a prerequisite of consciousness) whereas typically later components like the P3a and P3b are discussed as potential NCC-cos. In addition, it is indeed a concern for future research to parametrically modulate the TCE to rule out confounding from other perceptual effects.

5. Conclusions

Taken together, our data indicate that V4 plays a critical role in dynamically integrating luminance information into brightness perception. We suggest that two distinct perceptual processes might be involved in brightness coding: one "low level process" which is energy driven; the other "high level process" which is context driven. The low level, energy driven process responds faster (dominated by lower visual cortices, such as V1/V2, also VO/V4), while the high level, context driven process responds much slower (dominated by higher visual cortices, such as LO/V4). Either process could alone (independently) have the capacity to influence subjective awareness of brightness. In a more complex natural scene, it is likely that both systems are working together in sensing and interpreting the physical world, possibly together with contribution from higher mechanisms in the temporal, parietal, and prefrontal.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116277.

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