SSVEP as a no-report paradigm to capture phenomenal experience of complex visual images

Adélaïde de Heering, Arnaud Beauny, Laurène Vuillaume, Leila Salvesen & Axel Cleeremans

CO3, Centre for Research in Cognition & Neurosciences, Université libre de Bruxelles, Avenue F. Roosevelt, 50 CP 191, 1050 Bruxelles, Belgium.

Correspondence to:

Adélaïde de Heering

Centre for Research in Cognition & Neurosciences

Université Libre de Bruxelles

Avenue F. Roosevelt, 50 CP 191

B-1050 Belgium

E-mail: addeheer@ulb.ac.be

ABSTRACT

The goals of this study were (1) to develop a novel type of no-report paradigm capable of capturing people's phenomenal experience when they see complex images, and (2) to explore the extent to which such images can be processed in the absence of consciousness. To this end, we took advantage of a powerful technique derived from electroencephalography: the steady state visual evoked potentials (SSVEP) technique. We used faces embedded in sequences of non-face stimuli, which we manipulated the contrast of so as to create subliminal and supraliminal conditions. Our results are twofold. On the one hand, they indicate that the SSVEP response, which signalled the ability of the brain to categorize faces, was strongly reduced, but nevertheless maintained, when participants reported being unable to see the stimuli. In this condition, the response was confined to early visual stages, whereas it propagated through the ventral stream in conditions in which image contrast increased. On the other hand, the method appears as useful to consider as a novel instance of a no-report paradigm because it requires no overt behavioural response and because its outputs (signal magnitude and scalp topography) predict people's self-reported phenomenal experience.

Keywords: consciousness, subliminal, faces, steady states, no-report.

INTRODUCTION

Identifying the neural correlates of conscious experience remains a significant challenge in the field of cognitive neurosciences. Since the seminal work of Crick and Koch (1990), it has become clear that the very notion of a "neural correlate of consciousness" is problematic. It is unclear, for instance, whether we are looking for a single area, for a network of interacting areas, or for a specific kind of process to subtend conscious experience (Chalmers, 2000). Likewise, it is still unclear how to best distinguish the "true" neural correlates of consciousness from its prerequisites (NCC-pr) and from its consequences (NCC-co) - in other words, how to neutralize what is specific to conscious experience from other factors such as working memory or selective attention that are known to contaminate the identification of the specific mechanisms that underpin conscious experience (Aru, Bachmann, Singer, & Melloni, 2012; De Graaf, Hsleh, & Sack, 2012; Koch, Massimini, Boly, & Tononi, 2016). Further, multiple confounds have been identified that also compromise this endeavour. Lau and Passingham (2006), for instance, showed that performance, which is typically better when people report seeing a stimulus than when they do not, elicits its own neural correlates. Similarly, the typical requirement for participants to report on their conscious state also generates report-driven activity in the brain that may not be observed when people are not asked to produce them (Tsuchiya, Wilke, Frässle, & Lamme, 2015; see also Koch et al., 2016; Lamme, 2010; Odegaard, Knight & Lau, 2017). Lately, these concerns have motivated the development of so-called no-report paradigms, which offer the promise of building indirect measures of subjective experience, hence making it possible to avoid verbal or motor reports. Technically, such paradigms also offer an opportunity to get closer to real-life situations, during which individuals seldom reflect, or report, on their thoughts or experiences of the world. Thus far, amongst possible indirect measures are simple physiological measures, such as eye movements or pupil size, the modulations of which have been used to objectively and continuously map perceptual alternations from binocular rivalry stimuli, for example (Frässle, Sommer, Jansen, Naber, & Einhauser, 2014; for a review see Blake & Logothetis, 2002). Invasive local field potentials (LFP; Einevoll, Kayser, Logothetis, & Panzeri, 2013) and general flash suppression (GFS; Wilke, Logothetis, & Leopold, 2003; Wilke, Mueller, & Leopold, 2009) have also sometimes been used to shed light on which brain regions participate to subjects' phenomenology. Most of these measures nevertheless lack sensitivity (e.g., all-or-none responses) and flexibility (e.g., the requirement of fixating participants' head).

In this context, the major goal of this study was to develop a novel type of no-report paradigm based on electrophysiological methods. To do so, we relied on a sensitive paradigm originally designed to capture participants' brain response when it forms a category from very different faces and excludes the exemplars that do not belong to this category (Jacques, Retter, & Rossion, 2016; Rossion, Torfs, Jacques, & Liu-Shuang, 2015). This paradigm has been associated with a powerful technique derived from electroencephalography (EEG), the steady state evoked potentials (SS-EP) method (Regan, 1989), which only requires that participants view sequences of images flickering at a given frequency (e.g., 6 Hz = 6 images/second = image frequency) while their EEG is recorded (for evidence on infants with a similar paradigm, see de Heering & Rossion, 2015). In the current study, images were organized so that a face would re-appear every 5th item in a 6 Hz sequence, thus, at the slower frequency of 1.2 Hz (6 Hz/5 = face frequency). Crucially, the visibility of images, manipulated in terms of their overall contrast, was equally degraded for all images composing a given sequence, and also steadily increased over the course of the experiment. As such, participants did not expect faces to re-appear every 5th item in the low-contrast conditions, given that they were kept unaware of any kind of periodicity contained in the SS-EP sequences. In addition, the experimental design allowed us to address questions such as: Is it possible to identify the neural correlates associated to exposure to stimuli degraded to the point that participants report not having seen anything? Does this capability extend to the complex ability to form a visual category from different items? Where does such processing happen in the brain, and how does this activity propagate when the stimulus becomes visible to participants?

Given previous findings (King, Pescetelli, & Dehaene, 2016), we hypothesized that the face categorization paradigm we used here would be particularly sensitive to address such questions, even at subliminal stages - not only because of the documented power and sensitivity of the technique, but also because faces are stimuli that are both very salient and very familiar to people, which undoubtedly constitutes an advantage in any attempt to uncover the brain regions activated during subliminal processing (Navajas, Ahmadi, & Quiroga, 2013). We therefore expected to find significant brain activation at the frequency at which faces were introduced within the sequences, namely at 1.2 Hz (and harmonics) at a visibility level defined as subliminal to the group of participants. We did not have strong predictions about the location of this activity in the brain, but assumed that it could either be associated to very posterior regions (e.g., occipital lobe; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006), or involve face-selective occipito-temporal regions, but then to a lesser extent than what is typically observed at high visibility levels (Jacques et al., 2016; Rossion et al., 2015). We also predicted that the SS-EP technique would be sensitive enough to track down, over the course of a few trials only and at a sufficient spatial resolution for the goals of the current study, the involvement of different portions of the visual pathway as the face contrast increased.

