

Induced gamma-band activity elicited by visual representation of unattended objects

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Abstract

Object recognition is achieved through neural mechanisms reliant on the activity of distributed neural assemblies that are thought to be coordinated by synchronous firing in the gamma-band range (>20 Hz). An outstanding question focuses on the extent to which the role of gamma oscillations in object recognition is dependent on attention. Attentional mechanisms determine the allocation of perceptual resources to objects in complex scenes biasing the outcome of their mutual competitive interactions. Would object-related enhancements in gamma activity also occur for unattended objects when perceptual resources are traded off to the processing of concurrent visual material? The present electroencephalogram (EEG) study investigated event-related potentials (ERPs) and evoked (time and phase-locked) and induced (non time and phase-locked to stimulus onset) gamma-band activity (GBA) using a visual discrimination task of low or high perceptual load at fixation. The task was performed while task-irrelevant familiar or unfamiliar objects co-appeared in the surrounding central area. Attentional focus was kept at fixation by varying perceptual load between trials; in such conditions only holistic object processing or low-level perceptual processing, requiring little or no attention, are thought to occur. While evoked GBA remained unmodulated induced GBA enhancements, specific to familiar object presentations, were observed, thus providing evidence for cortical visual representation of unattended objects. In addition, the effect was mostly driven by object-specific activity under low load, implying that in cluttered or complex scenes attentional selection likely plays a more significant role in object representation.

Keywords: gamma band activity, visual object representation, attention, perceptual load, EEG

Introduction

Various attentional models have attempted to describe mechanisms through which stimuli, based on their task-relevance, are either ignored or selected for further processing (e.g., Treisman, 1969; Duncan, 1980). Spatial, feature-based and object-based attention are thought to rely differentially on a set of rapidly functioning neural mechanisms that allow enhancement of attended and suppression of unattended information (Reynolds and Chelazzi, 2004). Selective attention is essential for efficient processing as sensory information constantly competes for the limited set of available resources (Desimone, 1998). To address this Lavie (1995) proposed a model of attentional processing that takes into account the amount of perceptual information (referred to as 'perceptual load') that the visual system has to take into account in order to perform accurate discriminations. Perceptual load is enhanced when the number of items to be processed is increased, or when the task is altered to require discrimination between highly similar features or multiple feature conjunctions. Depending on the amount of load attentional mechanisms distribute perceptual resources across the rest of the scene to ensure efficient processing. One such mechanism reduces the processing of irrelevant information (referred to as 'distractors') when the perceptual load becomes high; another automatically allocates to other elements of a scene, when the perceptual load is low, even if they are task-irrelevant (Lavie, 1995).

A selective attention mechanism that controls the allocation of perceptual resources across visual scenes on the basis of stimulus relevance and task demands is very important for visual object representation. Attention is known to play an essential role in guiding the selection and processing of objects in everyday vision. Relevant objects are given processing priority and placed within the attentional spotlight (Schroeder, Mehta and Foxe, 2001) - they are foveated, recognised and acted upon. However to what level are unattended objects processed? Visual scenes contain large numbers of objects with varying amounts of clutter and mutual occlusion; these objects are constantly competing for processing resources. Their relevance for the individual's present motivational state influences the outcome of the competition as relevant objects are given

processing priority through attentional selection. But which representation type, if any, is formed for unattended objects?

It is generally considered that certain processing streams within the object recognition system do not require attention thereby allowing for implicit registration of unattended objects up to a certain level of representation (for overviews, see Murray and Jones, 2002; Thoma, Hummel and Davidoff, 2004). This level is mostly assumed to contain lower level representations of visual features within the image and their conjunctions (e.g., colour or shape) and to exclude higher level semantic-based information. Although certain studies found even unattended objects were habitually being processed up to the semantic level (e.g., Pins, Meyer, Foucher, Humphreys and Boucart, 2004; Altmann, Grodd, Kourtzi, Bühlhoff and Karnath, 2005), other studies which explicitly controlled attention indicated there is very little or no identification without attention (Lachter, Forster and Ruthruff, 2004). A recent behavioural study by Thoma et al. (2004) demonstrated that visual representations of ignored objects are holistic in nature while those of attended objects are analytic. In the hybrid model of object recognition these two types of visual representations occur in parallel and make contact with object memory independently; though only analytic representations contain explicitly delineated relations among an object's parts. Holistic representations do not define these relations explicitly or independently of the parts but instead represent them within a coordinate system that refers to one particular view of the object (Hummel and Stankiewicz, 1996).

Support for the hybrid model shows that the level of representation depends on the allocation of attention. A behavioural study by Murray and Jones (2002) adopted Lavie's (1995) model of perceptual load in order to systematically examine the relation between perceptual mechanisms of attentional selection and processing of object representations. A task was used in which local form information, embedded within a task-irrelevant global familiar object-shape, had to be matched in orientation between a reference and a target/distractor display. This local form information could either be of low or high perceptual load, which when randomly intermixed

between trials avoided strategic biases in attentional deployment. With attention constrained to the local form information by top-down influences no evidence of semantic processing of surrounding object-shapes was found under low or high load. Lower level pre-semantic processing of surrounding object-shapes still took place however since identical distractors seemed to be processed more favourably, presumably due to requiring little or no attention.

Visuo-spatial attentional selection and the deployment of perceptual resources have also been examined neuroscientifically. Recent studies have examined the role of peripherally presented perceptual load in determining the extent of neural processing of simple visual information. Handy and Mangun (2000) looked at the role of load using event-related potentials (ERPs) and obtained attentional modulations of P1 and N1 components. They suggested this reflected early changes in the magnitude of spatial-selective processing in extrastriate visual areas which increased with higher load. A related blocked design study by Handy, Soltani and Mangun (2001) observed a decrease for distractors presented under high foveal load occurring at the level of P1, N1 and N2; indicating that perceptual load did effect the early stages of processing of simple task-irrelevant information. In a recent functional magnetic resonance imaging (fMRI) study Schwartz, Vuilleumier, Hutton, Maravita, Dolan and Driver (2005) found that purely top-down increases in attentional load at fixation decreased responses to peripheral distractors at the level of early visual cortex. The effect was larger for higher-level visual areas suggesting attentional surround-suppression. High load therefore impacts on neurophysiological markers of early visual processing by reducing responses to simple information in the periphery.

However the question remains, what markers would be affected by complex visual information (i.e., objects) presented foveally under different types of perceptual load? Foveally presented items have preferential access to attention and therefore interfere more with the processing of task-relevant information (Beck and Lavie, 2005). The challenges posed by natural scenes in everyday life involve mutual occlusion of foveated objects amid varying degrees of background clutter. How does the brain manage to code each of these objects in a unified way? It

has been suggested that neural mechanisms subserving object processing rely on the activity of distributed neural assemblies. This activity is thought to be coordinated by synchronous firing in the gamma-band range (>20 Hz). Such event-related gamma band activity (GBA) can either be evoked (time- and phase-locked to stimulus onset) or induced (non time- and phase-locked). Evoked GBA is generally focused in the lower gamma-band frequency ranges (30-40 Hz) and has a stable latency of approximately 100 ms; it is modulated by task complexity (Senkowski and Herrmann, 2002; for an opposite finding see Posada, Hugues, Franck, Vianin and Kilner, 2003) and feature-selective processing demands (Busch, Schadow, Freund and Herrmann, 2006b) and reflects an early stream of sensory processing. Induced GBA shows greater variability in frequency (30-90 Hz) and usually peaks at approximately 250 ms with the peak latency related to the time point of object recognition (Martinovic, Gruber and Müller, 2007). Significant levels of induced GBA are elicited in studies that require identification of foveally presented familiar objects; it is likely that such induced GBA reflects a later stream of representational processing connected to visual memory processes (Gruber, Malinowski and Müller, 2004; Gruber and Müller, 2005). Induced GBA is therefore highly relevant for object recognition studies.

