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# The signature of undetected change: An exploratory electrotomographic investigation of gradual change blindness

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## Abstract

Neuroimaging-based investigations of change blindness, a phenomenon in which seemingly obvious changes in visual scenes fail to be detected, have significantly advanced our understanding of visual awareness. The vast majority of prior investigations, however, utilize paradigms involving visual disruptions (e.g., intervening blank screens, saccadic movements, “mudsplashes”), making it difficult to isolate neural responses toward visual changes cleanly. To address this issue in this present study, high-density EEG data (256 channel) were collected from 25 participants using a paradigm in which visual changes were progressively introduced into detailed real-world scenes without the use of visual disruption. Oscillatory activity associated with undetected changes was contrasted with activity linked to their absence using standardized low-resolution brain electromagnetic tomography (sLORETA). Although an insufficient number of detections were present to allow for analysis of actual change detection, increased beta-2 activity in the right inferior parietal lobule (rIPL), a region repeatedly associated with change blindness in disruption paradigms, followed by increased theta activity in the right superior temporal gyrus (rSTG) was noted in undetected visual change responses relative to the absence of change. We propose the rIPL beta-2 activity to be associated with orienting attention toward visual changes, with the subsequent rise in rSTG theta activity being potentially linked with updating preconscious perceptual memory representations.

This study represents the first neuroimaging-based investigation of gradual change blindness, a visual phenomenon that has significant potential to shed light

on the processes underlying visual detection and conscious perception. The use of gradual change materials is reflective of real-world visual phenomena and allows for cleaner isolation of signals associated with the neural registration of change relative to the use of abrupt change transients.

**Keywords:** change blindness, EEG, electrotopography, time-frequency, visual perception

## Introduction

Looking out of a window onto a busy street, we see people walking by, cars driving down the street, and perhaps even a plane or two flying high. Our moment-to-moment visual experience provides us with a subjective sense that virtually all aspects of our visual environment are perceived in an integrated, synchronous fashion. Nonetheless, a large body of research shows that a substantial amount of visual information in our environment fails to enter visual awareness (Huang et al. 2007). This point is readily demonstrated by the phenomenon of change blindness (Rensink et al. 1997), in which visual changes that are easily detected when explicitly pointed out nonetheless fail to be noticed by observers actively monitoring the target stimuli for change (Simons et al. 2000). Intriguingly, numerous studies have found evidence suggesting that despite not being consciously registered, undetected visual changes can often still be neurally registered (Busch 2013; Darriba et al. 2012) and exert an influence on subsequent behavioral outcomes (Ball et al. 2015; Busch 2013). These findings are in line with models proposing a graded view of visual awareness, particularly with regard to low-level visual stimuli (Nieuwenhuis and de Kleijn 2011; Overgaard et al. 2006; Windey et al. 2014).

The vast majority of prior change blindness neuroimaging investigations, however, have utilized visual disruption paradigms in which abrupt changes are introduced during blinks, saccades, intervening blank screens, movie cuts, or concurrently with onscreen “mudsplashes” (Simons 2000). Although these paradigms certainly capture instances of change detection failure and success, they may be less well suited to isolating the neural registration of change signals that fail to enter conscious awareness, in addition to the neural systems that are involved. One of the key reasons for the potential insensitivity of these paradigms is that the visual transients created by these disruptions may overwrite original scene information (Simons 2000)

as well as mask and draw attention away from change. For example, in saccade-contingent paradigms in which visual changes are introduced during saccadic movements, the smear of visual information on the retina likely serves as a global transient masking the change signal (Simons et al. 2000). These factors make it difficult to cleanly isolate signals associated with the neural registration of undetected visual change. Given that blindness to gradual change is driven by even basic phenomena such as motion (Saiki and Holcombe 2012; Suchow and Alvarez 2011), it is important to assess whether neural responses to the instantaneous visual changes utilized in disruption paradigms correspond with activity associated with gradual change processing in complex real-world environments. The need to examine gradual change processes is evidenced by visual change transients in real-world situations (e.g., incoming driving hazards in poor weather conditions; Hole 2007) and everyday social interactions (e.g., facial expression changes; David et al. 2006), which are often gradual in nature.