Relating such paradigm to participants' phenomenal experience ("what it feels like to see a face"; Boly et al., 2017) is a task harder to achieve because it does not simply require showing that low and high contrasted stimuli, and their underlying brain regions, are associated to low and high visibility ratings, respectively. This indeed would be totally uninformative to document on what their conscious experience is like. As previously suggested, such task requires in fact contrasting condition(s) for which stimulus content is equalized (Peters, Kentridge, Philips, & Block, 2017; Pitts, Padwal, Fennelly, Martínez, & Hillyard, 2014), as what is typically performed with binocular rivalry paradigms capable of highlighting different phenomenal experiences despite stimulus strength being kept constant across trials, and this regardless of whether the paradigm is associated to magneto- (Srinivasan, Russell, Edelman, & Tononi, 1999; Tononi, Srinivasan, Russell, & Edelman, 1998) or electro-encephalography in its frequency-tagging form (with distinct stimuli flickering at distinct frequencies; Sutoyo & Srinivasan, 2009; Zhang, Jamison, Engel, He, & He, 2011; see also Supèr, Spekreijse, & Lamme, 2001 for evidence in monkeys). With the same idea in mind, we paid particular attention to what happened at fixed contrast levels at which we confronted participants' objective and subjective measurements collected during the EEG session. In particular, we expected the two, indexed through brain activation (signal magnitude and scalp topography) and phenomenal experience that we evaluated here thanks to two visibility scales, to be correlated to each other, which would then validate the use of the current paradigm as a no-report paradigm.

RESULTS

Testing involved two sessions. In an initial behavioural session (SESSION 1), participants categorized briefly presented images (83.33 ms) as either a face (FA) or a non-face (NF). We adjusted the contrast of all images using a one up/one down staircase procedure (range = 0-5%, increment = 0.5%) to keep classification performance at chance level (50%), with the aim of defining the subliminal and supraliminal thresholds. A version of the "Perceptual Awareness Scale" (PAS; Ramsoy & Overgaard, 2004) indexing for participants' subjective visibility on a four-point scale (see methods for more details) was also administered at SESSION 1 to confirm these thresholds. In a second session (SESSION 2), we recorded the same participants' scalp EEG while they viewed the same set of images displayed in 6 blocks of 10 sequences and performed an orthogonal task (i.e., detection of the colour change of a fixation cross). The images composing each sequence were presented in continuous 6 Hz streams (i.e., 6 images per second) for 40 seconds, with a face image presented every 5^{th} item. Critically, the contrast of images was fixed within a block, and increased systematically from one block to the next to avoid expectations being built over the course of the experiment. After each sequence, participants were asked to report on the visibility of the images sequences were composed of by means of two visibility scales: a similar PAS scale as the one used in SESSION 1 and a quantitative version of it.

(1) Behavioural definition of subliminal and supraliminal thresholds

At SESSION 1, in which participants had to explicitly categorize single images as faces (FA) or non-faces (NF) (Figure 1A), the staircase converged over contrast levels ranging from 0.7% to 2.4%. The average convergence value was 1.4% (Figure 1B). Participants' proportion of correct responses for all eleven contrast levels ranged between 0.48 (SE = 0.03) at 0% contrast and 0.88 (SE = 0.06) at 5% contrast (Figure 1C). This indicates a regular increase of performance as a function of image contrast.

The lowest contrast level at which participants' classification performance was statistically higher than chance was 2% contrast (one-sample t-test: $t(14) = 2.704$, $p = .017$), which we defined as the supraliminal threshold. Amongst the conditions qualified by less contrast (i.e., 0%, 0.5%, 1% and 1.5% contrast), we selected the 0.5% contrast level as the subliminal threshold, for conservative purposes. It was indeed the first condition characterized by some signal (vs. 0% contrast), which contrast was the lowest. In this condition, variance was also low, which we took as a guarantee of homogeneity between participants' responses. Importantly, the PAS visibility ratings associated to the subliminal and supraliminal thresholds were significantly different from each other (t(14) = -7.254, p < .001) and approximated 0 for the former ("no impression of the stimulus", range: 0-0.93, X = 0.28; SE = .08) and 1 for the latter condition ("a brief glimpse experience", range: 0.34-1.22, X = 0.80; SE = .09) (Figure 1D), which we took as an additional argument to validate our choice of stimuli for SESSION 2 when the same participants' EEG was recorded.

