Boosting up gamma-band oscillations leaves target-stimulus in masking out of awareness: explaining an apparent paradox

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13 pages
2 figures

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Acknowledgements:
We thank Carolina Murd, Mari Hiio, Iiris Luiga, and Michael Herzog for help and useful discussions and Estonian Science Foundation for financial support (grant #7118).

Keywords: gamma oscillations, consciousness, visual masking, EEG
Abstract

Boost up gamma-band neuronal oscillations have been interpreted as a correlate of pertinent stimulus awareness. The validity of this observation-based conclusion can be rigorously tested if the basic methodological rule of investigating neural correlates of consciousness (NCC) is followed: the varying contents of consciousness should be contrasted with invariant stimulation. We asked whether reliable gamma-band oscillations recorded from primary visual cortex appear as signatures of target awareness in metacontrast masking with invariant stimulation parameters.

Surprisingly, clear target-stimuli awareness was associated with less expressed gamma power. However, because when target awareness was effectively masked more gamma power of the EEG response was found, and because this gamma-boost emerged at the post-target time when mask information was presented, we were able to explain our results as target substitution in consciousness by mask representation due to enhanced mask processing.
Boost up gamma-band neural oscillations correlate with stimulus awareness [9, 11]. Validity of this statement owes to the basic methodological rule in investigating neural correlates of consciousness (NCC): the varying contents of consciousness should be contrasted with invariant stimulation [3, 9]. Otherwise we confound stimulus-specific unconscious brain-process signatures with brain-process signatures interpreted as NCC. Manifold effective cognitive and pre-motoric processes in response to stimulation can go on without being reflected in awareness [4, 5] and it would be wrong to test stimuli-awareness by contrasting correct responding with incorrect responding (bias effects and illusions included). A considerable share of the correct responses may be based on correct guessing or just random responding and, on the other hand, vivid and subjectively confident seeing a target stimulus in awareness may be incorrect behaviorally because illusory percepts are a common effect in perception research. Therefore, a comparison is necessary between (i) brain-process signatures when responses are produced *without distinct conscious experience* and (ii) the signatures obtained when responses are accompanied by *clear conscious experience*. Experimental paradigms enabling this strategy include visual masking [2].

Metacontrast is a paradigm of masking where a brief target (e.g., a Landolt image often used to measure visual acuity) is briefly presented, followed by a spatially adjacent masking stimulus (e.g., a ring surrounding the Landolt) [2]. Importantly, a metacontrast masking experiment can be designed so that with the properly chosen target and mask durations, target and mask sizes, visual contrasts and stimulus onset asynchrony (SOA) between target and mask onsets, a combination of values of variables can be achieved that helps to satisfy our main methodological requirement: part of the trials where target identification is requested end up with target remaining subjectively invisible, but a comparably large number of trials leads to subjectively clear and distinct experience of the target image in visible perceptual representation.

Here, we asked whether reliable gamma-band oscillations recorded from primary visual cortex will appear as signatures of target awareness in metacontrast masking with invariant stimulation parameters. The central objectives were (1) to test if augmented gamma band EEG oscillations as measured from primary visual areas can be a reliable NCC for target stimuli, (2) to use a method where the often met
confound between correct responding and some measure of visual awareness (visual consciousness) is avoided. In order to follow the second objective, we used in addition to the commonly used rate of correct responses also a dependent variable that was set to measure subjective clarity of the target perception. The hypothesis put forward stated that trials associated with clear subjective visual experience of target stimuli should lead to augmented gamma band oscillatory response from occipital sensory areas.

Ten male subjects participated in the experiment (mean age 22 years, age range 20-25). All of them were right handed and reported normal or corrected to normal vision. Participants read and signed informed consent form and they were paid for participation. The study received ethical approval from the University of Tartu research Ethics Committee.