The extent to which integrative oscillatory activity underlying visual object representation is attention-dependent has previously been researched using induced gamma band responses as a measure of perceptual processing. There is some evidence supporting both the role of automatic, gestalt-like processes as well as the role of perceptual attentional mechanisms (Müller, Gruber and Keil, 2000; Müller and Gruber, 2001). Thus it is still an open question if attention is a necessary prerequisite for object-related enhancements in induced GBA. What happens with induced GBA when objects are unattended? Moreover, would GBA amplitude depend on the perceptual load, with highly taxing visual discriminations engaging more perceptual resources away from the task-irrelevant objects? Although induced GBA under conditions of different perceptual load has yet to be investigated, if it is a specific marker of integratory processes in object identification its amplitude should depend on the functioning of perceptual mechanisms of attentional selection.

The present electroencephalogram (EEG) study was conducted to provide answers to these outstanding questions: (1) do induced GBA enhancements specific for object processing also occur for unattended objects and (2) is their amplitude influenced by differential task demands introduced through changes in the perceptual load. ERPs and evoked and induced GBA were investigated using a visual matching task of low or high perceptual load at fixation that was attended while task-irrelevant familiar or unfamiliar objects co-appeared in the surrounding central area. The aim was to examine how much neural processing of surrounding familiar objects occurred when attention was directed to complex local form information. A further aim was to examine if this processing differs when perceptual load of task-relevant information was changed from low to high, thereby influencing the extent of the automatic reallocation of residual resources to spatially-coexistent distractors.

Based on previous findings on effects of stimulus size on both types of GBA (Busch, Debener, Kranczioch, Engel, & Herrmann, 2004) the small local-form stimuli should elicit none or very low event-related GBA (both evoked and induced). This assumption was first tested in Experiment 1 by employing only the local-form stimuli of low and high load without the surrounding distractors. This acted as a control for Experiment 2 which tested the hypothesised effects of distractors, either familiar or unfamiliar objects, under low and high perceptual load on ERPs, evoked and induced GBA. Induced GBA is elicited by foveal presentations of familiar but not unfamiliar words and objects (Fiebach, Gruber, & Supp, 2005; Gruber & Müller, 2005). Therefore, differential activations between familiar and unfamiliar objects were expected to be significant under low load due to the automatic reallocation of leftover resources to salient familiar stimuli and their representational processing. For high load it was expected that familiar objects would not be able to trigger significant increases in induced GBA in relation to unfamiliar objects, as perceptual capacities would be exhausted by the demanding high load task at fixation (Lavie et al, 2004). Evoked GBA, on the other hand, has been modulated by object familiarity in only one study (Herrmann, Lenz, Junge, Busch and Maess, 2004a). A methodological study by Morup,

Hansen, Herrmann, Parnas and Arnfred, (2006), using the same paradigm as Herrmann et al. (2004), has shown that the factorial structure of evoked GBA differs between familiar and unfamiliar objects; however, these differences were very small, with the two factors explaining less than 20% of the variance. Evoked GBA's object-specificity therefore remains doubtful since most studies do not find an effect of object familiarity (Tallon-Baudry, Bertrand, Delpuech and Pernier, 1996; Fiebach, Gruber and Supp, 2005; Gruber and Müller, 2005; Busch, Herrmann, Müller, Lenz and Gruber, 2006a; Gruber, Trujillo-Barreto, Giabbiconi, Valdes-Sosa and Müller, 2006). Robust previous findings indicate that evoked GBA is highly responsive to both bottom-up and top-down driven feature processing (e.g., Busch et al., 2006b) with the assumption being that it is a necessary prerequisite for significant increases in induced GBA (Herrmann, Munk and Engel, 2004b). It was therefore hypothesised that evoked GBA would be elicited but that it would dissociate from induced GBA, being preferentially modulated by task demands.

In order to complement the findings on event-related GBA, ERPs were also examined focusing on the following components: early components P1 and N1, and late components L1 and L2. Previous studies have found characteristic modulations of late components by stimulus familiarity; with unfamiliar stimuli eliciting a more negative L1 and a more positive L2 (Rugg, Soardi and Doyle, 1995; Gruber and Müller, 2005). As previously mentioned, Handy et al. (2001) observed more negativity for distractors under high load; occurring at the level of P1, N1 and N2. These authors speculated however that the P1 effect should be eliminated if load is subjected to trial-by-trial variations, as the attentional focus in these circumstances remains steady across load conditions. Since the allocation of attention was supposed to be equal at trial onset, due to unpredictability of both load and distractor type, it was expected that the early effects of load on P1 and N1 would not be observed. Effects of load could still occur at later processing stages, so it was expected that these differences might be observed on the late components L1 and L2.

Experiment 1

In the control experiment the central local form stimuli were piloted without any surround to verify the presence of behavioural effects of perceptual load and also to determine the optimal display times that would ensure desirable pacing for Experiment 2. EEG data was collected in order to establish that small foveal stimuli would not by themselves elicit significant enhancements in evoked or induced GBA. Since only familiar objects elicit significant increases in induced GBA (Gruber and Müller, 2005) this allows clear conclusions to be drawn about the interaction between object familiarity and perceptual load, which were to be examined in the main experiment.

Methods

Participants

Fourteen participants took part. Two had to be removed due to a technical error during EEG recording. Twelve participants (2 male) remained in the sample, aged 19-26 years (mean age 22.5 years). They were all healthy, right-handed university students and received class credit or a small honorarium for participation. Participants reported normal or corrected-to-normal vision. Individual written informed consent was obtained and the study conformed to the Code of Ethics of the World Medical Association.

Materials and procedure

In the centre of the screen an image was presented that contained three yellow boxes organized in a triangular fashion around a red fixation cross (see Figure 1).

insert Figure 1 about here

Participants were instructed to match the content of the upper box with the content of one of the two boxes below. The index and middle finger of one hand were placed on the two side by side buttons and participants were told to press the button that corresponded to the side of the box with the correct match.

Based on Murray and Jones (2002) tasks differing in perceptual load were created. 192 stimuli, which included the original Murray and Jones (2002) set, were presented in a randomised order, different for each of the participants. In the low perceptual load condition the upper and both of the lower two boxes contained line-forms and the participant had to match the content of the upper box to the lower box that contained exactly the same form. In the high load condition the lower boxes contained letters and participants had to match the line-form from the upper box with the letter that fully contained such a line-form within its shape. Participants were instructed to do this as quickly and as accurately as they could.

Participants first performed a practice block of 48 trials (24 per load level) that contained a subset of stimuli that were not used in the experiment itself. The practice was repeated until the participants reached a criterion of 80% correct – this usually required one repetition.

The experiment itself consisted of four blocks, with each block lasting approximately two minutes and containing 48 trials. Each trial consisted of a variable 500-800 ms baseline period during which a red fixation cross ($0.2^\circ \times 0.2^\circ$) was presented. This was followed by a stimulus picture that was displayed for 600 ms. The picture was then replaced by the fixation cross which remained on the screen for a period of 650 ms.

Stimuli ($1^\circ \times 1^\circ$) were shown on a white background and were presented centrally on a 19-inch computer screen, with a 70 Hz refresh rate, that was positioned 1 metre in front of the participant in a dimly lit soundproof testing chamber. Stimulus onset was synchronised to the vertical retrace of the monitor. The presentation and timing of the experiment were controlled using a Matlab Toolbox, allowing precise visual presentation and response-recording timings (Cogent, www.vislab.ucl.ac.uk/Cogent/; The Mathworks, Inc, Natick, Massachusetts).

