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Fasttrack article

Induced gamma activity is associated with conscious awareness of pattern masked nouns

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Abstract

The aim of this study was to explore the relationship between electroencephalographic (EEG) activity in the gamma frequency range and conscious awareness of a visual stimulus. EEG was recorded from subjects while they were shown backward-masked words only some of which they were able to discriminate correctly. The results showed that activity in the gamma frequency range increased with reported awareness of a word independently of whether it was correctly discriminated or not. It is concluded that gamma power is associated with awareness-dependent visual processing but not with processing that occurs in the absence of awareness.

Keywords: Electroencephalography; Gamma oscillations; Pattern masking; Awareness; Consciousness; Subjective reports

1. Introduction

The awake observer perceives the visual world as an organised, coherent field of objects, textures and colours. An object, for example a red book lying on a wooden table, is perceived as a perceptual gestalt despite the fact that the cells representing its different features (e.g. colour, form, location) may be spatially distributed in the brain. In order to provide us with a perceptual gestalt of such a visual image, there must be a mechanism that functionally associates or 'binds' these disparate visual features together. This is the so-called *binding problem*. One candidate mechanism for performing this function is the temporal correlation of neural responses in posterior cortex at frequencies in the gamma frequency range (30–80 Hz) (Gray et al., 1989; Singer and Gray, 1995; Rodriguez et al., 1999).

It has further been proposed that there is a close link between this feature-binding mechanism and the establishment of conscious mental states (Joliot et al., 1994; Crick and Koch, 1990). Notably,

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Crick and Koch (1990) have suggested that synchronous oscillations in the gamma frequency range may be necessary for the entry of sensory information into conscious awareness. In the decade since this conjecture was first made, however, little evidence has appeared in support of the strong hypothesis that synchronous gamma oscillations are 'causally implicated' in sensory awareness (Gold, 1999) and Crick and Koch have distanced themselves from their original proposal (Crick and Koch, 1998).

Notwithstanding this, some evidence does support the suggestion that gamma oscillations play a role in conscious awareness. Joliot et al. (1994), using magnetoencephalography, showed that two auditory clicks were capable of inducing separate gamma responses only when they were presented with an interstimulus interval above that at which subjective experience of two clicks was reported. Below this threshold, the two clicks induced a single gamma response, just like a single stimulus. Tallon-Baudry et al. (1997) report an experiment in which subjects viewed 'cloze' figures, in which a stimulus hidden in what appears to be a display of meaningless 'blobs' becomes subjectively visible only after the viewer has been alerted to its presence. Gamma activity associated with this stimulus was increased after subjects had been made aware of the stimulus. In animal studies, Fries et al. (1997) report that synchrony at gamma is correlated with conscious perception during interocular rivalry.

The aim of the present study was to examine the relationship between awareness and synchronous gamma oscillations, using a backward masking paradigm. It has been shown that a masked stimulus can influence response at the neural or behavioural level under conditions in which awareness is not reported (Macknick and Livingstone, 1998; Marcel, 1983; Dehaene et al., 1998). Masking paradigms have been used to distinguish between those brain processes that are dependent on awareness and those that are not. It has been proposed (Jack and Shallice, 2001) that while the process that control reflection on the nature of an experience, for example the thought ''I was aware of x'', is dependent on awareness of stimulus, correct discrimination of the identity of a masked stimulus from a small number of fixed choices does not require awareness. We predicted that synchronous gamma oscillations would occur in association with awareness-dependent processes, such as reported awareness, but not in association with awareness-independent processes, such as forced-choice discrimination.

2. Methods

2.1. Subjects

Thirteen volunteers (6 men, 7 women) aged 18–37 with normal or corrected-to-normal vision participated in the experiment. None had a history of neurological or psychiatric disease. Prior to commencing the study, ethical approval was obtained and all participants provided informed, written consent.

2.2. Procedure

The electroencephalograph (EEG) was recorded while participants viewed backward pattern masked words presented on an IBM compatible PC. Backward masking was at eight regularly spaced stimulus-mask onset asynchrony (SOA) intervals between 8 and 67 ms. Two additional trial types were also employed: one in which no stimulus was presented, and one on which no mask was presented.