Target stimuli were landolt-type targets. Instead of the standard ring-shaped landolts with gaps in the contour line we used four contoured squares with gap in one of the sides – either in the middle of the upper line, right side line, bottom line, or left side line (Fig. 1). The mask was a similar square, but with gaps in all sides (Fig. 1). Mask was slightly larger than target, with its contours adjacent to the target contours. The vertical and horizontal visual angle of the target “landolts” was 0.25 degrees; the gap size was 0.05 degrees; the vertical and horizontal visual angle of the mask was 0.3 degrees. The four target alternatives were specified according to the location of the gap in one side. “Landolt” targets and the mask were always presented in the middle of the screen. All stimuli were with negative contrast set to maximum possible level; they were presented in the center of a large luminous area having luminance equal to 105 cd/m². The presentation times and SOA were chosen in a behavioral pilot study with 3 subjects so that too high and too low performance levels as well as too clear and too much indistinct subjective experiences of target perception were avoided. This ended up with target “landolt” presentation duration equal to 35 ms, mask presentation duration also 35 ms, and SOA equal to 70 ms.

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Visual stimuli were presented on the computer monitor (Eizo Flex Scan, 80 Hz refresh rate). Subjects sat in the subject chair of the Nexstim Eximia EEG/TMS set, with a support for computer mouse on the right of them. The distance to the
monitor was 1.5 meters. Subjects wore the EEG cap with a set of necessary electrodes.

The task was twofold. First, after stimuli presentation, observers were confronted with pictures of the four possible landolt-type targets and had to make a forced choice to indicate which one was presented, thus the theoretical correct guessing rate was equal to 25%. Secondly, evaluation of the subjective level of confidence in having clearly experienced the reported target “landolt” in perception was required. This was completed by forced choice indication of one of the numerical values on the 4-point rating scale, the meaning of which was stated as follows: 1 – “confident in not having seen target distinctly”, 2 – “rather confident in not having seen target distinctly”, 3 – “rather confident in having seen target distinctly”, 4 – “confident in having seen target distinctly”. Trials with ratings 3 and 4 were classified as “aware trials” and trials with ratings 1 and 2 as “unaware trials”. (We could not use only 1 and 4 or all 1, 2, 3, and 4 of the response classes separately for obtaining reliable time-frequency data for the following reasons. First, as it turned out with 6 of the 10 subjects there were only 20 or fewer trials in one of the extreme categories already before the artefact elimination procedure. These circumstances would have made any reliable statistical effect with only one response class included separately in the analysis, unlikely. Second, and as was also clear from the results of the piloting experiments, the very nature of visual masking phenomena makes it very difficult to find many trials with highest confidence combined with many trials of lowest confidence when invariant stimuli conditions are used. But because invariance of stimuli was the essential requirement in our design in order to avoid artefacts stemming from physical differences of stimulation, we had to conform to this. If we would change physical conditions so that more maximally “aware” trials would be produced, we would have lost most of the unaware trials. By its very nature, visual masking does not allow extreme clarity of targets.)

Each subject performed 6 blocks of trials where each block consisted of 40 trials where the four versions of targets appeared in random order. After mouse-clicking on the “Next trial” icon on the display, a fixation dot (formed from the dark area sized as 4 screen pixels) appeared in the center of the monitor, followed after 700 ms by the target and mask. After 1500 ms from the offset of the masking stimulus the response icons appeared. Subjects responded by mouse-clicking two response icons: first indicating the “landolt” they concluded was presented and, second, the
Subjects experienced 10-15 practice trials before the experiment began. They were also instructed not to blink and not to move their eyes after clicking the “next trial” icon and before the response icons appeared.

EEG was recorded by Nexstim Eximia EEG system. EEGs were recorded against a reference electrode placed on the forehead. EEG data was collected from the electrodes AF1, AF2, F1, F2, C5, C3, Cz, C4, C6, P1, P2, Oz and Iz according to the 10-10 system. In addition, two electrodes were used for obtaining the VEOG. The impedances were kept below 5 kOhm. The sampling rate was 1450 Hz, all signals were filtered with a hardware based bandpass filter of 0.1-350 Hz. EEG was segmented into epochs measured from –400 ms to 700 ms relative to the target onset and baseline corrected with a baseline of –100 to 0 ms. Trials with voltage deviations higher than +40 µV or lower than –40 µV in any of the recorded channels were eliminated.