Halfway through the experiment participants were asked to change the responding hand. Participants were instructed to minimise eye movements and blinking during the display of a stimulus or the fixation cross.

EEG recording

EEG was recorded continuously from 128 locations using active Ag-AgCl electrodes (BioSemi Active-Two amplifier system) placed in an elastic cap, referenced to an additional active electrode (CMS – Common Mode Sense; with ground in additional electrode DRL – Driven Right Leg) during recording. EEG signal was sampled at a rate of 512 Hz. Horizontal and vertical electrooculograms were recorded in order to exclude trials with blinks and significant eye movements. EEG was segmented into epochs starting 500 ms prior and lasting 1500 ms following picture onset. EEG data processing was performed using the EEGLab toolbox (Delorme and Makeig, 2004) combined with self-written procedures running under Matlab (The Mathworks, Inc, Natick, Massachusetts). Artifact correction was performed by means of ‘statistical correction of artefacts in dense array studies’ (SCADS; Jungheofer, Elbert, Tucker and Braun, 2000). This procedure is widely accepted in the field and has been applied and described in several publications (e.g., Gruber, Müller, Keil and Elbert, 1999; Müller and Keil, 2004). The average rejection rate was 32.6% resulting in approximately 57 remaining trials per condition on average. Further analyses were performed using the average reference.

Behavioural data analysis

Reaction times (RTs) between 250 and 1250 ms (the maximum time allowed for responses) after stimulus onset on trials with correct responses were taken into further analysis. Mean RTs and error rates were computed for each participant. Differences in error rates and response speed between low and high perceptual load were analysed using paired t-tests.

Event related potentials analysis

A 25 Hz low-pass filter was applied to the data before all ERP analyses.

Two ERP components were assessed: P1 and N1. For each component regional means (shown in Figure 2, see Results) were assigned based on which electrodes exhibited maximal activity when data was collapsed across conditions. Average amplitudes across the electrodes at these sites in their respective time windows (80-120 ms for the P1, 130-190 ms for the N1) were then computed and the mean amplitude during the period 100 ms prior to stimulus onset (baseline) was subtracted. Mean latencies were not analysed as there were no hypotheses concerning them. Differences in amplitude between low and high perceptual load were analysed using paired t-tests.

Analysis of evoked and induced spectral changes

Oscillatory activity was analysed according to the standard procedure employed in a multitude of preceding studies (e.g., Gruber et al., 2004; Gruber and Müller, 2005). In brief, spectral changes in oscillatory activity were analysed by means of Morlet wavelet analysis (Bertrand and Pantev, 1994) which provides a good compromise between time and frequency resolution (Tallon-Baudry and Bertrand, 1999). This method gives a time-varying magnitude of the signal in each frequency band leading to a time-by-frequency (TF) representation of the signal and is described in-depth, together with suggested parameter definitions that allow for a good time and frequency resolution in the gamma frequency range, in previous studies (e.g., Gruber and Müller, 2005). In order to achieve good time and frequency resolution in the gamma frequency range the wavelet family was defined by a constant $m = f_0/\sigma_f = 7$, with f_0 ranging from 2.5 to 100 Hz in 0.5 Hz steps. This data was subsequently reduced to form 2.5 Hz-wide wavelets. Time-varying energy in a given frequency band was calculated for each epoch; this being the absolute value of the convolution of the signal with the wavelet for each complex spectrum.

Preliminary electrode sites used for time-by-frequency plots (TF-plots) and further peak amplitude analyses were selected on the basis of previous findings of maximal local gamma power

elicited by object categorisation paradigms – parietal for induced GBA (Gruber et al., 2004), and occipital for evoked GBA (Tallon-Baudry, Bertrand, Delpuech and Pernier, 1997). These sites were to be readjusted in order to envelop the area of maximal amplitude in case the observed grand mean topography happened to differ from previous findings. To depict these topographies wavelet analysis was recalculated for all 128 electrodes. Maps of oscillatory responses in the ± 5 Hz frequency band centred upon the maximal activity wavelet for each participant during the time window of maximal activity and were calculated for both conditions by means of spherical spline interpolations (Perrin, Pernier, Bertrand and Echallier, 1988).

For both types of GBA the time window of highest gamma amplitude was identified for the purposes of the analysis. The length of this time window was defined based on the observed grand-mean GBA; a common approach in previous studies (e.g., Busch, Debener, Kranczioch, Engel and Herrmann, 2004; Gruber & Müller, 2005).

In order to identify the time window and frequency range of the induced GBA peaks, mean baseline-corrected spectral amplitude (baseline: 100 ms prior to stimulus onset) was collapsed for all conditions together and represented in TF-plots in the 30-90 Hz range. Regional means of interest were then selected on the basis of grand mean topographies. Due to inter-individual differences in the induced gamma peak in the frequency domain a specific wavelet for each participant was chosen, designed for the frequency of his/her maximal amplitude in the gamma range based upon an average across both low and high load conditions. Centred upon this wavelet a frequency band of ± 5 Hz was subsequently formed for statistical analysis.

By definition evoked oscillatory activity is phase-locked to stimulus onset and was analysed through a transformation of the unfiltered ERP into the frequency domain. Evoked GBA is a response with low inter-individual variability in latency at frequencies between 30 and 40 Hz, with maximal activity usually occurring in a narrow time interval around 100 ms post stimulus-onset. Therefore a ± 5 Hz range was taken around a central wavelet of 35 Hz within a time window of 50-150 ms.

In short, GBA was analysed in the ± 5 Hz frequency band around the wavelets of interest; 35 Hz for evoked GBA and individual maximal wavelet for induced GBA. Means and standard errors (SEs) of the mean are reported throughout the results section. Differences against baseline in GBA amplitude at the site of the regional mean during the time window of maximal activity were tested using independent t-tests against zero.

Results

Behavioural data

Mean error rates and their SEs were as follows: low perceptual load $3.1 \pm 0.5\%$ and high perceptual load $12.3 \pm 1.7\%$. Mean RTs and their SEs, computed only from correctly answered items, were as follows: low load 652 ± 27 ms and high load 848 ± 24 ms. Highly significant effects were found with more errors and longer response latencies for higher load (error rate: $t(12) = -5.76, p < 0.001$; RTs: $t(12) = -14.56, p < 0.001$).

Event related potentials

Figure 2 depicts the ERPs. There were no significant effects of perceptual load on either of the components. Both P1 and N1 were maximal at occipital sites. P1 had a grand mean baseline-

insert Figure 2 about here

corrected amplitude of $1.95 \pm 0.39 \mu\text{V}$ for low and $1.99 \pm 0.31 \mu\text{V}$ for high perceptual load ($t(11) = -0.20, \text{n.s.}$). N1 had a grand mean baseline-corrected amplitude of $-3.47 \pm 0.75 \mu\text{V}$ for low and $-3.46 \pm 0.72 \mu\text{V}$ for high perceptual load ($t(11) = -0.03, \text{n.s.}$).

Evoked and induced spectral changes

Figure 3 shows grand mean baseline-corrected TF plots and topographies of event-related GBA collapsed across experimental conditions.

insert Figure 3 about here

Gamma-band amplitude evoked by stimulus presentations between 30 and 40 Hz during a time window of 50-150 ms showed a slight increase at occipital sites (Figure 3a) throughout the lower gamma-frequency ranges. This increase was not significant for either low load (0.05 ± 0.04 μV , $t(11) = 1.22$, n.s), or high load (0.004 ± 0.03 μV , $t(11) = 0.16$, n.s).

