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## Human non-phase-locked gamma oscillations in experience-based perception of visual scenes

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### Abstract

Perception results from ongoing interactions between stimulus-driven visual processes and cognitive context. These reciprocal relations are emphasized when a visual stimulus is degraded, forcing the perceiver to fill the missing information in, based on internal representations. The neural mechanisms by which internal representations facilitate visual perception are still unclear. Here we investigated the role of EEG oscillations in the gamma band, thought to reflect the elaboration of internal visual representations, in the experience-based perception of visual scenes. Twelve subjects were trained with degraded images of natural scenes. EEG was recorded while they performed a detection task on trained and untrained degraded stimuli. Non-phase-locked gamma band responses in a large frequency spectrum (55–85 Hz) were observed around 200 ms post-stimulus onset at posterior sites, and were larger when subjects reported an accurate perception based on previous experience. These results suggest that mid-latency gamma oscillations in the visual cortex underlie the experience-based perception of visual scenes.

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At first glance, degraded pictures as shown in Fig. 1a appear as meaningless black blobs on a white background. However, a single exposure to their grey-scale versions entails a dramatic change in perception: one then no longer fails to detect the duck and the squirrel in the formerly meaningless images. This example illustrates how perceptual organization may rely on information not present in visual input. In the same way, everyday visual perception is guided not only by retinal input, but is also largely determined by the cognitive context, the perceiver's expectations, motivations, and previous experience [2]. In other words, visually degraded stimuli emphasize the interactions existing between the perceptual organization of visual input, and the internal representations, forged by previous experience [11]. Yet, the neural mechanisms

subtending such perception through visual experience are currently not well understood (e.g. Ref. [3]).

EEG recordings conducted on human subjects have revealed the existence of transient high frequency oscillations (> 30 Hz), referred to as gamma band oscillations (GBOs, see Refs. [5,9,16] for reviews). These oscillations can be either phase-locked (PL) or non-phase-locked (NPL) to the stimulus onset. Early PL GBOs correlate with elementary visual properties and selective attention [1,7]. NPL GBOs occur generally between 180 and 300 ms post-stimulus onset. They are mainly located on posterior visual sites and are thought to reflect the elaboration of complex visual representations in the brain [8,14,15]. Reflecting intrinsic EEG dynamics, NPL GBOs are also likely to subtend the integration of cognitive context and sensory processing [4].

In the present study, the role of NPL GBOs was investigated in a situation where a visually coherent representation is elaborated, based on the previous experience of the observer. Subjects were presented with degraded images that were not recognized unless previously associ-

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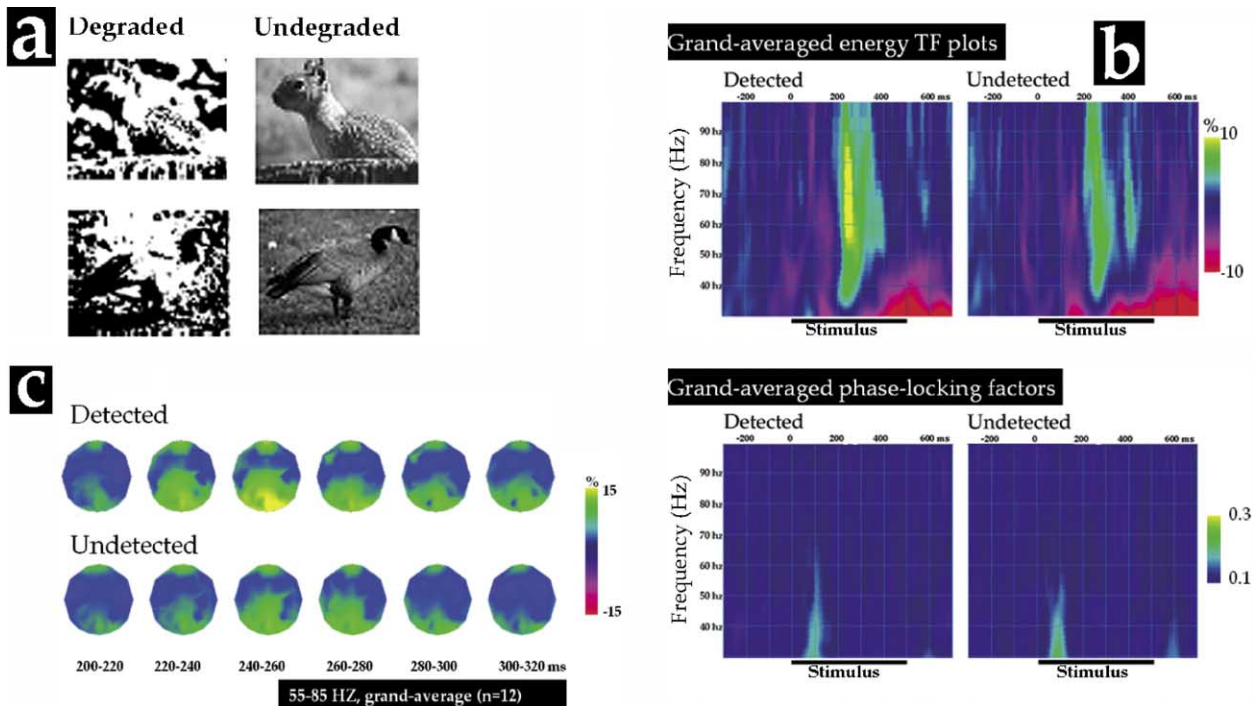