Individual EEG data was sorted into segments according to trial types defined by four possible combinations of interest: (1) correct/aware, (2) correct/unaware, (3) incorrect/aware and (4) incorrect/unaware. Behavioral results were as follows. The subjects were correct on 45% of trials which is significantly better than expected by chance (25%) – T=4,991, \( P < 0.001 \). When we considered the four different confidence ratings, there was an effect of confidence on correctness in our experiment (repeated measures ANOVA with the factor confidence: \( F(3, 27) = 35,678, P < 0.0001 \)). As for the EEG analysis the trials were sorted to two categories – aware and unaware, we also made a similar behavioural analysis with these two levels of awareness and obtained a significant effect of awareness on correctness (repeated measures ANOVA with the factor awareness: \( F(1,9) = 33,361, P < 0.0001 \)). This means that when a subject was correct, his/her confidence also tended to be higher. However, the analysis of the relation of correctness and confidence for the individually averaged data taken from all 10 subjects showed that correlation between the level of confidence and level of correctness was not significant (\( r = - 0.168, P > 0.600 \)). This result appears because there are subjects who, despite of their low correctness rate, are confident in having perceived the target clearly and also subjects
who show the opposite – their rate of correct responses is quite high, but confidence in seeing the target clearly is not high.

When comparing the EEG oscillatory responses we made two comparisons. First, trials where observers were confident in having seen the target distinctly were contrasted with trials where observers did not see target clearly or not at all. For this, the above mentioned combinations (1)+(3) were contrasted with (2)+(4). Within each subject we included a similar number of aware and unaware trials in the analysis. The same number of correct and incorrect trials for both awareness conditions was analyzed in order to exclude the confound of the expected NCC with behavioral correctness of responding (the latter possibly including correctly reported trials without distinct awareness of the target and incorrectly reported trials despite the clear subjective awareness). The number of correct and incorrect trials within the awareness conditions was equal to the smaller number of correct and incorrect trials from the conditions. Trials from the bigger sample were excluded randomly. This resulted on average in 91 trials per subject per condition. In addition, we made the common comparison between correct and incorrect trials, corresponding to the combinations (1)+(2) vs. (3)+(4). Similar number of trials for the correct and incorrect condition was used within each subject. However, the possible confound with the factor ‘awareness’ was not avoided as the goal was to use the methods commonly applied. This resulted on average in 84 trials per condition per subject.

To eliminate the confounding vertical EOG high frequency activity apparent in the forehead reference electrode, the EEG for time-frequency analysis was re-referenced to the average of all electrodes. The spectral dynamics in oscillatory activity were explored by means of time-frequency analysis implemented in EEGLAB [6] running under Matlab (Mathworks, Inc.). The event-related spectral perturbation (ERSP) index was computed. This requires the calculation of the power spectrum over a sliding latency window and then averaging this power spectrum across the trials. The color of each data point in the image of spectral perturbation indicates the power relative to baseline (in dB). In order to achieve good time and frequency resolution all over the gamma frequency range we used a complex Morlet wavelet transform with the number of wavelet cycles increasing with the frequency (5 cycles at 20 Hz to 10 cycles at 70 Hz). This method allows obtaining better frequency resolution than by applying a constant cycle length [6].
The time-varying power was calculated in the frequency range from 20 Hz to 70 Hz with 50 linear 1-Hz wide wavelet steps. We used a baseline of 400 ms. In order to analyze the power changes across the time and frequencies the mean baseline log power spectrum was subtracted from each spectral estimate, which led to the baseline-normalized ERSP. For comparing the power changes across the conditions, the common average baseline log power spectrum was subtracted.

In order to analyze oscillatory activity that is not phase-locked to the stimulus, the analysis was performed separately for each single trial and the power values of the resulting time-frequency representations were averaged. The ERSPs between the conditions ‘aware’ and ‘unaware’ were compared using a permutation-test, where a distribution for the null hypothesis is estimated by accumulating surrogate data by shuffling the means from the conditions within the subjects. A large number of tests was performed simultaneously which led to the inflation of Type-1 error. To correct for this problem, a more conservative significance threshold was chosen ($P < 0.0005$).