Spectral amplitude induced by stimulus presentations showed a slight enhancement in a time window from approximately 170 to 410 ms after stimulus onset in a frequency range between 30 and 80 Hz (Figure 3b). This enhancement was also not significant when tested against zero for either low load (0.01 ± 0.03 μV , $t(11) = 0.25$, n.s) or high load (0.04 ± 0.03 μV , $t(11) = 1.32$, n.s.).

Conclusion

Behavioural effects of perceptual load were obtained both in error rates and RTs. Early ERP components P1 and N1 were not significantly modulated by perceptual load. This confirms our hypothesis and is in accordance with Handy et al's (2001) predictions that under constant attentional allocation the early effects of load should be eliminated. It was also determined that low and high load local-form stimuli did not produce significant enhancements in either evoked or induced GBA. This leads to the conclusion that the matching tasks of either low or high load do

not have the capacity to elicit significant event-related GBA, such as the one usually observed in object recognition tasks, when presented in isolation.

Experiment 2

In Experiment 2 the local form stimuli of low and high perceptual load were co-presented with either familiar or unfamiliar task-irrelevant objects. Behavioural effects of load in the absence of effects of distractor type were expected since this has been observed in previous studies where load varied from trial to trial (e.g., Murray & Jones, 2002). To repeat the crucial hypotheses; induced GBA elicited by presentations of familiar as opposed to unfamiliar objects was expected to show enhancements, driven by increases in activity under low load. Additionally it was expected that evoked GBA would dissociate from induced GBA by showing enhancements with increases in perceptual load irrespective of distractor type.

Methods

Participants

Nineteen participants took part. Three had to be removed from the sample due to excessive EEG artifacts. The remaining sixteen (4 male), aged 19-46 years (mean age 24.5 years) were all healthy, right-handed university students and received class credit or a small honorarium for participation. Participants reported normal or corrected-to-normal vision. Individual written informed consent was obtained and the study conformed to the Code of Ethics of the World Medical Association.

Materials and procedure

The central stimuli from Experiment 1 were superimposed over a background that could contain either a familiar object or an unfamiliar object. The unfamiliar objects were created from

familiar objects by image distortion (see Figure 4 for examples). Intersecting the factors of load and familiarity four conditions were formed: low load familiar, low load unfamiliar, high load

insert Figure 4 about here

familiar and high load unfamiliar. 96 stimuli were shown for each of the four conditions. As the object set contained 384 images, each of the 192 local form stimuli were shown twice during the experiment and were assigned to two pairs of images, familiar and unfamiliar.

The objects in the images were 1.4° to 4.5° of visual angle in size. The presentation was randomised and counterbalanced to ensure that if one participant saw one half of the images in familiar and the other half in unfamiliar form a second matched participant would see them presented in opposite conditions, i.e., if one saw the ‘cat’ the other would see the distorted version of the ‘cat’.

The experiment consisted of four blocks lasting approximately five minutes and containing 96 trials each. Each trial consisted of a variable 500-800 ms baseline period during which a red fixation cross (0.2° x 0.2°) was presented. This was followed by a stimulus picture that was displayed for 650 ms. The picture was then replaced by the fixation cross which remained on the screen for a period of 750 ms (see Figure 5 for trial outlook).

insert Figure 5 about here

The experiment used the same tools and equipment as Experiment 1. Stimulus presentation setup and response collection were also the same. Participants were instructed to perform the task as in Experiment 1 and were told to ignore the irrelevant background images.

EEG recording

For general information on EEG recording procedure see methods section for Experiment 1. The average rejection rate in this experiment was 25.9% resulting in an average of approximately 64 remaining trials per condition.

Behavioural data analysis

Reaction times between 250 and 1400 ms (the maximum time allowed for responses) after stimulus onset on trials with correct responses were taken into further analysis. Mean RTs and error rates were computed for each participant. Differences in error rates and response speed between conditions were analysed with a 2 x 2 repeated measures ANOVA with the within-subject factors of perceptual load (low and high) and distractor type (familiar or unfamiliar object).

Event-related potentials analysis

As in Experiment 1 a 25 Hz low-pass filter was applied to the data before all ERP analyses. Two early (P1, N1) and two late (L1, L2) ERP components were assessed. For each component regional means (shown in Figure 6, see Results) were assigned to areas encompassing maximal activity electrodes when data was collapsed across conditions. Average amplitudes across electrodes at these sites in the respective time window (see Table 1, Results section) were then computed and the mean amplitude during the period 100 ms prior to stimulus onset (baseline) was subtracted. Mean latencies were not analysed since no differences were predicted. Each component was subject to a 2 x 2 repeated measures ANOVA comprising the within-subjects

factors of perceptual load (low and high) and distractor type (familiar and unfamiliar objects). Means and standard error rates are reported throughout the results section. Post-hoc tests were performed using paired t-tests.

Analysis of Evoked and Induced Spectral Changes

Oscillatory activity was analysed according to the same general procedure described in the methods section of Experiment 1. The time windows and regional means were selected on the basis of grand mean TF plots and topographies and GBA was analysed in the ± 5 Hz frequency band around the wavelets of interest; 35 Hz for evoked GBA and individual maximal wavelet for induced GBA. The evoked GBA did not exhibit a specific peak and therefore a 30-40 Hz range was chosen in order to make the findings comparable to previous studies (Herrmann et al., 2004a; Gruber and Müller, 2005).

In order to obtain differential activity in the gamma-band that reflected object-specific processing, activity elicited by unfamiliar objects was subtracted from the activity elicited by familiar objects within every load level; i.e., low load familiar minus low load unfamiliar; high load familiar minus high load unfamiliar. The same procedure was employed to obtain differential activity in the gamma-band related to task demands only, with activity elicited by low load subtracted from activity elicited by high load tasks within every object familiarity level (i.e., high load unfamiliar minus low load unfamiliar; high load familiar minus low load familiar). The sites with maximal amplitude changes between conditions were identified from the topographies of differential activity obtained by the subtractions. GBA amplitude was tested at these sites with a 2x2 repeated measures ANOVA with the within-subject factors of perceptual load (low and high) and distractor type (familiar or unfamiliar object). Tests were performed on the activity in the ± 5 Hz frequency band around each participant's maximal wavelet for induced GBA and on the activity in the 30-40 Hz range for evoked GBA. Subtractions of GBA elicited by different conditions have already been used in studies that employed stimuli which were highly comparable

between conditions (e.g., the coloured checker boards used in the attentional study by Müller and Keil, 2004). Such subtractions make it possible to isolate the activity related to a specific function. It was expected that the overall amplitudes in Experiment 2 would be rather small, as the small visual material for the matching task (Experiment 1) and unfamiliar objects (Gruber and Müller, 2005) elicit very little event-related GBA on their own. By topographically localising the differences between closely matched conditions, load or familiarity, one is able to maximise the signal by focusing on the aspects that are most likely to reflect the representational processes of interest. Means and standard errors are reported throughout.

Results

Behavioural data

Mean error rates with SEs were as follows: low load unfamiliar object, $2.2 \pm 0.5\%$; low load familiar object, $1.9 \pm 0.3\%$; high load unfamiliar object, $11.8 \pm 1.4\%$; and high load familiar object, $13.6 \pm 1.7\%$. Mean RTs with SEs were: low load unfamiliar object, 699 ± 14 ms; low load familiar object, 705 ± 15 ms; high load unfamiliar object, 916 ± 14 ms; and high load familiar object, 925 ± 17 ms. There were no interactions between the two factors of perceptual load and distractor type (error rates: $F(1,15) = 1.56$, n.s.; RTs: $F(1,15) = 0.13$, n.s.). There was a main effect of perceptual load with a very significant increase in errors ($F(1,15) = 82.6$, $p < 0.001$) and slowing of responses for high as opposed to low load ($F(1,15) = 912.38$, $p < 0.001$). The factor of distractor type had no effect on error rates ($F(1,15) = 0.86$, n.s.) or speed of responding ($F(1,15) = 2.7$, $p = 0.12$).