For each trial a central fixation point was presented for 1300 ms, followed by a blank screen for 400 ms and then the stimulus word. The stimulus word remained on screen for 8 ms. In the 8 ms SOA masking condition the stimulus word was followed directly by the mask. Otherwise, the screen was left blank until mask onset. The mask remained on screen for 200 ms. The screen was then blank for 2000 ms. A prompt then appeared requiring subjects to press one of four buttons with their left hand to report their state of awareness (see below). Immediately after this response was made, two words were displayed to the left and right of fixation, the stimulus word and a distracter. The participant was required to identify the stimulus word by pressing one of two buttons with their right hand. The stimulus word appeared on each side with equal frequency. Words were between 4 and 7 letters long with a mean length of 4.7 letters.

Trials were presented in 8 blocks of 40 trials. Participants experienced two different types of trial blocks, which were interleaved using a counter-balanced latin-square design. For blocks in the *bottom–up* condition, each trial involved a novel stimulus word and distracter word. In the *top–down* condition the same two words were used on every trial of the block, with each word acting as the stimulus word for half the trials. The order of trials within blocks was randomised for each subject.

Stimulus and distracter word pairs were matched for frequency. All were high-frequency nouns printed in upper case. The mask was selected at random on each trial from a set of four non-letter symbol strings. All stimuli were displayed in white on a black background.

2.3. Subjective report categories

The response categories in which subjects reported their awareness of the masked word were based on the results of a pilot study that consisted of a brief version of the procedure described above. In the pilot study, participants were able to make responses using up to 10 subjectively determined categories of awareness and were encouraged to describe their subjective experience of the stimulus. This procedure was adopted to establish a standardised model by which subjects might interpret their own experiences and communicate them accurately to the experimenter. It is argued that an adequate model is essential for the collection of reliable self-report data (Jack and Shallice, 2001). Inspection of response and transcribed verbal data from the pilot study suggested that subjective experience of the masked stimuli in this experiment could be best classified into four categories. These are listed below. These categories were explained to subjects prior to the main experiment. The words shown in brackets were presented as a prompt to subjects on every trial.

1. The stimulus could be clearly seen and identified (clearly visible)
2. The stimulus was not clear, but could be seen sufficiently well for the subject to be confident of the identity of the word (identification)
3. There was some partial conscious visual information about the stimulus, or a 'hunch' about the identity of the word (letters or shape)
4. There was no conscious information whatsoever about the stimulus, and the most the subject experienced was the impression that something may have appeared prior to the mask (flash/nothing)

Participants were asked to pay particular attention to their use of category 4 and were instructed ''It is very important that you only use this category when you have no conscious information at all which might allow you to identify the stimulus''. This was emphasised in the attempt to prevent participants from responding that they were unaware when in fact they only lacked confidence in their awareness report. For clarity the four categories are described here as (1) *clearly visible* (2) *identified* (3) *something* and (4) *nothing*.

2.4. EEG recording and analysis

EEG was recorded in a sound-attenuated and electrically shielded testing chamber from 28 scalp sites using an ECI electrode cap fitted to the subject's head with a ground electrode placed 1.5 cm anterior to the vertex. Vertical and horizontal electrodes were placed above and below the right eye and laterally from both eyes. A reference electrode was placed on the left ear but all EEG data were converted to average reference prior to analysis. Recording and digitisation were carried out using a Neuroscan Synamps amplifier with signal bandpass 0.15–100 Hz with a sampling rate of 500 Hz. Impedances were kept below 10 kΩ. The results reported below concern data from four electrode sites: midline parietal (Pz), midline occipital (Oz) and left and right temporal (T5 and T6, respectively).

After exclusion of epochs contaminated with artefact the EEG was subjected to a wavelet analysis. This produced a time–frequency decomposition giving estimates of signal amplitude (i.e.

square root of power) across the gamma frequency range with high temporal resolution.

The wavelet analysis involved the convolution of the EEG by complex Morlet's wavelets that have a Gaussian shape in both the time and frequency domain (Torrence and Compo, 1998). Wavelets were normalised so that their total energy was 1 and the internal frequency, ω_0 was 5.336. The wavelet convolution provided a real and imaginary amplitude and the modulus of these values was taken as the amplitude of induced gamma at that time and frequency point. Amplitude was used rather than power as its distribution was close to a normal distribution. The frequency range analysed was 16–80 Hz with eight steps per octave. The wavelet amplitude at each frequency was baseline corrected by subtracting the mean amplitude in the -100 to 0 ms interval.