Time-frequency plots of activity were obtained. The power of brain responses as a function of oscillation frequency and time from target onset from the aware/unaware comparison is illustrated in Fig. 2. We expected stronger gamma power when target awareness was the case. Contrary to our expectation, on the electrode Iz which was the closest electrode to V1 locations implied in early processing of stimuli signals, 30-Hz gamma-band activity was weaker in the trials with clear target awareness and stronger in the trials where effective masking was the case (Fig. 2; $P < 0.0005$). We did not initially use the Bonferroni correction because it is too conservative (as the estimates of neighboring time-frequency points are highly correlated) leading to the underestimation of the real experimental effects. However, to confirm that our results were robust, we made a Bonferroni correction by assessing fewer frequencies and fewer time points (20 x 50, respectively, in the time range -100 ms to 400 ms) on a higher significance threshold [$0.05/(20 \times 50) = 0.00005$]. The Bonferroni correction validated both of the significant differences on Fig. 2 and the corresponding new time-frequency plot with depicted significantly different gamma-band activity level looked virtually identical to what is shown in Fig. 2.
At first, our result appears as a paradox inconsistent with the host of evidence about augmented gamma band neural responses as a genuine NCC for target awareness [9, 11]. Yet, there is an important aspect in our experimental design that helps to explain the apparently paradoxical outcome. The boost of heightened gamma activity emerged about 70-130 ms post-target, being significant from 70-100 ms (Fig. 2). Let us make a little calculation: the earliest occipital V1 responses to visual featured stimulation appear 30-100 ms after stimulus onset [10] and the SOA value used here was 70 ms, therefore the EEG-activity could not show the specific activity related to the masking stimulus, as it would arrive in visual cortex not earlier than after 100 ms. However, this activity immediately preceded the arrival of the masking stimulus in the visual cortex. Gamma-activity immediately preceding the moment when visual signals arrive in cortex can have their beneficial effect upon stimulus processing (Aru & Bachmann, unpublished). As the target-awareness was lower in the case of stronger oscillatory gamma activity immediately preceding the arrival of the mask-related cortical activity, we interpret this activity as being beneficial for the masking stimulus. Therefore, our results support consciousness-related masking-theories where instead of inhibition of target-related signals masking results from stronger mask-processing. Thus mask substitutes the target in working memory and becomes available for response instead of the target [1, 7, 8]. Either reentrant signals from higher-level cortical nodes back to V1 help the newly arriving mask signals substitute the target signals for visible representation [7, 8] and/or in addition to the fast geniculo-cortical responses a delayed thalamo-cortical modulation response is induced so that when mask-specific signals arrive later, they take advantage of the slow modulation caused by target, with mask becoming emphasized instead of the target [1]. (See, however, [12] for an alternative view explaining the decrease in late V1 activity due to the offset-activity, elicited by the offset of the target. Thus the increased target visibility, accompanied by a decrease in late gamma-activity might mean that target offset was effective in reducing mask processing. In this case, however, it is difficult to understand why there is no clear increase in target-related activity with better target visibility.)

However, as we stated earlier, in the time-range 70-100 ms the representation of the masking stimulus probably has not arrived in the visual cortex yet. Therefore, the gamma-boost for unaware trials is probably not related to the specific cortical processing of the masking stimulus, as required in the case of theories.
postulating the importance of recurrent intracortical processing [7,8]. We postulate that it rather reflects the slow non-specific modulatory activity caused by the preceding target. Mask just happens to be presented at the optimal time-point, but the gamma-burst is actually induced by the target. By the arrival of the representation belonging to the masking stimulus in visual cortex (after 100-130 ms), it can immediately take advantage of this non-specific activity, become augmented, more salient, substituting the target in awareness. Thus the trials that are marked with relatively enhanced mask processing for conscious-level visual representation easily mean deprivation of target-related information for the same purpose. The observed likely signature of enhanced mask processing explains that and why mask substitutes target in visual awareness. When mask-input processing was actually not augmented (Fig. 2, middle panel), target escaped from masking, appearing in awareness.