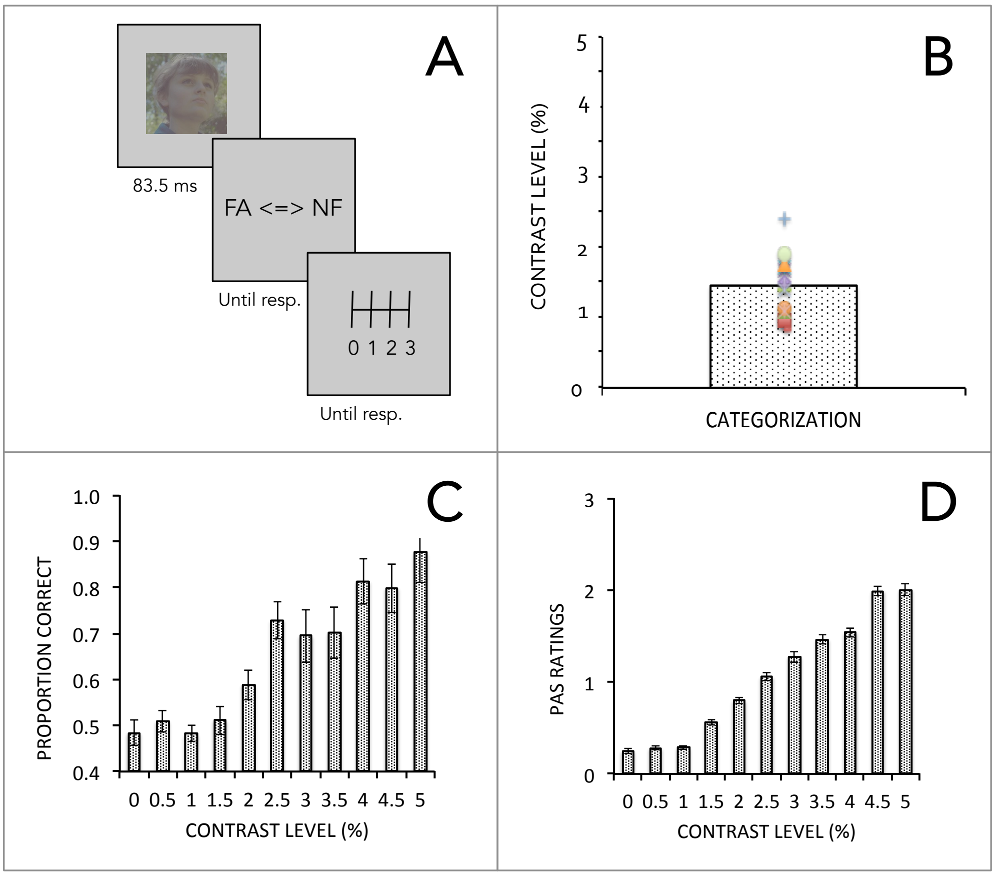

Figure 1. A. Participants saw briefly presented images whose overall contrast level ranged between 0-5%. They categorized each as either a face (FA) or a non-face (NF) before rating image visibility on a 4-point PAS scale (0 to 3). B. A staircase procedure identified 1.4% image contrast as the threshold for chance level (50% correct) categorization performance. C-D. There was a steady increase in the proportion of correct responses and in subjective visibility ratings as a function of image contrast.

(2) Preliminary exploration of the visibility (subjective) and of SSVEP (objective) measurements

At SESSION 2, participants were successively tested on 6 blocks presented in a fixed order (0%, 0.5%, 1%, 1.5%, 2% and 100% contrast). They were very accurate at detecting the colour-change of the fixation cross at each contrast level, even if their performance decreased at higher contrast levels given that the cross was somewhat less distinct from the background at higher contrast levels ($F(5,60) = 3.745$, $p = .005$). Importantly however, participants allocated their attention to the fixation cross in a similar way at comparable contrast levels (e.g., 0% and 0.5% contrast), as indicated by the absence of significant differences between adjacent contrast levels (post-hoc Bonferroni tests: $ps > .05$). After each sequence, participants' subjective impression of having seen the stimuli was also assessed by means of two visibility scales, a qualitative scale resembling the 4-point PAS scale and a quantitative scale through which participants had to report the number of images, up to 240, they felt they had been able to categorize within a given sequence. Participants carefully completed that task, distributing their responses across the full range of ratings. The shapes of the overall distribution of these scores were distinct, with an exponential increase associated to increasing visibility for its qualitative version and a rather stepwise shape for its quantitative version (Figure 2).

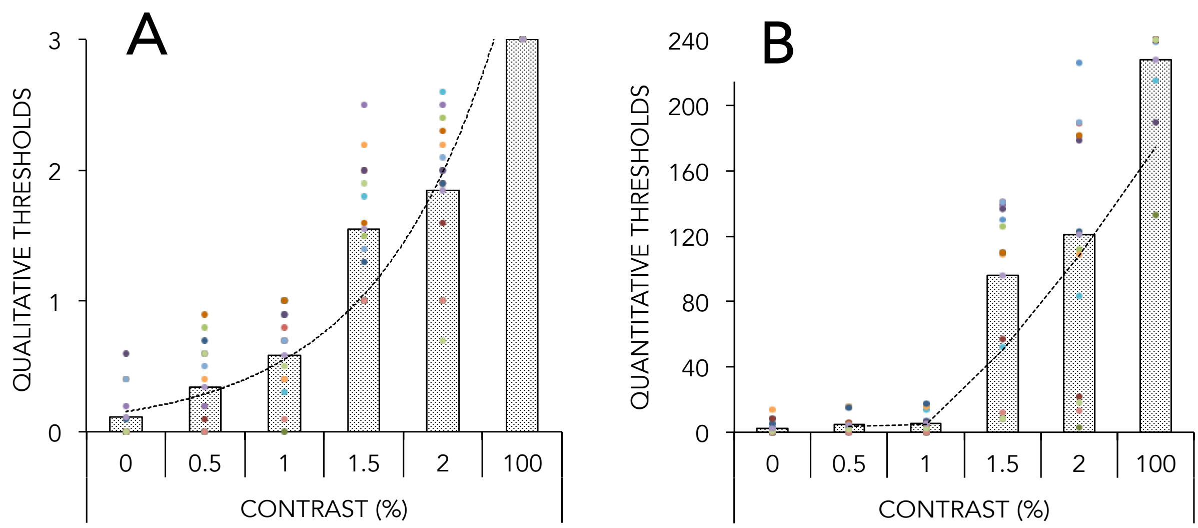

Figure 2. Participants' ratings at the qualitative (A) and quantitative (B) visibility scales collected after each SSVEP sequence. Ratings progressively increased with increasing contrast and followed distinct trajectories according to the scale, namely an exponential (A) and a stepwise distribution (B). Bars illustrate group performance. Dots illustrate averaged performance recorded at an individual level.

When images were presented at 100% contrast, that is, when they were completely visible to participants, we replicated the findings of previous studies (Jacques et al., 2016; Rossion et al., 2015) with a massive activation at the medial occipital lobe in response to the succession of the 6 images per second (Figure 3). Such responses typically signal for visual processes that are common to both faces and non-faces (Jacques et al., 2016). A similar scalp topography was also present for images not contrasted at all (0% contrast) but in a significantly reduced fashion (paired t-test: $t(14) = 3.447$, p

= .004) because in this condition, participants only experienced a grey square flickering on a lighter grey background (Figure 3). These peaks were highly significant and reached their highest magnitude at electrode Oz (averaged brain response to the 6 Hz component and its 3 consecutive significant harmonics at 100%: SNR = 15.55 (SE = 1.7) and at 0%: SNR = 9.91 (SE = .88)) (Figure 3). As in other studies (Quek, Liu-Shuang, Goffaux, Rossion, 2018), their magnitude also monotonically decreased with decreasing discernibility across blocks (100% to 0% contrast: $F(5,70) = 13.73$, $p < .001$). In addition, these images elicited strong face responses significantly up to 16.8 Hz, which suggests that participants' brain automatically detected their apparition every 5th item (Jacques et al., 2016; Rossion et al., 2015; Figure 3C). These face-selective responses emerged significantly (z-score threshold fixed at 3.09, 1-tailed, $p < .001$) from the medial occipital cortex (Iz: z-score at 1.2 Hz = 8.18, mean SNR = 2.62) and propagated through the ventral visual stream, bilaterally (LOT: P7-P07-P9 complex: mean SNR = 3.75 (SE = .33); one-sample t-test against 1: $t(14) = 9.27$, $p < .001$; ROT: P8-P08-P10 complex: mean SNR = 3.47 (SE = .27); one-sample t-test: $t(14) = 8.35$, $p < .001$), without any statistical difference between the two hemispheres (ROT *vs.* LOT: paired t-test: $t(14) = .980$, $p = .344$). Images at 0% (i.e., dark grey squares flickering on a light grey background) did not elicit any significant face response, at none of the above-mentioned regions-of-interest (ROI).