Fig. 1. (a) Examples of the degraded stimuli used in the experiment as well as undegraded, original, images. (b) (Top) Grand-averaged time-frequency (TF) tables are depicted for detected and undetected conditions, when posterior scalp regions (parietal and occipital) are collapsed. Amplitude values are expressed as percentages relative to baseline level (300 ms prior to stimulus onset). (Bottom) Phase-locking factor grand-averaged across subjects and for posterior scalp regions is illustrated for the two conditions. (c) Scalp topography of gamma energy modulations (55–85 Hz frequency range;  $n = 12$ ) over time and across conditions.

ated with non-degraded versions of the same pictures. Hence, under identical stimulation conditions, subjects could either activate a coherent and meaningful representation, or fail to do so, depending on previous experience. If complex neuronal assemblies oscillating in the gamma frequency range subtend the elaboration of coherent visual representations in the human brain, pre-experienced degraded images should produce larger posterior NPL GBOs than non-pre-experienced degraded stimuli.

Twelve subjects (eight females, mean age 23.6 years) participated in the experiment. All subjects had normal or corrected-to-normal vision. They gave their informed consent and were paid for their participation. Eighty grey-scale pictures of animals in natural scenes were contrast-binarized (Fig. 1a) in such a way that they could not be identified as meaningful scenes without any pre-exposure to undegraded (grey-scale) versions. All stimuli were presented at the centre of the screen and subtended a  $5.1/4.1^\circ$  visual angle (8 cm/6.5 cm on screen, viewing distance: 90 cm).

The experiment comprised two stages: (1) a training stage, during which subjects learned to detect animals in degraded images, followed a few days later by (2) the experimental EEG session. (1) Subjects were trained with half of the 80 degraded images (image sets counterbalanced across subjects) in five sessions scheduled on five consecutive days. They saw each degraded image paired

with its undegraded counterpart (three repetitions of each pair, presentation duration: 1000 ms) and were explicitly instructed to learn to detect the animal in the degraded images. At the end of the training, subjects were presented with trained and untrained degraded images (mixed and random order), appearing one at a time for 500 ms, and were instructed to overtly name the animal if they detected it. Performance criterion was reached when 85% of the trained images were accurately named. (2) The EEG session was made of four blocks of 150 trials. Trained and untrained degraded stimuli, as well as new undegraded scenes, appeared one at a time during 500 ms (five stimulus repetitions). After each stimulus presentation, subjects had 1200 ms (randomized between 1100 and 1300 ms) to report as quickly and accurately as possible by a key press whether they had detected the animal in the image or not.

EEG was recorded (500 Hz sampling rate) on 58 tin electrodes mounted in an Electrocap<sup>®</sup> (standard 10–20 system locations and additional intermediate positions) with the left earlobe as physical reference (impedances below 5 k $\Omega$ ). Four facial bipolar electrodes monitored horizontal and vertical EOG. The signal was amplified by Synamps<sup>®</sup> amplifiers and band-pass filtered online at 0.01–100 Hz. We used an online 50 Hz-notch filter and an offline 68–72 Hz FFT band-pass filter to eliminate interference due to alternative electrical current and video monitor refresh rate, respectively. EEG was re-referenced offline to linked

earlobes and segmented in [–500, 1000 ms] time epochs. After artefact rejection (excluding epochs exceeding –100/100  $\mu\text{V}$  threshold), the number of trials was equalized across conditions (trained/detected and untrained/undetected) for each subject, resulting in a mean of 126 trials averaged by condition per subject.