Event Related Potentials

Figure 6 depicts the ERP components and Table 1 provides information on their properties. A 2 x 2 repeated measures ANOVA was used to compare across conditions (perceptual load; distractor type).

insert Figure 6 about here

insert Table 1 about here

P1 was maximal at occipital sites and showed no interaction between the two factors ($F(1,15) = 1.58$, n.s.) and no main effect of load ($F(1,15) = 0.78$, n.s.). There was an effect of distractor type ($F(1,15) = 5.34$, $p < 0.05$) being enhanced under high load for unfamiliar items in comparison to familiar items ($t(15) = 2.27$; $p < 0.05$). There were no modulations of the N1 component (load: $F(1,15) = 0.21$, n.s.; distractor type: $F(1,15) = 0.08$, n.s.; interaction of the two factors: $F(1,15) = 1.41$, n.s.). L1 was modulated both by load ($F(1,15) = 31.45$, $p < 0.001$), being enhanced for unfamiliar items, and by distractor type ($F(1,15) = 8.19$; $p < 0.05$), being enhanced for high load stimuli. There was no interaction between the two factors ($F(1,15) = 1.50$, n.s.). L2 was enhanced under high load ($F(1,15) = 8.52$, $p < 0.05$) with a modulation by distractor type ($F(1,15) = 4.06$, $p = 0.06$) that approached statistical significance. There was a trend for enhancements for familiar objects under low load ($t(15) = -1.97$, $p = 0.07$).

Evoked and induced spectral changes

Figure 7a shows grand mean baseline-corrected TF plots for evoked GBA. Figure 7b shows the topography for data collapsed across experimental conditions. Figure 7c shows grand mean amplitudes at the regional mean for each condition. Figure 7d shows topographies of the grand means of subtractions between levels of evoked GBA denoting object specificity within every load type, familiar minus unfamiliar, or task-specificity within every distractor type, high load versus

low load. Figure 7e shows grand mean amplitudes for each condition at the sites of maximal differences represented in Figure 7d.

insert Figure 7 about here

Gamma-band amplitude evoked by picture presentations during a time window of 50-150 ms showed an increase at occipital sites in the 30 to 40 Hz gamma-frequency range (Figure 7a and 7c). This activity extended into the lower frequencies, up to 20 Hz, in accordance with findings on evoked GBA in visual information processing tasks (Keil, Stolarova, Heim, Gruber and Müller, 2003). When tested against zero, as shown in Figure 7b, above-baseline activity was found for low load familiar ($t(15) = 2.43, p < 0.05$) and for both high load conditions (unfamiliar: $t(15) = 3.14, p < 0.01$; familiar: $t(15) = 2.83, p < 0.05$). Significant evoked GBA increases against baseline were not observed for low load unfamiliar objects ($t(15) = 1.5, n.s.$).

Subtractions within load type and distractor type revealed that maximal differences in activity were situated at central occipital sites (Figure 7d). A 2x2 repeated measures ANOVA showed that activity at these sites in the 30-40 Hz range (Figure 7e) remained unmodulated by object familiarity ($F(1,15) = 0.05, n.s.$) or perceptual load ($F(1,15) = 1.57, n.s.$).

Figure 8a shows grand mean baseline-corrected TF plots for induced GBA. Figure 8c shows the topography for grand mean data collapsed across experimental conditions. Figure 8b shows grand mean amplitudes at the regional mean (defined as electrode sites with maximal activity, see Figure 8c) for each condition separately. Figure 8d shows topographies of grand mean subtractions between levels of induced GBA denoting object specificity within every load type, familiar minus unfamiliar, or task-specificity within every distractor type, high load minus low

load. Figure 8e shows grand mean amplitudes for each condition at the sites of maximal differences represented in Figure 8d.

insert Figure 8 about here

Spectral amplitude induced by picture presentations showed an enhancement in a time window from approximately 170 to 450 ms after stimulus onset in a frequency range between 40 and 90 Hz (Figure 8a). This enhancement was highly significant when tested against zero for the low load familiar object condition ($t(15) = 4.83, p < 0.001$) although it was not significant for the low load unfamiliar object condition ($t(15) = 1.44, n.s.$). Both high load conditions elicited induced GBA which was significantly increased compared to baseline (unfamiliar object: $t(15) = 2.72, p < 0.05$; familiar object: $t(15) = 3.38, p < 0.005$).

Differential task-specific activity was computed by subtracting induced GBA elicited by low load tasks from the induced GBA elicited by high load tasks for each participant and then calculating a grand mean across participants to obtain task-related activity within every distractor type. The same type of subtractions (familiar minus unfamiliar object) was performed within every perceptual load level to obtain object-specific activity in the induced GBA. Figure 8d shows that the highest differences were centred on left parieto-occipital sites. When the activity at these sites (Figure 8e) was tested with a 2x2 repeated measures ANOVA a highly significant main effect of object familiarity was found ($F(1,15) = 8.75, p < 0.01$). This effect was mostly driven by increases in induced GBA under low load ($t(15) = -2.25, p < 0.05$) while the object-specific change under high load was not significant ($t(15) = -0.56, n.s.$). There was no main effect of task demands ($F(1,15) = 0.02, n.s.$).

From comparisons between Figures 7b and 8b and the t-tests against zero it is clear that induced GBA was most significantly enhanced for familiar objects under low load. Evoked GBA amplitude was most significantly enhanced for high load items. While induced GBA amplitude was significantly enhanced by object familiarity at left parieto-occipital sites (Figure 8e), occipital evoked GBA remained unmodulated (Figure 7e). Post-hoc tests have shown that object-specific increases in induced GBA were most evident under low perceptual load.

Discussion

In line with previous studies (Lavie, 1995; Murray and Jones, 2002; Lavie, Hirst, de Fockert and Viding, 2004) the obtained behavioural results exhibited main effects of load but not of distractor type suggesting that the attentional focus was consistently assigned to the central stimuli in both low and high load conditions. In line with these findings the early components P1 and N1 were not modulated by load thus confirming Handy et al's (2001) predictions. Therefore, we conclude that throughout the experiment attention was equally allocated to the central stimuli irrespective of perceptual load.

The role of event-related GBA as a neural marker of representational processing of unattended objects can therefore be appraised. According to our hypotheses, some representational processing of unattended objects should occur under conditions of low perceptual load and induced GBA should be a marker of this object-specific activity. In fact none of the studied ERP components (P1, N1, L1 and L2) showed any specific modulations by object familiarity under low load. Significant levels of evoked GBA always preceded enhancements in induced GBA, as predicted by Herrmann et al. (2004b). However, evoked GBA failed to show any significant modulations. The only component that showed specific sensitivity to object familiarity was the induced GBA. This object-specific activity was centred at left parieto-occipital sites; this was especially pronounced when perceptual load was low.