Thus, these preliminary findings confirm that participants' SSVEP measurements and their visibility ratings as they are used here can be associated without contaminating each other. As such, they provide novel avenues to examine people's phenomenology when they see complex visual images such as faces.

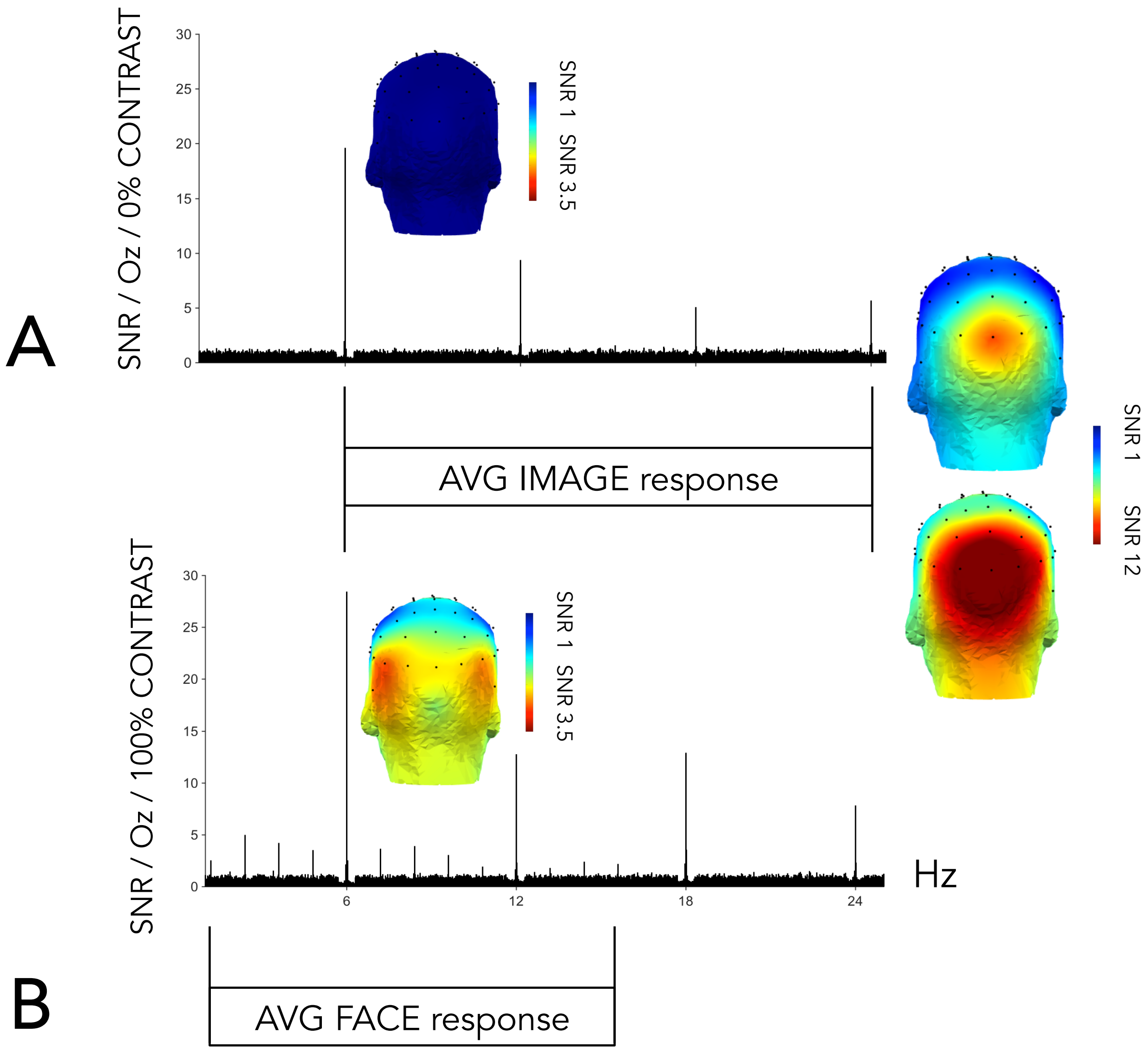

Figure 3. SNR spectrum and scalp topography generated at 0% (A) and 100% contrast (B) in response to images (6 Hz = 6 images/second) and faces (1 image out of 5; 1.2 Hz and harmonics). Both conditions lead to significant brain activations in response to images at 6 Hz up to 24 Hz. Face responses are only visible at the 1.2 Hz component and its harmonics up to 16.8 Hz at 100% contrast. No significant face response is recorded at 0% contrast.

(3) SSVEP measurements capture brain activation in response to complex visual images that participants report not having seen

Given that one goal of the study was to explore whether the current paradigm would be sensitive to faces presented subliminally, and if so, whether such exposure would generate detectable activation in the brain, we looked for any face response at 0.5% contrast that would resist the methodological constraints (SNR distribution and z-score threshold) imposed at 2% contrast. At 2%, the face response resembled the one computed at 100%, with a shift towards more central electrodes (Figure 4). It peaked maximally at electrodes O1 (SNR at 1.2 Hz = 1.65 (SE = .27); z-score = 3.49) and spread significantly over the left (PO3; SNR at 1.2 Hz = 1.58 (SE = .23); z-score = 3.15) and right hemisphere (PO8; SNR at 1.2 Hz = 1.61 (SE = .19); z-score = 3.19), without contaminating other harmonics for 2 out of 3 of these electrodes (O1, PO8 but not PO3). At 0.5% contrast, the only electrode significantly responding to the repetition of faces throughout the sequences was Iz, located over the primary visual cortex (SNR = 1.53 (SE = .19); z-score = 3.88). Interestingly, the magnitude of the signal recorded at this electrode did not increase with increasing contrast or (subjective) visibility recorded at SESSION 1 (2-tailed Pearson correlations: contrast: r = -2.252, p = .364; visibility: r = -0.129, p = .648). Its magnitude was also not statistically different from what was recorded for O1 at 2% contrast (t(14) = -.399, p = .696) and did not spread to other harmonics (Figure 5). In between these thresholds and therefore at 1% and 1.5% contrast, the face responses did not reach significance at none of the 64 electrodes at the 3.09 z-score threshold. When lowered at 2.53 (1-tailed, p < .01), the z-score threshold helped revealing, at 1% contrast, responses at posterior electrodes, namely at O1 (SNR at 1.2 Hz = 1.39 (SE = .12); z-score = 2.35) and P1 (SNR at 1.2 Hz = 1.34 (SE = .17); z-score = 2.46). This was not the case at 1.5% contrast, which we attribute to the fact that many more images have been accessed in this condition (Figure 2B, right). Future studies are needed to confirm that this sudden experience is indeed disruptive to participants, resulting in their attention being randomly allocated over the sequence rather than being locked to the periodic stimulus, which has in turn be shown to reduce significantly the amplitude of SSVEP responses (Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015).