One paradigm that is ideal for isolating the neural signature of undetected visual changes is the gradual change blindness task in which visual changes are gradually introduced into a continuously presented scene, without the use of visual disruptions (Simons et al. 2000). Contrasting neural activity associated with present-but-undetected visual changes to activity associated with correctly classified absent changes has the potential to more cleanly isolate the neural signature associated with visual changes that are registered without entering conscious awareness. Building on this possibility, the present study utilizes high-density EEG to contrast these response conditions using a gradual change blindness paradigm with detailed, ecologically valid visual scenes.

Because all scenes in this study are presented under free-viewing conditions, the temporal smearing of the visual registration of presented changes precluded the use of phase-locked-based event-related potential measures. Instead, tomographic analysis of induced oscillatory activity within bounded temporal windows during the scene-viewing intervals is utilized. The source analysis of oscillatory activity was conducted using standardized low-resolution brain electromagnetic tomography (sLORETA), an improvement of the widely used LORETA algorithm (Pascual-Marqui et al. 1994). In addition to being extensively used to estimate neural generators of evoked potentials (Pascual-Marqui et al. 2002), sLORETA is also widely used to estimate generators of neuronal oscillations (Meltzer et al. 2009; Yun

et al. 2012) from multichannel surface recordings. Results from the sLORETA method are supported by combined imaging methods such as EEG-functional MRI (fMRI) (Meltzer et al. 2009) and EEG-PET (Pizzagalli et al. 2003).

On the basis of previous work that has examined change blindness as it relates to time-frequency activity in visual disruption-based designs (Darriba et al. 2012; Park et al. 2010), the two primary bandwidths of interest in this study lie in the beta and theta range. Both Darriba et al. (2012) and Park et al. (2010) utilized successive display paradigms to assess time-frequency-related activity associated with change blindness-related responses. Darriba et al. (2012) utilized sinusoidal gratings with changes in orientation, whereas Park et al. (2010) employed face stimuli with changes in facial features. Both investigations found post-change activity in the beta and theta bandwidths to be implicated in change detection and blindness responses. Scalp-level beta activity was associated with the presence of change regardless of detection in Darriba et al. (2012), and only with conscious detection in Park et al. (2010). Theta activity, on the other hand, was associated with the conscious detection of change in both studies. Darriba et al. (2012) also found differences in activity in the beta range to precede theta-related effects.

Apart from these two change blindness studies (Darriba et al. 2012; Park et al. 2010), other investigations have also linked beta activity, particularly over posterior regions, with visual detection performance (Krancioch et al. 2007) and attentional arousal in the visual system (Gola et al. 2013; Kamiński et al. 2012). The results of this prior work are in line with proposals of beta-band activity being one of the primary communication bandwidths within the visual-attentional network (Gross et al. 2004; Wróbel 2000).

With regard to the link between theta activity and visual change detection (Darriba et al. 2012; Park et al. 2010), other researchers have also found theta activity to play an important role in visual attention (Fan et al. 2007). Frequently this activity has been linked to visual working memory load (Boonstra et al. 2013) and other aspects of visual memory capacity (Vandenbroucke et al. 2015). Notably, with regard to both of these bandwidths, recent work has implicated engagement of right parietal region-focused functional beta and theta networks in visual stimulus discrimination, with suppression of these networks linked to symptoms of visual neglect (Yordanova et al. 2016). Additional support for the involvement of activity in