For comparison between conditions, amplitude was calculated before averaging across trials. As this included both phase-locked and non-phase-locked components of the EEG signal, the resulting amplitude values are 'induced' rather than 'evoked' gamma amplitudes.

Two sorts of statistical analysis were conducted on the gamma amplitudes observed at each of the four electrodes. In the first, trials for which the subject indicated some awareness of the stimulus, albeit partial (awareness categories *clearly visible*, *identified* and *something*), were classified as *aware* trials, and trials in awareness category *nothing* were classified as *unaware* trials. The gamma amplitudes between the four conditions (correct/aware, correct/unaware, incorrect/aware, and incorrect/unaware) were compared using *t*-tests. *T*-values were calculated for each time–frequency point which meant that a very large number of *t*-tests was performed for each time–frequency plot which, if uncorrected, would have lead to an inflated Type-1. To overcome this problem, a method of Type-1 error control adapted from topographical mapping of EEG was used. This method uses a randomisation testing procedure to correct for multiple comparisons and provides realistic estimates of the true *P*-values (Burgess and Gruzelier, 1999). All *t*-tests were two-tailed and the *t*-values converted to *z*-values.

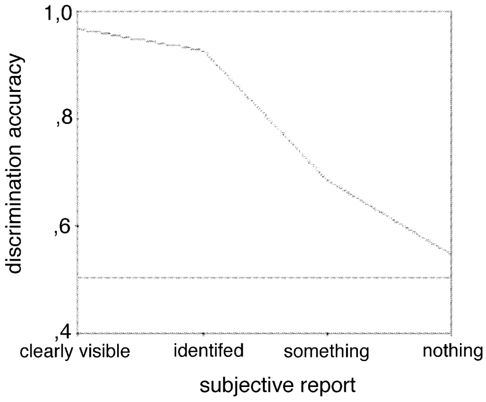


Fig. 1. Behavioural data. Discrimination performance increases with reported awareness. Chance is 0.5. Performance when no awareness is reported (category 4) is significantly greater than chance ($t_{(9)}=2.635$, $P<0.0025$).

In the second analyses, ANOVAs were used to compare the amplitude of the gamma signal in a defined time interval following the stimulus across subjective report categories (*clearly visible*, *identified*, *something*, *nothing*) for both correct and incorrect trials.

3. Results

Three participants were excluded as they responded in awareness category 4 *nothing* on too few trials to permit statistical analysis.

3.1. Behavioural data

For discrimination performance (percentage correct) there were significant main effects of subjective report category ($F_{(3,76)}=38.2$, $P<0.001$) and SOA ($F_{(9,71)}=6.7$, $P<0.001$), but not condition (*top–down* vs. *bottom–up*) ($F_{(1,79)}=1.3$, $P=0.24$). For this reason, data were averaged across top–down and bottom–up conditions for all subsequent analyses. There was also a clear association between awareness report category selected and SOA, with many more 'seen' responses reported at higher SOA intervals.

Participants showed above chance discrimination even when they reported no awareness of the stimulus (i.e. *nothing*, ''absolutely no information about the stimulus influenced my discrimination choice''; $t_{(9)} = 2.635$, $P < 0.025$; Fig. 1). Our experiment thus showed evidence of a subliminal priming effect, as previously described (Marcel, 1983).

As might be expected, there was a strong association between correct response and level of awareness (Fig. 1a). Most of the incorrect responses were associated with a response in categories 3 and 4. In order to show that gamma activity is associated with awareness and not with correctness, we thus analysed both correct and incorrect trials.

3.2. Awareness for correct trials

We compared gamma activity for correct/aware ($n = 3382$) and correct/unaware trials ($n = 405$). *Z*-scores and *P*-values for each time–frequency location can be seen in Fig. 2a–d. At electrode Oz, gamma activity began at about 250 ms poststimulus and continued for 500 ms, with a large cluster of statistically reliable time–frequency locations occurring between 40 and 50 Hz at about 650 ms. At electrode T6, statistically significant differences between correct/aware and correct/unaware trials were observed at two time–frequency locations, one at 40 Hz with a latency of 450 ms, and the other at 30 Hz, 650 ms after the presentation of the masked word.

In order to get an idea of the extent of the difference between the two conditions at these time–frequency locations, we calculated percent change values for each significant ($P < 0.05$) pixel. Values ranged from 6.2 to 12.4%, and averaged 10.4% for electrode Oz, and 8.5% for electrode T6. Percent change values for each time–frequency pixel which showed a difference between correct/aware and correct/unaware trials are shown in Fig. 2f.