Overall, it appears from these results that the human brain is capable of evoking a category from very different face images even in the absence of phenomenal experience. At a subliminal stage, the characteristics of the brain response are, however, very different from what is recorded at conscious (supraliminal) stages, especially in terms of the brain regions underlying this complex activity. Future studies could assess whether this conclusion also stands at an individual level, which would require the use of longer or of a greater number of SSVEP sequences to increase within-block statistical power.

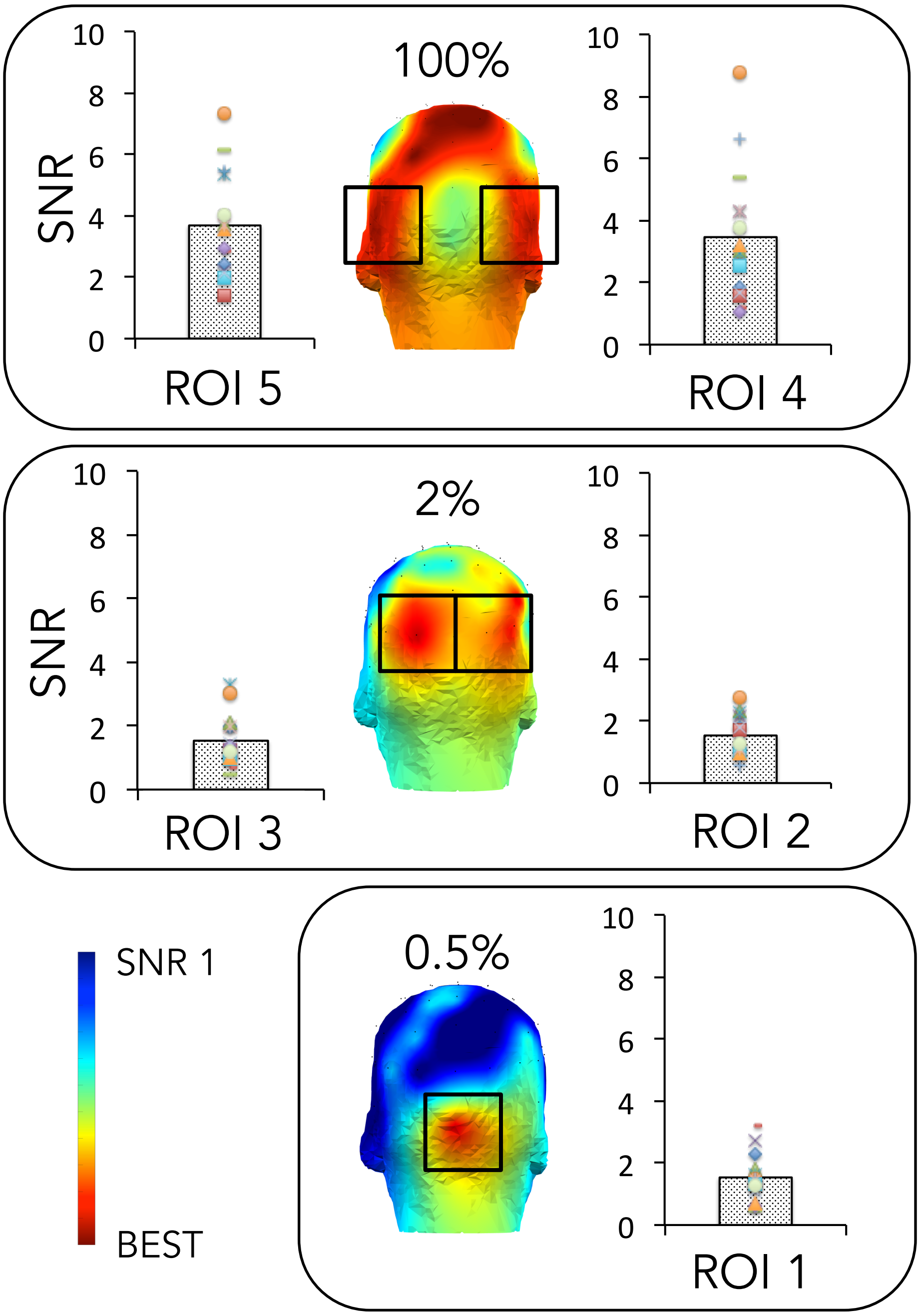

Figure 4. The face signal extracted at 1.2 Hz is confined to a very posterior electrode at a subliminal stage of activation (ROI 1 capturing face response at 0.5% contrast - max SNR = 1.5) and then propagates along the ventral stream, bilaterally, towards ROI 2 and ROI 3, which capture the face response at 2% contrast (max SNR = 1.7) and further to ROI 4 and ROI 5, which capture the face response at 100% contrast (max SNR = 4).