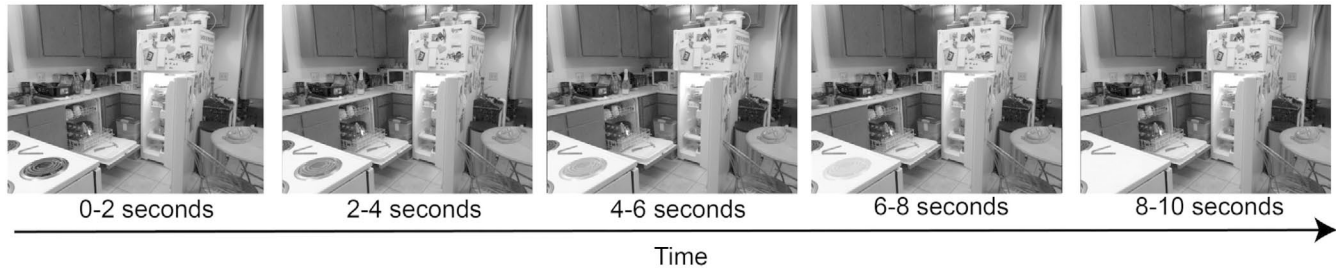
the right parietal region with change blindness-related phenomena comes from fMRI investigations that found activation in parietal lobe regions in change detection (Beck et al. 2001; Pessoa and Ungerleider 2004) and undetected change registration (Pessoa and Ungerleider 2004). Transcranial magnetic stimulation (TMS)-induced disruption over this area has been shown to directly increase change blindness rates (Beck et al. 2006; Tseng et al. 2010), reduce conscious perception reports (Babiloni et al. 2007; Kihara et al. 2011), and disrupt visual working memory (Morgan et al. 2013). Prior work has also shown that TMS to the right parietal region triggers subjective disappearances of visual stimuli (Kanai et al. 2008) or a hemineglect-like profile (Hilgetag et al. 2001).

In summary, the current study represents the first neuroimaging-based investigation of gradual change blindness. Participants free-viewed a series of environment scenes, a subset of which contained gradual visual changes. To preface our results, participants in this study did not detect changes on a sufficient number of trials to allow for strong conclusions regarding the neural signature of conscious change detection. We were, however, able to contrast neural activity associated with processing scenes in which no visual changes occurred with the processing of scenes in which gradual visual changes were present but undetected, thereby isolating activity associated with the neural registration of visual change in the absence of conscious awareness.

## **Materials and Methods**

### *Participants*

Twenty-five participants (13 women, 12 men; age =  $19.69 \pm 1.30$  yr, mean  $\pm$  SD, range 18–22 yr) were recruited from the research subject pool at the University of Nebraska-Lincoln, receiving course credit and \$10 for their participation. All experimental procedures were submitted to and approved by the University of Nebraska Lincoln Institutional Review Board and carried out in accordance with the board's guidelines and regulations for human subjects. All participants provided written informed consent after receiving a detailed explanation of the experimental procedures, had normal or corrected-to-normal vision, and reported right-handed dominance as measured by the Edinburgh Handedness Inventory (Oldfield 1971).



**Fig. 1.** Sample change stimuli movie. All changes were presented in a continuous graded fashion over 8 s after an initial 2-s baseline interval. Images on the task were presented in full 24-bit color.

### *Task procedure*

The experiment was conducted in a single 30-min session. Participants viewed a total of 60 scenes presented as 10-s-long movies (Fig. 1), with a 2-s blank screen presented in between each scene. In 40 of the 60 scenes, after a 2-s interval in which no changes occurred, a single object gradually faded into the screen, changed color, or faded out of the screen over the remaining 8 s. Multiple types of change were used so that participants were unable to anticipate a specific change type and instead were required to monitor broadly for any alteration to the scene. No scene changes were present in the remaining 20 scenes. Change and no-change trials were randomly intermixed.

All presented changes were sufficiently gradual to not produce a strong visual transient while simultaneously being easily detectable when directly attended to. Participants received instruction to monitor the scenes for changes and were given verbal examples of the possible change types. Before the test trials, observers received three practice trials (one of each change type: appearance, disappearance, color change) in which the location of the change was identified in advance. Participants responded on a button box the instant they detected a change occurring on screen. All stimuli were  $1,440 \times 810$  pixels ( $38.25 \times 21$  cm) on a  $1,920 \times 1,080$ -pixel LCD monitor (size:  $51 \times 28$  cm; 60-Hz refresh rate), occupying  $21.65^\circ$  of horizontal and  $16.28^\circ$  of vertical angle from a viewing distance of 100 cm.

### *EEG data acquisition*

Data were recorded using a Hydrocel Geodesic Sensor Net (256 high-density AgCl electrodes) connected to a high-input impedance NetAmps 300 amplifier using Net Station version 4.4.2. Participants were seated 1 m away from the presentation monitor and made responses

via button box. Recordings were collected using a vertex sensor (Cz), later re-referenced to an average reference. Electrode impedances were below 40 k $\Omega$ , a level appropriate for the system that had been designed to accommodate high impedances. The data were analog filtered from 0.1 to 100 Hz and digitized at 1,000 Hz.