A series of studies had previously failed to find any differential processing of familiar against unfamiliar objects in the evoked GBA (Tallon-Baudry et al., 1996; Fiebach et al., 2005; Gruber and Müller, 2005; Gruber et al., 2006). Herrmann et al. (2004) has thus far been the only study that found a significant increase in evoked GBA for familiar objects. Just as in Herrmann et al. (2004), object identity in this study was task irrelevant and its processing was therefore incidental. Such incidental processing can be bottom-up driven, relying on image-features that are unique to salient object configurations; e.g., the geometrical stability and the qualities of elongation and symmetry axes specific to objects (see Marr, 1982). Evoked GBA is an early marker sensitive to both bottom-up and top-down influences (Busch et al., 2006b) and is extremely responsive to object properties; even more so than early ERPs (Busch et al., 2004). On the basis of many studies on shape familiarity and figure-ground factors (Peterson and Gibson, 1993; Peterson and Gibson, 1994a; Peterson and Gibson, 1994b; for an overview see Peterson and Skow-Grant, 2003) it was concluded that object memories constitute a configural cue that contributes to early perceptual organisation, it is therefore very difficult to argue in favour of a particular mnemonic role for evoked GBA separate from its function as a marker of feature-based processing that is sensory in origin (Karakas and Basar, 1998). Further research should focus on the importance of task-relevance of object identity since this is likely to play a crucial role in determining whether evoked GBA shows a more bottom-up effect of configural processing when identity is task-irrelevant (Herrmann et al., 2004) or a more top-down effect of task-relevant processing of image's features for the purpose of identification (Tallon-Baudry et al., 1996; Fiebach et al., 2005; Gruber and Müller, 2005; Gruber et al., 2006).

This study did not support the hypothesis that evoked GBA would be a sensitive marker for increases in task demands. This negative finding is similar to Posada et al.'s (2003) study which found no effects of task complexity on evoked GBA by contrasting a simple colour-to-button visual association task with a more complex rule-based task. It runs contrary to Senkowski & Herrmann's (2002) finding that increased task complexity augments evoked GBA. Senkowski &

Herrmann (2002) contrasted a complex task to a passive viewing task, which suggests that changes in demand need to be sufficiently large in order to modulate evoked GBA amplitude. Posada et al. (2003) found an effect of task complexity on induced gamma-band oscillations at right parietal sites and explained it by additional attentional top-down influences introduced by the need to perform a rule-operation in the complex task. In the current study, due to randomly intermixed trials of low and high load, attention remained constrained to the local-form stimuli by top-down influences. This explains why induced GBA remained unmodulated by changes in task demands between the low and high load.

It is also necessary to contrast Experiment 1, which found no significant GBA for low or high load tasks in isolation, with Experiment 2, which found both evoked and induced GBA were significantly enhanced against baseline when high load distractors were paired with unfamiliar objects. This implies that a simple increase in the complexity of the stimulus results in above-baseline increases in activity. These enhancements are likely to be an outcome of more intense suppression of the surrounding spatially-coexistent distractors while performing a perceptually demanding high load task. This explanation is in accordance with the biased competition model of attention which applies in particular to the processing within the ventral visual stream responsible for object recognition (e.g., see Desimone, 1998). It suggests that the competition arising from more complex stimulus configurations could in itself result in enhanced levels of event-related GBA. This is not surprising since synchronisation of responses in the visual cortex at the frequencies of 20-65 Hz has been shown to result from intercortical coupling mechanisms whose effectivity rises as central activation increases (Herculano-Houzel, Munk et al. 1999). Furthermore, neurons which receive the inhibitory postsynaptic potentials of GABAergic interneurons form the root of these high frequency components in network-driven synaptic activity since their potentials carry more synchronicity and power in the gamma-band range (Hasenstaub, Shu et al. 2005). Interneuronal involvement has also been explicitly acknowledged by the representational hypothesis of Tallon-Baudry and Bertrand (1999). Similarly, a modulation of the

P1 by distractor type was also found in this study, with specific enhancements for unfamiliar objects under high load. This leads to the supposition that an interplay between concurrent early enhancement of central task-relevant information and suppression of co-localised distractors might reflect on the P1 effect (Luck, 1995).

Field Code Changed

Returning to the crucial finding that induced GBA is the only object-specific marker of representational neural processing, ERP components L1 and L2, that relate to the processing of objects, did not show such specificity. The late ERP component L1 was modulated by object familiarity and load, being monotonously enhanced both for high load and for unfamiliar objects. L1 enhancements for unfamiliar objects are in line with previous findings (Gruber and Müller, 2005). The late component L2 showed a trend to increase under high load for familiar objects. This supports Gruber and Müller (2005) who also found a trend towards L2 enhancements for repetitions of familiar objects showing that this late component, related to semantic processing, is responsive to familiar object identities. These robust ERP findings are in accordance with existing literature but this study's main contribution lies in its ability to demonstrate that induced GBA is the most relevant marker of representational processing of unattended objects. This further strengthens Tallon-Baudry and Bertrand's (1999) representational hypothesis which claims that induced GBA is a neural marker of cortical object representation.

Increases in induced GBA for familiar objects were driven by enhancements in activity under low load in accordance with Lavie's (1995) model. This model claims that high load effectively reduces distractor perception and predicts that under high load no priming should be possible. Since induced GBA is a priming-sensitive component (Gruber and Müller, 2002; Gruber et al., 2004; Fiebach et al., 2005; Gruber and Müller, 2005) the lack of object-specific effects under high load could also have been predicted thus further supporting the representational hypothesis.

Finally the lack of object-specific effects under high load has important implications for the role of attentional selection in visual representation of objects. High load conditions with foveally

co-localised items can be perceived as a simplified model of object processing in complex visual scenes. From our findings it is clear that selective attention does have a crucial role to play in the processing of objects under high perceptual demands. Such high demands loosely approximate everyday situations in which the visual system is faced with multitudes of ambiguous, cluttered visual scenes. Objects under low load conditions seem to hold a privileged status in the processing hierarchy and can capture perceptual resources, which is reflected in specific increases of induced GBA. Under high load conditions however processing is determined by perceptual mechanisms of attentional selection. In situations that involve competition between different stimuli these mechanisms ensure the most efficient processing of attended content with a general suppression of surrounding information. Taken together this evidence further supports the idea that high frequency oscillatory synchrony, and in particular its induced component, is likely to be a fundamental mechanism both for automatic coherent percept formation and for perceptual information processing and attentional selection, also evidenced in a recent magnetoencephalographic study on induced GBA (Vidal, Chaumon, O'Regan and Tallon-Baudry, 2006). As object coding is heavily reliant on perceptual, mnemonic and attentional processes this explains why visual representation of objects is specifically marked by enhancements in induced high-frequency oscillatory synchrony.

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Table 1. ERP Components: time windows and mean baseline-corrected amplitudes (n=16)

Component	Time window (ms)	Low perceptual load Amplitude in μV (Mean + SE)		High perceptual load Amplitude in μV (Mean + SE)	
		Unfamiliar	Familiar	Unfamiliar	Familiar
P1	80-120	3.08 ± 0.61	2.93 ± 0.54	3.33 ± 0.65	2.88 ± 0.64
N1	130-190	-0.18 ± 0.86	-0.42 ± 0.93	-0.43 ± 0.94	-0.29 ± 0.89
L1	200-370	2.01 ± 0.94	1.45 ± 0.91	2.85 ± 0.93	2.52 ± 0.89
L2	480-600	-0.15 ± 0.68	0.26 ± 0.60	0.65 ± 0.53	0.98 ± 0.57

Legends to Figures:

Figure 1. Examples of stimuli. **a)** low load items; **b)** high load items; **c)** low and high load items organised around a fixation cross so that the upper position is taken by the line-form that is to be matched with one of the two line-forms in the lower boxes (lines for low load, letters for high load); **d)** trial outlook.