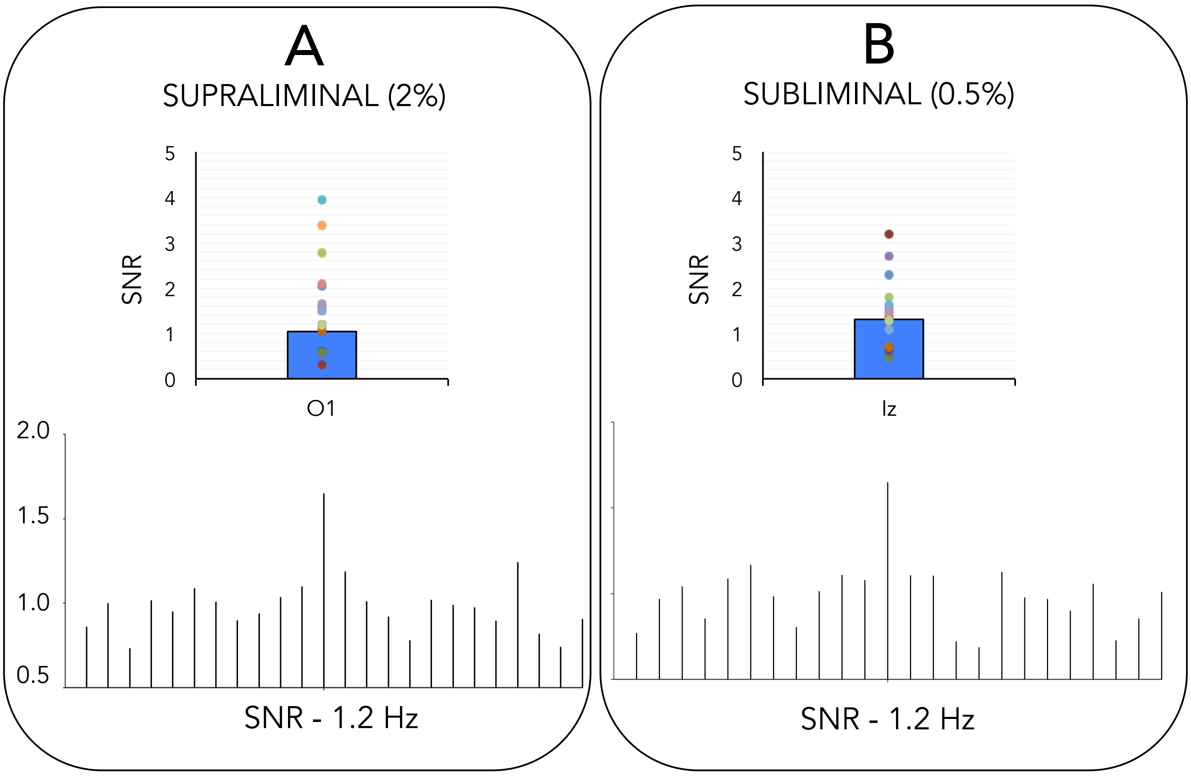

Figure 5. The brain response recoded in response to faces (1.2 Hz) peaked maximally and significantly at electrode O1 at 2% contrast (A; supraliminal threshold) and at electrode Iz at 0.5% contrast (B; subliminal threshold). The magnitude of these two peaks was not statistically different.

(4) SSVEP measurements capture the propagation of complex categorization responses along the ventral stream as contrast increases

When looking at the scalp topographies generated at 0.5%, 2% and 100% contrast, the signal recorded in response to faces propagated along the ventral stream as stimulus contrast increased (Figure 4). In addition to this spatial propagation, the signal also increased in term of its amplitude as more anterior parts of the ventral stream were concerned. In fact, it significantly differed between the brain regions underlying face categorization at 2% and 100% contrast, in both the right (from ROI 2 to ROI 4: $t(14) = -3.466$, $p = .004$) and the left hemisphere (from ROI 3 to ROI 5: $t(14) = -5.223$, $p < .001$) but not between those regions underlying face categorization at 0.5% and 2% contrast, in none of the hemispheres (from ROI 1 to ROI 2: $t(14) = -0.086$, $p = .933$; from ROI 1 to ROI 3: $t(14) = -0.034$, $p = .973$) (Figure 4).

(5) The magnitude of face categorization responses and their scalp topography are good predictors of subjects' phenomenal experience

So far we have observed that the amount of contrast embedded in the faces participants are exposed to is highly predictive of the magnitude of the SS-EP response and of the scalp topography at which the response is maximally observed. The current SS-EP paradigm may nevertheless only be considered as a no-report paradigm if it can predict participants' phenomenal experience. To demonstrate that this is the case, and for the reasons developed earlier, we focused on what had been recorded at 2% contrast because the visibility ratings associated to this condition reached neither ceiling nor floor, as it was the case at 100% or at 0%-0.5% contrast (Figure 2B). An ROI could also be delineated in this condition, which was not the case at 1% or 1.5% contrast.

At 2%, participants' averaged SNR in response to faces correlated positively to their quantitative visibility ratings, indexed by the number of images they reported having categorized within SSVEP sequences of this block, in the right hemisphere, at ROI 2 (1-tailed Pearson correlation: $r = .484$, $p = .034$), and in the left hemisphere, at ROI 3 (1-tailed Pearson correlation: $r = .467$, $p = .040$). More specifically, these correlations reached their maximum at PO8 (1-tailed Pearson correlation: $r = .587$, $p = .011$) and P6 electrodes (1-tailed Pearson correlation: $r = .562$, $p = .015$) within ROI 2 and at O1 (1-tailed Pearson correlation: $r = .536$, $p = .020$) and PO7 electrodes (1-tailed Pearson correlation: $r = .452$, $p = .045$) within ROI 3 (Figure 6A). Similar correlations relating participants' SNR to their PAS ratings collected at SESSION 1 or to their qualitative visibility ratings collected at SESSION 2 did not reveal any significant result. Beside the observation that, at this contrast level (2%), the amplitude of the signal recorded at face-selective electrodes predicts phenomenal experience, we also observed that information about participants' phenomenology could be derived from the brain regions they recruit at this contrast level. The amplitude of the face signal indeed clearly increased across the 3 subgroups of 5 participants differing in how many images they report having seen on average across the 2% block (Figure 6B).

We therefore suggest that, in addition to the magnitude of the face categorization response, scalp topography is another good predictor of phenomenology. Future studies could involve testing whether this observation can be generalized to other contrast levels. To do so, one would first have to develop more sensitive scales, that is, scales that discourage participants from only expressing extreme ratings. It would also be interesting to replicate the current findings after having increased the number of participants included in each subgroup, which would most probably reveal an occipital, and therefore subliminal-like, activation in the subgroup which visibility ratings are the lowest.