### *EEG preprocessing*

The ongoing EEG from participants was first digitally filtered in using a 0.3- to 30-Hz zero-phase shift finite impulse response bandpass filter. The Automatic Artifact Removal (AAR) toolbox (Gomez-Herrero et al. 2006) was used to reduce ocular and electromyographic artifacts using spatial filtering and blind source separation. The data were then segmented into 10-s intervals with each segment beginning at the onset of a scene stimulus presentation. Bad channels were then identified across all segments for each participant via their poor overall correlation ( $<0.40$ ) between neighboring channels. Bad channels were also identified within each segment via either unusually high differences between an electrode's average voltage and that of its neighbors ( $>30 \mu\text{V}$ ) or by extreme voltage differences within an electrode ( $>100 \mu\text{V}$  minimum to maximum). A channel was also rejected if more than 20% of its segments were classified as being bad. All identified bad channels were replaced using whole head spline interpolation.

After the identification and interpolation of bad channels, trials with more than 10% interpolated channels were discarded. All participants had a minimum of 14 retained trials ( $25.08 \pm 7.36$ ) in each of the two critical conditions (change not detected,  $31.68 \pm 4.05$ ; no change,  $18.48 \pm 1.90$ ). The number of trials per condition was deemed acceptable for reliable fast Fourier transform (FFT)-based frequency analysis on the basis of prior work in the area indicating 20–30 trials to be a sufficient trial range (Frank et al. 2015). The number of detected changes ( $7.68 \pm 4.27$ ) and false alarms ( $1.32 \pm 1.75$ ) was deemed insufficient for reliable spectral analysis. Retained segments were then re-referenced to an average reference configuration and divided into five 2-s epochs (0–2, 2–4, 4–6, 6–8 and 8–10 s post-stimulus onset, respectively).

### *sLORETA analysis*

Standardized low-resolution brain electromagnetic tomography (sLORETA) was used to localize the cortical source generators of scalp-recorded activity in five frequency bands: theta (6.5–8 Hz), alpha



(8.5–12 Hz), beta-1 (12.5–18 Hz), beta-2 (18.5–21 Hz), and beta3 (21.5–30 Hz). The Talairach coordinates of the 256 electrode positions of the EGI Hydrocel system were first used to compute an sLORETA transformation matrix. Following transformation to an average reference, the EEG activity of cross-spectra of each participant by condition and time window was then computed (Frei et al. 2001) and transformed using the transformation matrix into sLORETA files containing the three-dimensional (3D) cortical distribution of cortical generators. sLORETA computations were carried out using a 3-shell, 6,239-voxel, 5-mm-resolution head model by using the MNI152 template with the 3D solution restricted to gray matter in Talairach space. Differences in oscillatory cortical sources between groups in each frequency band were assessed via voxel-by-voxel nonparametric mapped permutation within-subjects *F*-ratio tests with a global frequency-wise normalization. Correction for multiple testing for all voxels and frequency bands was implemented via nonparametric randomization (5,000 permutations) with the threshold set to  $P < 0.01$ .

## Results

### *Behavioral analysis*

The change detection hit rate (HR) was  $19.20 \pm 2.14\%$  (mean  $\pm$  SE) with a  $6.60 \pm 1.75\%$  false alarm (FA) rate. Hit and FA rates were uncorrelated [Pearson  $r(23) = 0.260$ ,  $P = 0.210$ ] but significantly different within participants [ $t(24) = 5.288$ ,  $P = 0.000$ ,  $d = 1.067$ ]. Signal detection measures indicated above-chance detection performance with a conservative bias ( $A = 0.696$ ,  $B''_d = 0.967$ ). Change detections were significantly correlated between each change category type [disappearance and appearance,  $r(25) = 0.574$ ,  $P = 0.003$ ; appearance and color change,  $r(25) = 0.455$ ,  $P = 0.022$ ; color change and disappearance,  $r(25) = 0.495$ ,  $P = 0.012$ ]. Participants exhibited significantly higher detection rates for changes involving the disappearance of scene elements (HR =  $24.50 \pm 0.03\%$ ) relative to appearance [HR =  $16.00 \pm 0.02\%$ ;  $t(24) = 3.630$ ,  $P = 0.001$ ] or color changes [HR =  $15.56 \pm 0.03\%$ ;  $t(24) = 3.428$ ,  $P = 0.002$ ], with no significant difference in HR between the last two change categories [ $t(25) = 0.170$ ,  $P = 0.866$ ]. These results should be viewed with caution given that although changes in the stimuli were designed to be difficult to detect, the materials were not piloted to ensure the parameters of the change stimuli were equivalent across all change categories.