ANOVA analysis was conducted on the amplitude of the signal averaged across all four electrodes, at around 40 Hz (35–45 Hz) sampled 500–700 ms poststimulus. Results showed that gamma amplitude for correct trials in this interval increased linearly with subjective report category (Fig. 2e). This linear increase was statistically significant ($F_{(1,9)} = 5.42$, $P < 0.025$).

3.3. Awareness for incorrect trials

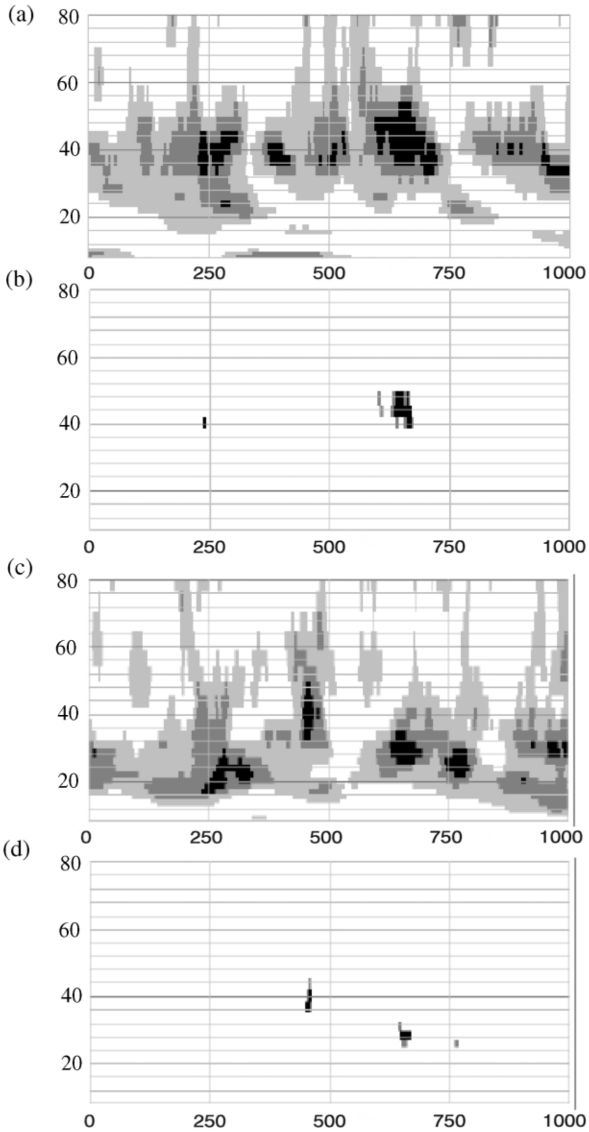
Even when subjects report awareness of a stimulus, they may not identify it correctly. The implication is that the subject experiences an illusory percept, perhaps due to incorrect completion by top–down processes of highly degraded visual information. In the present study, 661 trials (69% of all incorrect responses) were rated as having been associated with some level of awareness (mostly awareness level 3, *something*, with 58.4% of all incorrect responses).

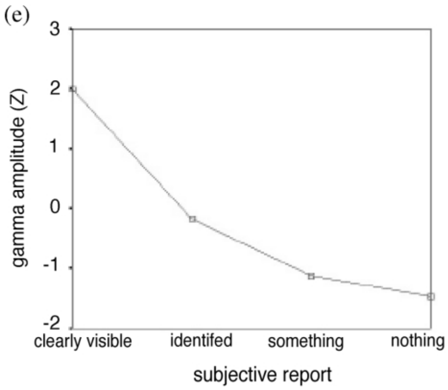
Identical analyses to those for correct trials were thus undertaken for incorrect trials. For the electrode Oz, incorrect/aware trials ($n = 661$) showed no statistically significant difference from incorrect/unaware trials ($n = 351$) (Fig. 3a). However, at electrode T6, a statistically reliable ($P < 0.05$) difference between the two conditions was observed at about 650 ms poststimulus, at a frequency of about 35 Hz (Fig. 3b,c). A difference of 11.7% between the two conditions was observed for this voxel.