The continuous Morlet wavelet transform (CMT) of EEG epochs was used to identify stimulus-induced oscillations. Explored frequencies ranged from 30 to 100 Hz in steps of 1 Hz (for more technical details see Ref. [12]). CMT was applied on each individual trial and then averaged across trials for each subject. This enhanced both PL and NPL activities. To reveal the time-locked modulations of oscillation amplitude, results were expressed as relative increase or decrease, as compared to a pre-stimulus reference period (i.e. –300 to 0 ms; Fig. 1b–d). There was no significant difference across conditions in this pre-stimulus interval ( $P > 0.12$ ). Phase-locking of oscillatory activities was estimated by computing the phase-locking value (PLV [10]). This value, ranging from 0 (NPL) to 1 (strictly PL), reflects the phase distribution across trials as a function of time and frequency. The gamma energy modulations were analyzed separately for the trained/detected and the untrained/undetected conditions, referred to as *detected* and *undetected* conditions below. Mean time-frequency (TF) windows of energy were extracted in each subject and condition (detected and undetected) at four electrode sites, allowing us to examine NPL GBO temporal and spatial distribution: frontal (FP1, F3A, F1, F3, F5, FPZ, FZ, FP2, F4A, F2, F4, F6), central (C1A, C3A, C5A, C1, C3, C5, CZA, CZ, C2A, C4A, C6A, C2, C4, C6), parietal (C1P, C3P, P3, P1, PZA, PZ, C2P, C4P, P2, P4), and occipital (P1P, P3P, O1, PZP, OZ, P2P, P4P, O2) regions. Repeated-measure ANOVAs were applied to assess the effects of and interaction between *site* (frontal vs. central vs. parietal vs. occipital), electrode *lateralization* (left vs. midline vs. right) and *detection* (detected vs. undetected) factors. When appropriate,  $P$  values were adjusted by Greenhouse–Geisser correction. Post-hoc comparisons were performed using polynomial contrasts.

During EEG recording, subjects reported the detection of the animal in 74.5% ( $\sigma \pm 19\%$ ) of the trained images whereas they did not detect anything in 65% ( $\sigma \pm 33\%$ ) of the untrained images. Subjects were faster in detected ( $790 \pm 12$  ms) than undetected ( $926 \pm 8$  ms) conditions ( $F(1, 11) = 71.41$ ,  $P < 0.0001$ ), indicating the clear behavioural benefit of previous experience with undegraded images in the former case. Grand-averaged TF plots ( $n = 12$ ) revealed an increase in energy in the 55–85 Hz band, in both detected and undetected conditions (Fig. 1b). These GBOs started at 200 ms, and peaked around 250 ms, mainly over parietal and occipital scalp sites ( $F(1.3, 14) = 13.1$ ,  $P < 0.001$ ). *Detection* interacted significantly with *site* ( $F(2.5, 27) = 9.02$ ,  $P < 0.001$ ) in the 220–280 ms time interval. Detected trials led to significantly larger amplitudes than undetected trials on occipital

sites ( $P < 0.05$ ) but not on parietal, central nor frontal sites ( $P > 0.2$ ). The PLV transform showed that these GBOs were not accompanied by an increase of phase-locking to stimulus onset (Fig. 1b, bottom part). Two PL peaks of phase-locking occurring at lower frequencies (30–45 Hz) around 100 ms after stimulus onset and 100 ms after stimulus offset were observed. These responses did not, however, differ between conditions.

In summary, presenting degraded visual stimuli induced NPL GBOs starting at around 200 ms post-stimulus onset, predominantly at posterior electrodes. This is in agreement with previous evidence that NPL GBOs in human EEG are related to the visual processing of shapes, be they learned and meaningful or not to the perceiver [13–16]. However, increased GBO amplitude, observed when the same stimuli were recognized, suggests that these activities also subtend top-down influences of prior knowledge on bottom-up visual processing, as previously hypothesized [4].

An important aspect of the current findings is that the modulations in GBO energy result from the pre-acquired ability of the subject to segment the scene correctly and not from variations in gestalt grouping criteria. Indeed, all images were identically degraded and the set of stimuli selected for training was counterbalanced across subjects. An account in terms of exposure frequency is also unlikely; although the detected stimuli were more frequently presented than undetected stimuli during the training procedure, recent evidence shows that repetitive presentation of visual stimuli decreases, rather than increases, the energy of NPL GBO [6].

This directly supports the hypothesis that human NPL gamma oscillations not only reflect the bottom-up elaboration of coherent visual representation, but also subtend the modulation of visual processes by the perceiver's internal representations and cognitive context [4,13]. These findings are also in agreement with neuroimaging evidence from a similar previous study in humans, showing the involvement of several posterior regions such as the fusiform gyrus, and the medial and lateral parietal cortices in mediating such experience-based perception of objects [3]. Our findings extend these observations by showing that such integrations take place during a short time epoch, at a relatively early latency following stimulus onset (here between 200 and 300 ms). Further experiments will have to clarify whether top-down influences on gamma activity result from long-range synchronization between distant cortical areas [17].

This study thus showed that experience-based perception of objects embedded in degraded visual scenes involves an increase of GBOs of neural populations in the human visual cortex around 200 ms following stimulus onset. These observations support the hypothesis that high frequency oscillations are an important component of top-down influences on visual perception.

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