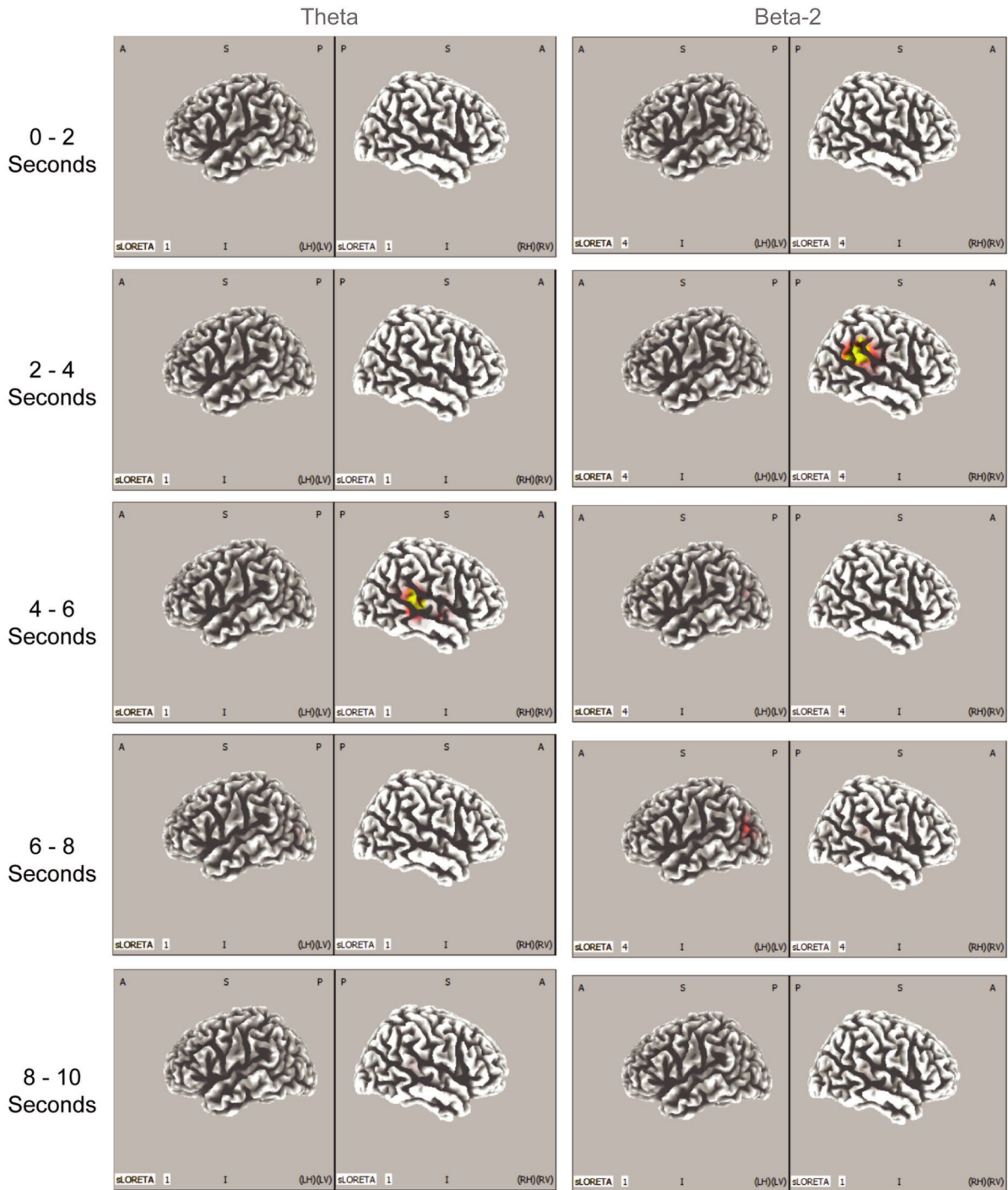
### *sLORETA results*

All analyses contrasted conditions of undetected visual change (miss) and correctly rejected no visual change (correction rejection). Correction for multiple testing for all voxels and frequency bands was implemented via nonparametric randomization (5,000 permutations) with the threshold set to  $P < 0.01$ . No significant differences were observed between the conditions in any of the investigated frequency bandwidths in the baseline viewing interval (0–2 s) during which no visual changes were present in either condition. The initial introduction of change in the 2–4 s time window was, however, accompanied by significantly higher levels of beta-2 activity (18.5–21 Hz), localized to BA40 [right inferior parietal lobule (rIPL); MNI coordinates:  $X = 65$ ,  $Y = -40$ ,  $Z = 30$ ; nonparametric permutation-corrected  $P = 0.005$ ,  $\log F$  threshold = 0.540], in miss responses (change present without conscious