Figure 2. **a)** Grand mean baseline-corrected ERP waveforms averaged across electrodes. Shaded areas indicate components of interest. **b)** Scalp topographies of P1 and N1 components reflecting grand mean data averaged across all conditions. Boxes indicate electrode sites included in the regional mean. Note: different voltage scales.

Figure 3. Evoked **(a)** and induced **(b)** GBA. **(I)** Grand mean baseline-corrected TF-plots averaged across 128 electrodes and all conditions. Black boxes indicate the time-window for statistical analysis. **(II)** Grand mean 3D spherical spline amplitude-maps (averages across all conditions) based on the ± 5 Hz frequency band centred on the wavelet of interest (35 Hz for evoked, individual maximal wavelet for induced) during the selected time-window. Black boxes indicate electrode sites included in the regional mean.

Figure 4. Examples of stimuli. **a-I)** low load, familiar objects; **a-II)** high load, familiar objects; **b-I)** low load, unfamiliar objects; **b-II)** high load, unfamiliar objects.

Figure 5. Trial outlook for Experiment 2.

Figure 6. Left column: scalp topographies of P1, N1, L1 and L2 from grand mean data averaged across all conditions. Boxes indicate electrode sites included in regional means. Right column: Grand mean baseline corrected ERP waveforms at the regional means. Shaded areas indicate components of interest. (LF: low load familiar; LU: low load unfamiliar; HF: high load familiar; HU: high load unfamiliar). Note: different voltage scales; also note that P1 and N1 both are shown at P1 sites only as there is considerable overlap resulting in highly similar waveforms.

Figure 7. Evoked GBA. **(a)** Grand mean baseline-corrected TF-plot averaged at the regional mean sites (see panel b) across all conditions. Box indicates the time window for statistical analysis. **(b)** Bar plot of amplitudes of evoked GBA for each condition at the regional mean during the selected time window, with SE bars. **(c)** Grand mean 3D spherical spline amplitude-map (average across all conditions) based on the ± 5 Hz frequency band centred on the 35 Hz wavelet during the selected time-window. Box indicates electrode sites included in the regional mean. **(d)** Grand mean 3D spherical spline amplitude-maps of subtractions performed to isolate object-specific activity for each load (I and II) and load-specific activity for each distractor type (III and IV). Amplitude maps are based on subtractions of grand-mean baseline-corrected amplitudes within the ± 5 Hz frequency bands centred on the 35 Hz wavelet during the selected time-window; sites of maximal differences are indicated by the box (LF: low load familiar; LU: low load unfamiliar; HF: high load familiar; HU: high load unfamiliar). **(e)** Bar plot of amplitudes of evoked GBA for each condition at the sites of maximal differences during the selected time window, with SE bars. * indicates significance against zero at $p < 0.05$, ** at $p < 0.01$. Note: different voltage scales.

Figure 8. Induced GBA. **(a)** Grand mean baseline-corrected TF-plot averaged at the regional mean

(see panel b) across all conditions. Box indicates the time window for statistical analysis. **(b)** Bar plot of amplitudes of induced GBA for each condition at the regional mean during the selected time window, with SE bars. **(c)** Grand mean 3D spherical spline amplitude-map (average across all conditions) based on the ± 5 Hz frequency band centred on the maximal individual wavelet for each participant during the selected time-window. Box indicates electrode sites included in the regional means. **(d)** Grand mean 3D spherical spline amplitude-maps of subtractions performed to isolate object-specific activity for each load (I and II) and load-specific activity for each distractor type (III and IV). Amplitude maps are based on subtractions of grand-mean baseline-corrected amplitudes within the ± 5 Hz frequency bands centred on the wavelet of interest during the selected time-window; sites of maximal differences are indicated by the box (LF: low load familiar; LU: low load unfamiliar; HF: high load familiar; HU: high load unfamiliar). **(e)** Bar plot of amplitudes of evoked GBA for each condition at the sites of maximal differences during the selected time window, with SE bars. * indicates significance against zero at $p < 0.05$, ** at $p < 0.01$. Note: different voltage scales.