Sampling data from the same time–frequency location as for correct trials (35–45 Hz, 500–700 ms poststimulus), no linear association with subjective report category was observed. However, visual inspection of the data suggested that this was due to an increase in gamma power for subjective report category 2 (*identified*) compared to category 1 (*clearly seen*). Given that the data from category 1 included only 23 trials, we excluded trials in subjective report category 1 (*clearly seen*) from the reanalysed data. A linear trend for increasing gamma amplitude with report category was observed (Fig. 3d) which approached significance ($F_{(1,9)} = 2.94$, $P = 0.061$).

4. Discussion

The study aimed to examine the relationship between synchronous gamma oscillations and visual awareness. The results show that gamma amplitude is increased, over posterior cortex, between 250 and 750 ms following a presentation of masked noun stimuli for trials on which a high level of subjective awareness is reported. This increase occurs independent of whether the subject





(f)

Electrode	%change	Low-freq	Hi-freq	Start (ms)	End (ms)
oz	7.15	38.30	41.77	236	240
oz	10.01	41.77	45.55	636	640
oz	9.62	45.55	49.67	638	642
oz	10.85	41.77	45.55	642	646
oz	10.69	45.55	49.67	644	648
oz	11.32	41.77	45.55	648	652
oz	10.91	45.55	49.67	650	654
oz	11.34	41.77	45.55	654	658
oz	12.38	41.77	45.55	660	664
oz	11.80	45.55	49.67	662	666
oz	10.60	38.30	41.77	662	666
oz	12.27	41.77	45.55	666	670
oz	10.13	38.30	41.77	668	672
t6	6.23	35.13	38.30	450	454
t6	7.60	35.13	38.30	456	460
t6	8.73	38.30	41.77	458	462
t6	8.91	27.09	29.54	648	654
t6	8.49	27.09	29.54	656	662
t6	8.90	27.09	29.54	664	670

Fig. 2. Time–frequency amplitudes in the 8–80 Hz range in the 0–1000 ms poststimulus period for correct/aware vs. correct/unaware trials, at electrodes (a) Oz and (c) T6. Statistical reliability of the difference at electrodes (b) Oz and (d) T6. Gamma power shows an association with subjective report category. Z-scores are shown on the left-hand map (black, $z < -2$; dark grey, $-2 < z < -1$; light grey, $-1 < z < 0$; white, $z > 0$), and P-values on the right hand map (grey, $P < 0.1$; black, $P < 0.05$). Percent change values, with precise time–frequency locations, for significant voxels in Fig. 2b and d are shown in (f).

makes a correct response on a forced-choice discrimination task.

For correct trials, we found that gamma amplitude increased linearly with the level of subjective awareness of the stimulus reported by the subject. However, when a subject makes a correct response on a forced-choice discrimination task, it cannot be inferred that the brain has performed the appropriate information processing for the task. A correct response could also be made by chance. It is