detection) relative to correct rejections (no change present with no false alarm) (Fig. 2). A slight increase in beta-2 in BA39 (left middle temporal gyrus, MNI coordinates:  $X = -55$ ,  $Y = -70$ ,  $Z = 25$ ) was also observed in the 4–6 s time window that failed to surpass the  $P$  value-corrected threshold (nonparametric permutation-corrected  $P = 0.064$ ,  $\log F$  threshold = 0.572).

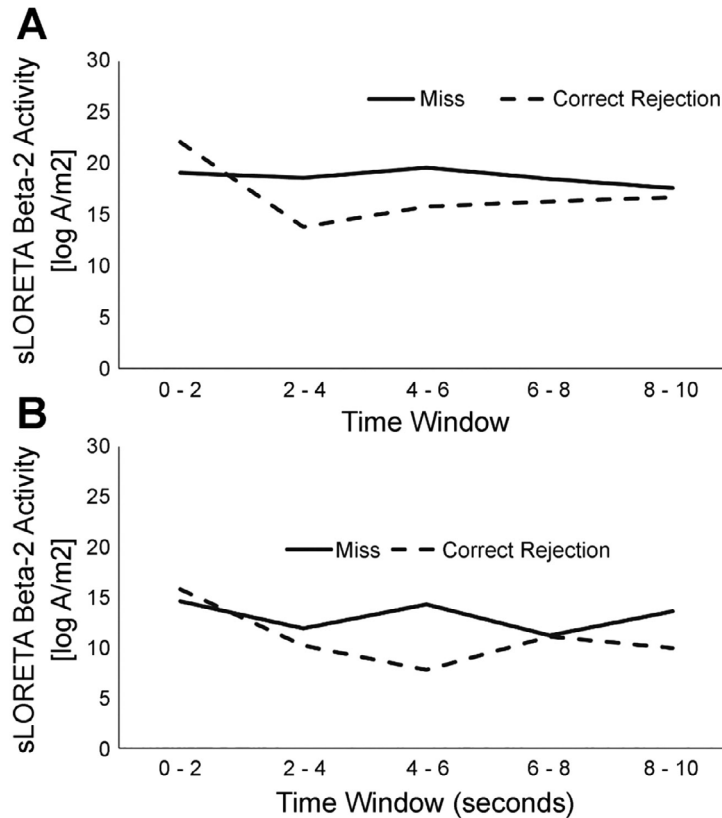
Progression of change in the 4–6 s window was accompanied by significantly higher levels of theta activity (6.5–8 Hz), localized to BA22 [right superior temporal gyrus (rSTG); MNI coordinates:  $X = 70$ ,  $Y = -35$ ,  $Z = 10$ ; corrected  $P = 0.009$ ,  $\log F$  threshold = 0.572], in miss relative to correction rejection responses (Fig. 2). Plots of sLORETA current density in the rIPL and rSTG as a function of time window are presented in Fig. 3. No significant differences were noted in the 6–8 and 8–10 s time windows in any of the analyzed bandwidths.