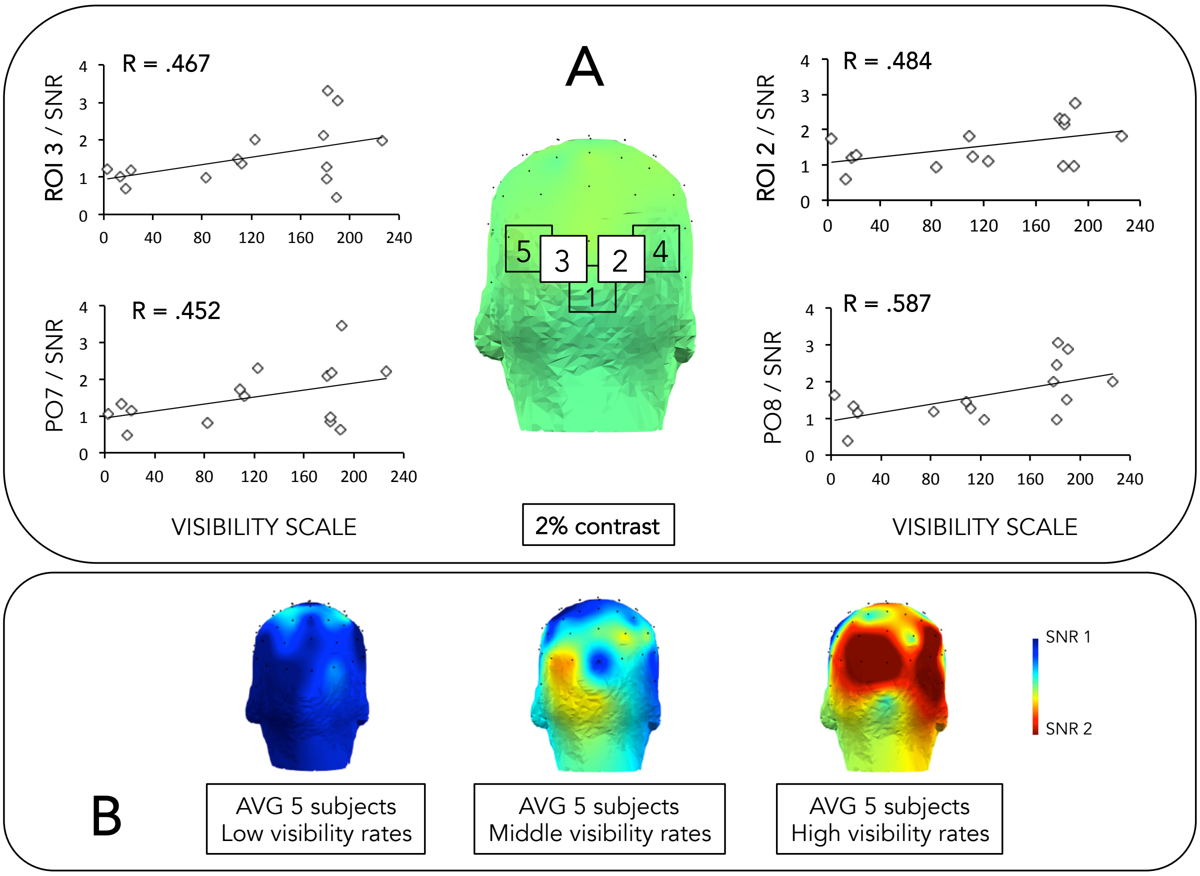

Figure 6. A. Five regions-of-interest (ROI) were tracked down along the visual pathway. At 2% contrast, participants' face categorization responses (1.2 Hz) strongly correlated with their visibility judgement of how many images they estimate to have categorized in both the right (ROI 2) and left (ROI 3) hemisphere. Within these ROIs, the strongest correlation was observed at PO7, PO8, O1 and P6. B. At 2% contrast, spatial localization also predicted participants' phenomenal experience, as attested from the scalp topographies generated for subgroups of participants critically differing in how many images they reported having seen, on average, across the block.

DISCUSSION

The main goal of this study was to assess whether a paradigm that does not require from participants to give any overt (verbal or motor) response can also be used to access their phenomenology. To address this question, we tested a group of 15 participants in two consecutive testing sessions requiring them to view the same set of complex visual images (faces, non-faces) varying systematically in term of their overall contrast. The main goal of SESSION 1 was to establish, through a staircase procedure as well as through subjective reports, participants' visibility thresholds. At the group level, images at 0.5% and 2% contrast were taken as subliminal and supraliminal for conservative purposes. The main goal of SESSION 2 was to explore the extent to which the brain is sensitive to the periodic presentation of face images. To do so, we compared participants' brain activation in response to faces embedded in sequences of non-face stimuli, which contrast differed. We predicted we would find a face categorization response at contrast levels for which participants reported having seen the stimuli (2% contrast and above), which would sign for the ability of their brain to categorize faces at supraliminal levels, even if they are degraded in term of their visibility. Given the nature of the stimuli and of the paradigm we used here, we also expected to find a response in the brain even when reaching the threshold for which participants report not having seen the stimuli. Two visibility scales (qualitative, quantitative) were provided to participants at the end of each SSVEP sequence with the goal of apprehending their visibility of the images they had been exposed to.

We think the results of this study are remarkable for two main reasons.

The first reason is that they document the exceptional capabilities of the human brain. Because of the power and the sensitivity the SSVEP technique provides, we were able to show, over 6-7 minutes of stimulation only, that the brain is capable of processing, but also of creating a visual category from very different faces, even at a stage that had been defined at an earlier session as subliminal to a group of participants. This is spectacular given the low visibility and the complexity of the stimuli involved in the task: faces which overall contrast has been set to 2%. Similar observations have been made in the past, but with stimuli of lower complexity (e.g., gratings; King et al., 2016; letters: DelCul, Baillet, & Dehaene, 2007) and in other contexts (e.g., working memory: Soto, Mäntylä, Silvanto, 2011; Soto & Silvanto, 2014). Interestingly, the face response extracted at this subliminal stage (0.5% contrast) was peculiar in the sense that it showed both harmonic and spatial restriction. Harmonic restriction relates to the fact that the face signal did not propagate significantly beyond 1.2

Hz, which corresponds to the frequency associated to the automatic response of the brain to the introduction of faces every 5th item in the sequences. Such observation is consistent with the finding that stimuli of low visual complexity typically engage fewer harmonics than those of high visual complexity (Norcia et al., 2015; Regan, 1989). Spatial restriction was obvious from that the weak, but significant, signal captured in response to subliminal faces remained confined to a single electrode located at the medial occipital lobe, which is typically activated by low-level visual information such as the orientation of lines embedded in the stimulus. The observations we made at 1% and 1.5% contrast were mixed, which we attributed to a lack of power in two conditions for which participants reported having experienced more images than at 0.5% contrast. Beyond this point (2% contrast and above), we found that the face signal increased in amplitude and that it propagated spatially along the ventral stream as contrast increased. Importantly, these results can be attributed neither to attention, which was held constant throughout the experiment (see results on the fixation cross; Lamme, 2003; Koch & Tsuchiya, 2007; Tsuchiya, & Koch 2014), nor to working memory (no face-related information to be memorized; Lamme, 2010; Soto, & Silvanto, 2014).

Critically, these observations are in line with the view that unconscious information remains locally active in the brain, while it is made globally available to multiple brain systems once information becomes conscious (Dehaene & Changeux, 2011; see also, Dehaene, Sergent, & Changeux, 2003; Dehaene & Naccache, 2001; Sergent, Baillet, Dehaene, 2005). At the same time, they raise two questions. The first one stems from the fact that we did not observe any prefrontal activation in response to faces, even at 100% contrast. To us, this should however not be taken as evidence that this brain region has not been recruited at all during the task. Its activity could indeed have been captured at other frequency bins than those associated to the repetitive introduction of faces within sequences or even have been spread indistinctly over these bins if the cognitive abilities associated to this brain region (e.g., monitoring) had been recruited along the sequences. The second question is related to the finding of a subliminal activation in a brain region typically responding to features of weaker visual complexity than faces (e.g., line orientation). We attribute this result to re-entrant feedback information originating from higher-level regions onto the medial occipital lobe (Lamme & Roelfsema, 2000; Pollen, 1999). Another possibility is that the subset of apparently heterogeneous faces we used in the current study engaged in fact some repetitive structures (e.g., roundish shape) that the striate cortex could detect. To disentangle these two proposals, one could test another group of participants on the same subliminal sequences but presented this time at inverted orientation. A low-level visual explanation would only be considered if medial occipital activations are also observed in response to inverted subliminal faces.