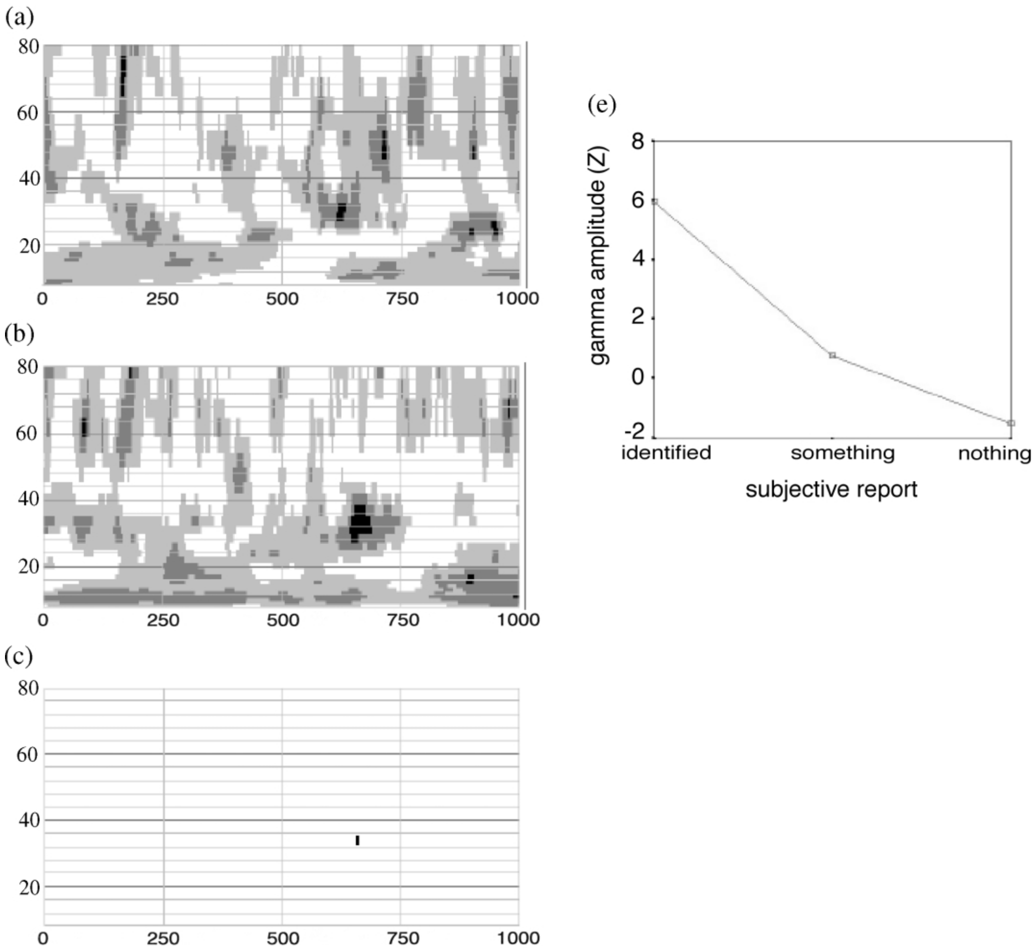


Fig. 3. (a) Time–frequency amplitudes for incorrect/aware vs. incorrect/unaware trials, for electrodes (a) Oz and (b) T6. Statistical reliability of the difference, for electrode T6, is shown in (c). No statistically significant time–frequency locations were observed for electrode Oz in this comparison. Gamma power shows a linear association with subjective report category (d).

not possible to determine whether a correct trial is thus ‘genuinely correct’ (i.e. correct because of appropriate information processing) or a guess. Our results for correct trials may thus have occurred because subjects were more likely to be ‘genuinely correct’ when they reported high levels of awareness. Our results for correct trials alone, thus, do not necessarily suggest an association between gamma power and subjective awareness.

However, we showed that an almost identical pattern of results occurred for incorrect trials. On incorrect trials, it can be inferred that awareness-independent mechanisms which permit the selection of the correct choice have broken down. However, on a large number (69%) of incorrect trials, subjects reported at least some awareness of the stimulus. The most plausible explanation is that on these trials, subjects experienced an illusory perception of a word or word-fragment which was not actually there. On these trials, more gamma activity was observed than on trials in which no awareness whatsoever of the stimulus was reported.

Previous research has suggested that the perception of unmasked nouns is associated with an increase in gamma power at approximately 30 Hz, between 500 and 800 ms after the stimulus (Pulvermuller et al., 1996, 1999). We found increased in activity at between 30 and 40 Hz at between 250 and 750 ms poststimulus, in close accord with these studies. It is interesting to note that the gamma activity observed in association with a higher level of subjective report on incorrect trials onset later than that for correct trials. One explanation is that the perception of a heavily degraded stimulus (most of the responses in this comparison came from awareness category 3 *something*) involves greater top–down processing than perception of clearly seen stimulus, and so takes longer. Further, the finding that this late activity for both correct and incorrect trials was observed at a slightly lower frequency (30–35 Hz as supposed to 40 Hz for correct trials) is consistent with the view that wider cortical assemblies, such as those involving top–down processing, may reverberate at lower frequencies (Pulvermuller et al., 1999).

We found that for correct trials, statistically significant differences between aware and unaware trials occurred both at occipital (Oz) and temporal (T6) regions. However, for incorrect trials, differences were only observed at electrode T6. One explanation for this is that for correct trials, both awareness-dependent and awareness-independent processes may contribute to responding in subjective report category *aware*. Awareness-independent processes, such as priming, may involve posterior brain regions such as the occipital cortex, whereas awareness-dependent processes may require the activation of downstream processing structures such as those found in temporal cortex. On incorrect trials, we propose that only awareness-dependent processes are activated when subjective awareness of the stimulus is reported. Thus, gamma activity was only observed over the temporal cortex (electrode T6).

In conclusion, we found that the amplitude of the posterior brain EEG signal close to 40 Hz is associated with awareness-dependent processes, such as those required to subjectively report the experience of having seen something.

Acknowledgments

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