In addition, stronger oscillatory activity in the case of unaware trials at about 300 ms around 45 Hz was obtained from the electrodes Iz and Oz. The first significant difference where there was stronger EEG gamma activity for aware trials than for unaware trials was observed at 250 ms between 40 and 45 Hz and at 350 ms between 45 and 50 Hz, measured from the frontal electrodes AF1 and AF2, respectively.

In order to be even more confident that there is not an effect of target correctness as large as the effect of clarity of target awareness, we did also a time-frequency analysis of correct vs. incorrect trials. As can be seen from Fig. 3, no significant differences in gamma-band power were found when correct and incorrect trials conditions were compared -- neither in the early time range nor later. Therefore, the comparison aware vs. unaware should be preferred to the more common comparison of correct vs. incorrect in the science of consciousness. This consideration has two important reasons. First, subjects can give correct responses, although they have no awareness of the target. Second, they can be aware of the target, although their response is actually incorrect. Our conscious vision is prone to illusions and clear, but non-veridical percepts are a common finding in consciousness research. Although the situation where the subject claims that (s)he is aware of the target but is actually incorrect is paradoxical, we should trust the subjective measures if we study consciousness, because it is important how distinct the conscious percept is, independent of the correctness. Further research has to show what the crucial differences between correct/aware and incorrect/aware trials are in experimental setups like ours. In our experiment, we were able to find the early correlates of
consciousness only because we used the difference aware/unaware instead of correct/incorrect.

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Awareness of a task-relevant visual object can be traded for the dominance of a task-irrelevant object. The 30-Hz gamma-band oscillations in V1, if they happen to be augmented exactly at the time when initial sensory signals from the following irrelevant object firstly arrive there can be considered as a “negative-NCC” for a target object. Among the many masking theories [2], the theories assuming mask enhancement or emphasis as the cause of target’s deprivation of awareness [1, 7, 8] have received strong support.

**Acknowledgements**

We thank Carolina Murd, Mari Hiio, Iiris Luiga, and Michael Herzog for help and useful discussions and Estonian Science Foundation for financial support (grant #7118).
References

Figure legends:

Figure 1

Schematic of experimental procedure including examples of stimuli and timing of stimuli presentation. Target was presented for 35 ms, followed by 35 ms empty inter-stimulus interval and then by 35 ms mask presentation; thus SOA=70 ms. Mask stimulus contours flanked the target contours surrounding them from a slightly more peripheral distance. Observers had to perform 2 tasks: (a) identify the target (one alternative among 4 possibilities) and (b) evaluate target’s visibility using a 4-point scale (1 – “confident in not having seen target distinctly”, 2 – “rather confident in not having seen target distinctly”, 3 – “rather confident in having seen target distinctly”, 4 – “confident in having seen target distinctly”).

Figure 2

Time-frequency plots of the power of brain’s oscillatory responses measured with EEG from occipital central location (electrode Iz). Target exposure set at 0 ms. When target was not perceived in awareness, a distinct gamma-band activity around 30 Hz frequency emerged between 60 ms and 130 ms (post-target time epoch), corresponding to the time delay with which mask-related first signals arrive visual primary cortex (upper panel). When target was well perceived in awareness, no clear-cut augmented oscillatory responses were recorded (middle panel). Statistical comparison of target/aware and target/unaware conditions revealed stronger gamma-activity at sub-100 ms delay (lower panel; $P < 0.0005$).

Figure 3

The time-frequency plots from the electrode IZ for the correct vs. incorrect comparison. Note that there are no significant differences at the $P < 0.001$ level.
Figure 1

Response: (a) identify (b) rate target visual clarity

mask 35 ms

SOA = 70 ms

target 35 ms
Figure 2

UNAWARE

AWARE

“t-Test” (based on permutations)

p < 0.0005
Figure 3