## **Discussion**

The results of this study show significant changes in EEG cortical activity in response to gradual visual changes that failed to reach conscious awareness. During the initiation of visual change, increased beta-2 activity, localized to the rIPL, was observed in undetected-change miss responses relative to no-change correct rejections. This shift was followed by increased levels of theta activity that localized to the rSTG. These interconnected (Karnath 2009) regions have been independently and jointly (within the temporoparietal junction) implicated in a wide range of attention and change related phenomena.



**Fig. 2.** Electrotomographic results. Shown are differences in EEG power spectra within the theta (6.5–8 Hz; A) and beta-2 (18.5–21 Hz; B) bandwidths between miss and correct rejection responses in the analysis time windows, corrected for multiple comparisons using a nonparametric permutation test. Areas in yellow and red/orange indicate voxels significant at the  $P \leq 0.01$  and  $P \leq 0.10$  levels, respectively ( $n = 25$ ). A, anterior; S, superior; P, posterior; I, inferior.



**Fig. 3.** Changes in sLORETA current density over the 5 time windows in the right inferior parietal lobule (MNI coordinates:  $X = 65$ ,  $Y = -40$ ,  $Z = 30$ ) in the beta-2 (18.5–21 Hz) range (A) and in the right superior temporal gyrus (MNI coordinates:  $X = 70$ ,  $Y = -35$ ,  $Z = 10$ ) in the theta (6.5– 8 Hz) range (B).

Activity in right parietal regions has been linked with visual change registration (Beck et al. 2001; Pessoa and Ungerleider 2004), with the application of repetitive TMS to the region being associated with increased change blindness (Beck et al. 2006; Tseng et al. 2010) and visual search and perception disruption (Kanai et al. 2008), as well as symptoms of spatial neglect (Hilgetag et al. 2001). The rIPL specifically has been shown to play a key role in visual attention and has been implicated in visual-spatial neglect (Verdon et al. 2010). Though the rIPL was initially viewed as part of the dorsal stream, subsequent work soon showed the rIPL did not fit well into a pure dorsal role and possibly serves as a nexus between dorsal and ventral systems (Milner and Goodale 2006). In addition to likely playing a role in spatiotemporal integration (Shapiro et al. 2002), the rIPL has repeatedly been implicated in responding to novel (Gur et al. 2007) and threshold-level

stimuli (Park et al. 2014). Of particular relevance to the current study, the rIPL has been implicated in orienting spatial attention (Yin et al. 2012), particularly with regard to orienting attention toward changes in unattended (Corbetta et al. 2000; Yin et al. 2012) and unexpected (Kincade et al. 2005) locations. Additional evidence for this role comes from research demonstrating the application of TMS to this region to be associated with impaired orientation of visual attention to stimuli presented outside the current attentional focus (Kihara et al. 2011).

In line with the varied roles of the rIPL, center-posterior beta activity, which in one prior study localized directly to the rIPL (Volberg and Greenlee 2014), has also been linked with the visual integration of information (Volberg and Greenlee 2014), visual detection (Kranczioch et al. 2007), and attentional arousal (Gola et al. 2013; Kamiński et al. 2012). In line with these findings, beta activity has been proposed as a potential candidate carrier signal for visual attention (Gross et al. 2004; Wróbel 2000).

Fluctuations in beta activity have also been previously linked with change blindness (Darriba et al. 2012; Park et al. 2010). The first of these investigations was conducted by Darriba et al. (2012), who showed suppression of beta activity in the presence of change independent of conscious detection. The second was conducted by Park et al. (2010), who did not examine beta differences between change-blind and change-absent conditions but did note increases in beta activity to be associated with change detection. Collectively, these findings suggest that beta activity plays a key role in the conscious and subconscious change registration.

Given that differences in stimuli presentation methods exert significant dissociative influences on beta activity enhancement and suppression (Güntekin and Tülay 2014), numerous methodological differences between the studies by Darriba et al. (2012) and Park et al. (2010) and the current study make it difficult to draw firm conclusions on the factors underlying observed differences in this frequency range. The pattern of beta-2 fluctuations, in combination with their localization to the rIPL, does suggest this effect is driven by maintenance of beta-related activation in this region in the presence of change relative to its absence. Speculatively, this result may be related to activity associated with integrating the incoming visual change information (Kranczioch et al. 2007; Volberg and Greenlee 2014) into the presented scene. It is also possible that the presence of change might have boosted levels of visual attention oriented toward the scene via

low-level registration of the visual change signal (Gross et al. 2004; Wróbel 2000). Given that this study was not able to analyze the shift in signal induced by actual gradual change detection, however, further study is needed to test these potential hypotheses.