Figure 1

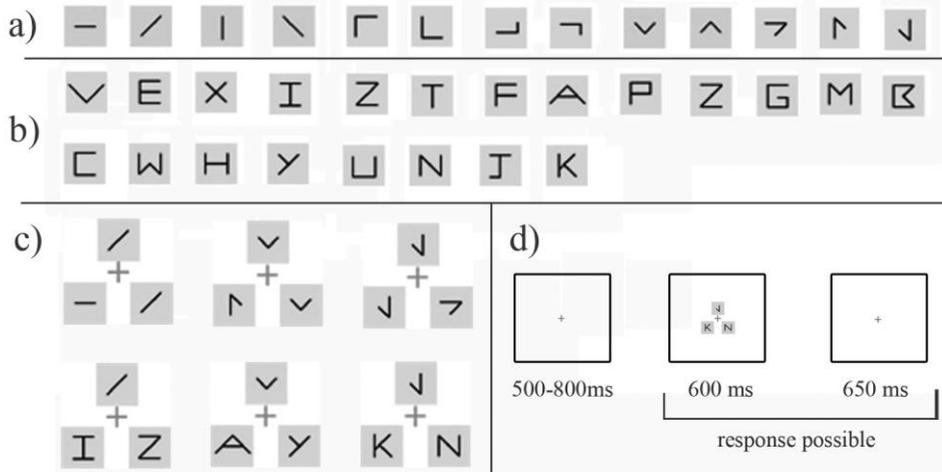


Figure 2

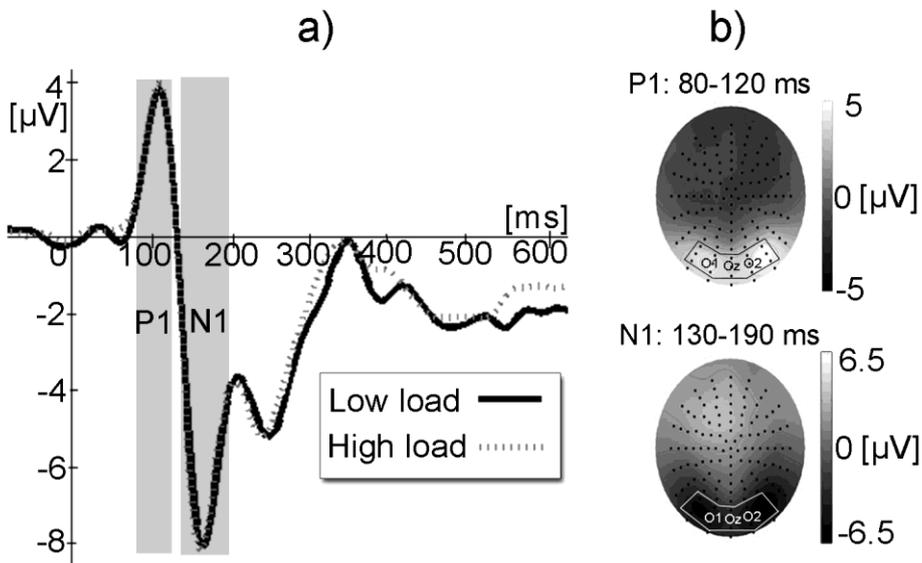


Figure 3

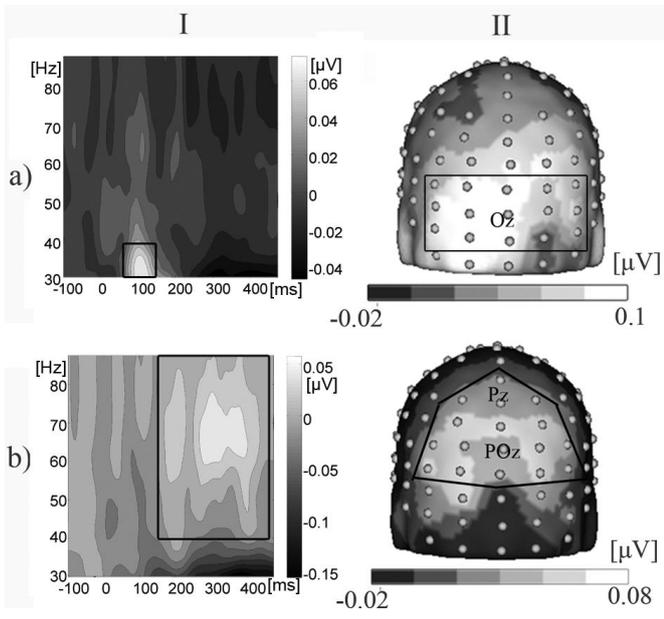


Figure 4

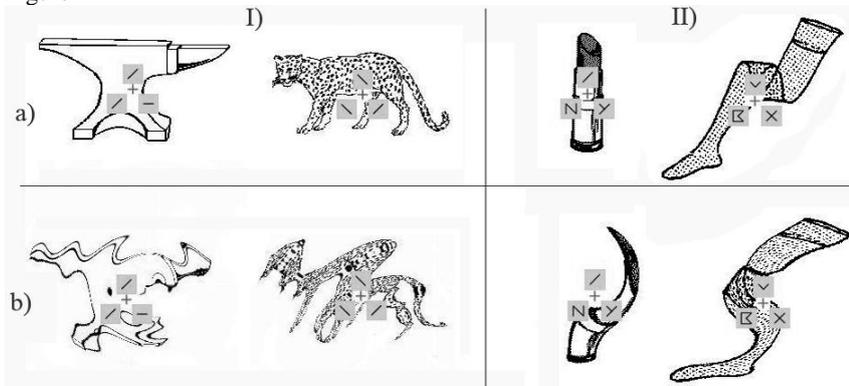


Figure 5

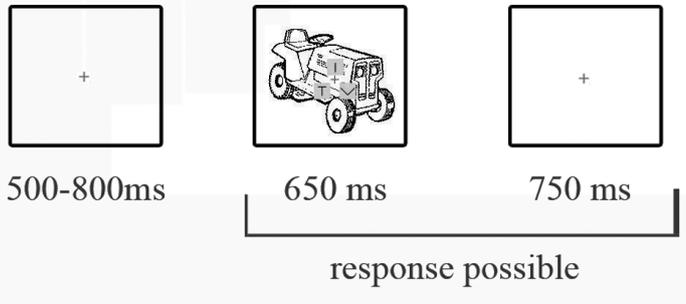


Figure 6

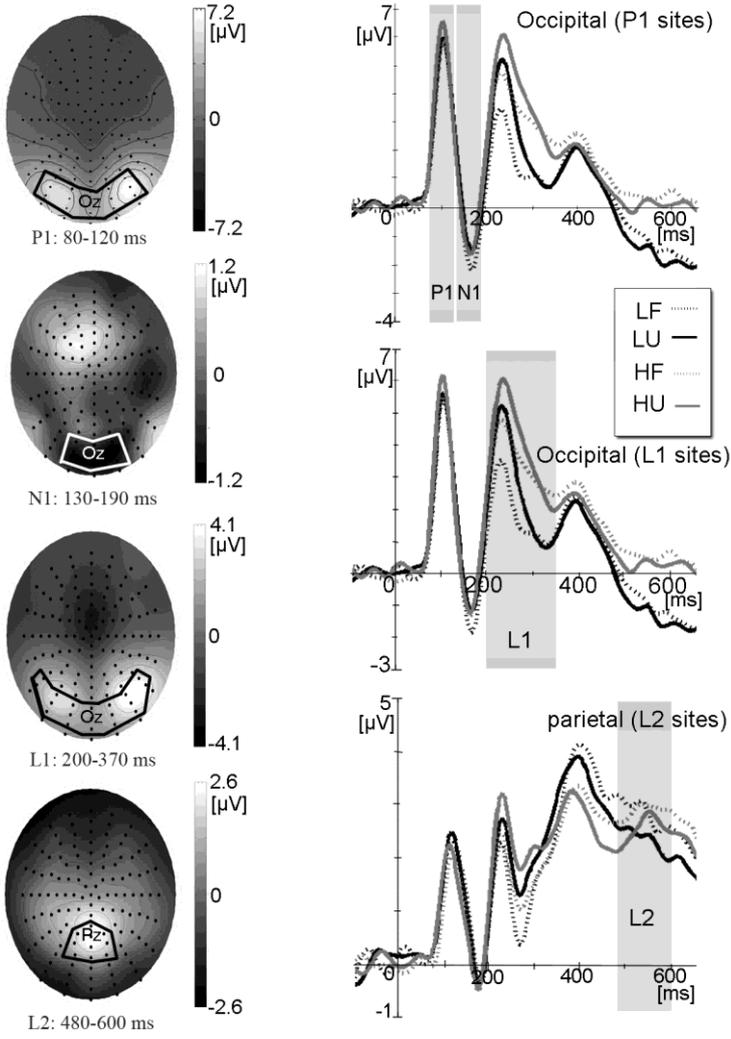


Figure 7

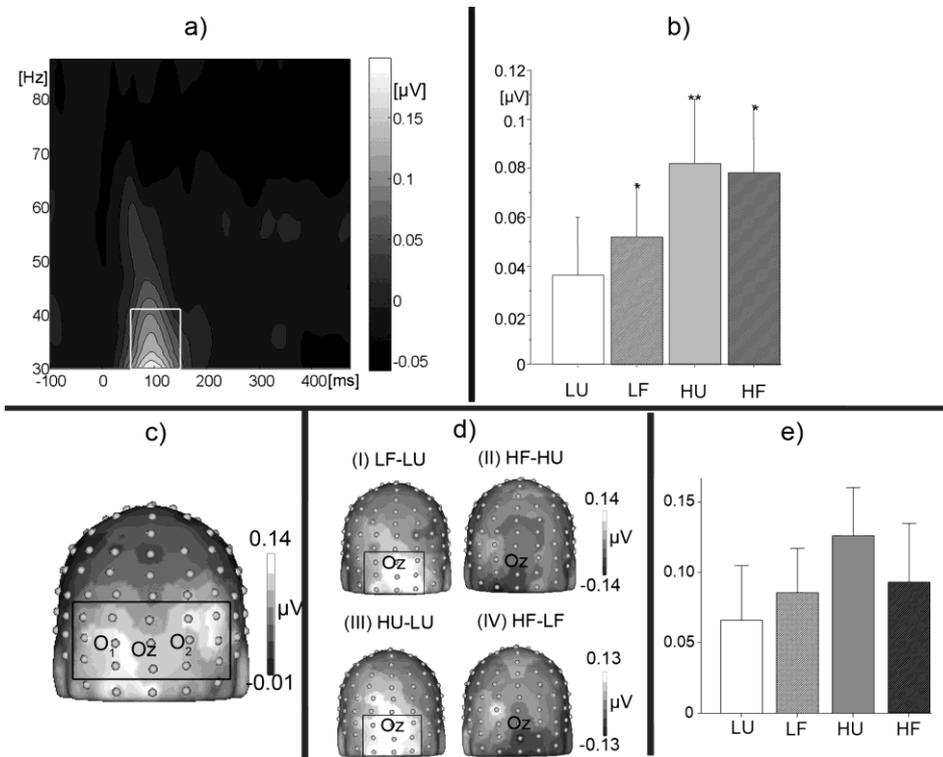


Figure 8