The results of this study also show increased levels of theta activity localized to the rSTG. Similarly to the rIPL, the rSTG has also been proposed to be an interface between dorsal and ventral streams (Karnath 2001; Park et al. 2011). The region has been associated with many aspects of visual attention (Corbetta et al. 2008; Shapiro et al. 2002), including attention reorientation (Thiel et al. 2004), exploratory visual search (Ellison et al. 2004; Gharabaghi et al. 2006), visual encoding (Demiral et al. 2012), and spatial neglect-related phenomena (Ellison et al. 2004; Karnath 2001). Within this body of work, it is interesting to note that theta activity in the rSTG has been specifically linked with visual attention, particularly alerting-related processes (Fan et al. 2007). Collectively, these prior findings suggest that the post-change initiation rSTG theta activity observed in this study may be associated with a graded (Nieuwenhuis and de Kleijn 2011; Overgaard et al. 2006; Windey et al. 2014) registration of visual transients that fail to meet the threshold for conscious awareness. In line with links between the rSTG, visual encoding, and retrieval (Demiral et al. 2012), as well as strong associations between theta activity and visual memory functions (Boonstra et al. 2013; Vandenbroucke et al. 2015), it is also possible that the increase in theta activity may reflect the contextual updating of preconscious aspects of visual memory (Baars and Franklin 2003) to incorporate the presented changes into the post-change scene representation. Both of these interpretations are in line with theta-related findings noted by prior change blindness investigations by Darriba et al. (2012) and Park et al. (2010) as well as with the pattern of observed change in the theta signal in this region over time. Again, given that this study was not able to assess changes in theta activity as a function of actual change registration, further work is needed to assess these hypotheses.

Both the rIPL and rSTG have been proposed to play a key role in biasing information flow within both the ventral and dorsal streams (Shapiro et al. 2002). Collectively, these two areas make up a large portion of the right temporoparietal junction (rTPJ) which, in line with the prior discussion, is also believed to play a key role in the stimulus-driven or bottom-up “circuit-breaking” attentional processing to reorient attention toward task-relevant but currently unattended

stimuli (Corbetta et al. 2008; Shulman et al. 2007). In support of this view, electrical stimulation of this region has also been associated with improved detection of threshold visual stimuli (Beauchamp et al. 2012). Other researchers, however, have recently argued that processing-related timing issues suggest that activation in the rTPJ region may instead reflect contextual updating or the integration of internal representations of the current context with new incoming sensory information (Geng and Vossel 2013). The present results are consistent with the notion that both perspectives are correct, with an early alerting response in rIPL being soon followed by contextual representation updating via involvement of perceptual memory-related processing in the rSTG.

In summary, the present study provides the first demonstration of gradual undetected visual changes in the environment having a significant moderating influence on activity in neural bandwidths and regions associated with visual attention. In support of prior proposals of change detection processing (Beck et al. 2001; Corbetta et al. 2008), neural activity associated with undetected change registration was localized to regions associated with dorsal and ventral stream integration, the rIPL (Milner and Goodale 2006; Shapiro et al. 2002) and rSTG (Karnath 2001; Park et al. 2011; Shapiro et al. 2002). Speculatively, it is possible that the observed beta-2 activity in the rIPL may be involved in deploying visual attention toward gradual visual changes in the environment, with subsequent levels of increased theta activity in the rSTG being associated with updating preconscious contextual representations in perceptual memory. Further work is needed to test these potential hypotheses.

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**Author contributions** — JEK and MDD conceived and designed research; JEK and JEC performed experiments; JEK analyzed data; JEK interpreted results of experiments; JEK prepared figures; JEK drafted manuscript; JEK, MDD, RFB, and JEC edited and revised manuscript; JEK, MDD, RFB, and JEC approved final version of manuscript.

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