The second reason of why these results are particularly interesting is that they constitute evidence that SSVEP measurements, at least in their present form, can be used to predict participants' phenomenology. They also emphasize the benefit of using a quantitative rather than a qualitative visibility scale. In particular, the magnitude of participants' brain responses and their scalp topography were good predictors of their phenomenal experience. At a fixed contrast level (2% contrast), these two parameters could therefore be used in the future to predict what is subjects' (subjective) visibility of the images they are exposed to, and this is especially true at electrodes typically engaged during face-selective tasks (Jacques et al., 2016; Rossion et al., 2015). As such, we benefit now from a novel no-report paradigm applicable to vulnerable populations such as infants or patients, which phenomenology is often difficult to evaluate.

Overall, this study is part of a larger attempt to delineate how the brain produces phenomenal experience. It specifically tags, by means of a powerful paradigm derived from electroencephalography, what are those neural correlates associated to the categorization of faces when they vary in term of their contrast. We found that subliminal faces were weakly but significantly categorized at the medial occipital lobe and that the magnitude of the categorization response increased as image visibility increased. Increasing contrast also drove different brain regions being activated along the ventral stream, from more posterior to more anterior regions of the brain. Crucially, scalp topography and signal amplitude predicted participants' phenomenology, which offers the promise of identifying the neural correlates associated to the conscious experience of complex visual stimuli with greater precision in the future.

METHODS

PARTICIPANTS

The Research Ethics Boards of the department of Psychology of the Université libre de Bruxelles (Belgium) approved the experiment. We tested 15 French-speaking adult participants (5 male; all right-handed; mean age: 22 years, SD = 3; 1 participant excluded because more than 2 sequences/block could not be included in the analyses). All received financial compensation in exchange for their participation, gave written informed consent, and reported normal or corrected-to-normal vision.

STIMULI

We used a previously described set of 200 x 200-pixel coloured images (de Heering & Rossion, 2015). The set contained 48 face images and 248 natural object images (e.g., animals, houses, fruits/vegetables, flowers/plants, man-made objects). Face images varied in terms of colour composition, age, sex, viewpoint, lighting conditions, and background (Figure 7). After equalizing the overall contrast and luminance of these images, we used Adobe Photoshop CS6 to create 11 image sets of varying visibility by parametrically changing each image's contrast from 0% (signal absent) to 5% (signal present), in 0.5% steps. All 11 sets were used for SESSION 1 (behaviour). For SESSION 2 (EEG), we selected 5 of them (0%, 0.5%, 1%, 1.5%, 2% and 100% contrast). Images in SESSION 2 were slightly bigger (6.7 x 6.7 degrees of visual angle) than those used in SESSION 1 (5.7 x 5.7 degrees of visual angle).

Figure 7. Examples from the original set of images (100% contrast) as well as simulated version of what could be the same images but presented at 2% (supraliminal) and 0.5% contrast (subliminal). For the needs of EEG recordings (SESSION 2), images were embedded in 40-second sequences and flickered at 6 Hz (6 images/s). A face stimulus was introduced every 5th item and therefore re-appeared within the sequence at the slower frequency of 1.2 Hz (6Hz/5).

PROCEDURE

The experiment included an initial behavioural test (SESSION 1) followed by an EEG component (SESSION 2). These sessions were scheduled either on the same day or on two successive days and were not counterbalanced across participants (i.e., behavioural testing always preceded EEG recording). On both testing days, participants sat comfortably at a distance of 50 cm from a laptop Lenovo computer (refresh rate = 60 Hz). Stimuli were always presented in the centre of the screen.

SESSION 1 consisted of a behavioural task designed to yield both an *objective* and a *subjective* index of participants' categorization threshold of faces. To this end, we presented each of the 48 faces twice, along with an equal number of object images, for a total of 192 randomized trials. For each briefly presented image (83.5 ms duration), participants performed two tasks. First, they categorized the image as either a face (FA) or a non-face (NF) (i.e., two-alternative forced-choice, or 2AFC). We used a one up/one down staircase to control their contrast value (start at 3.5% contrast, contrast ranging from 0% to 5%, in 0.5% increments), with the aim of precisely identifying which contrast level the group needed to categorize faces and differentiate them from non-faces at exactly chance (50%) level. Second, participants gave a subjective rating of the visibility of each image on a four-point version of the "Perceptual Awareness Scale" (PAS) (Ramsoy & Overgaard, 2004; Sandberg, Timmermans, Overgaard, & Cleeremans, 2010). They had to choose between (0) no impression of the stimulus (no experience), (1) a feeling that something has been shown, with a content that cannot be specified any further (brief glimpse), (2) an ambiguous experience of the stimulus, with some aspects being experienced more vividly than others and a feeling of almost being certain of it (almost clear experience), or (3) a non-ambiguous experience of the stimulus with no doubt about its own answer (clear experience). Responses for both tasks were not speeded, i.e., participants could take as long as they wanted to respond.

SESSION 2 was dedicated to SSVEP recordings. Here we presented participants with the images from SESSION 1 and used the SSVEP approach described earlier (see Jacques et al., 2016; Quek & Rossion, 2017; Retter & Rossion, 2016). Participants viewed them in a continuous stream and experienced them as flickering against a grey background (image presentation frequency = 6 Hz, i.e., 6 images/second). Each image appeared on screen for just 83.33 ms, and was followed by a blank interval of 83.33 ms, for an image cycle duration of 166.66 ms. Contrary to Jacques and collaborators (2016), we used a square-wave contrast modulation and therefore contrast variations changing from 0% contrast to maximal contrast in one cycle. The goal was indeed to precisely control the amount of contrast participants was exposed to during a given sequence, and to ensure that the presentation duration of each image corresponded precisely to that used during the behavioural session (i.e., 83.33 ms). Within the stream of non-face images, we embedded a face image as every 5th item, corresponding to a face-presentation frequency of 6Hz/5, or 1.2Hz. This manipulation ensures that face-selective neural activity is evoked at a pre-specified point in the EEG frequency spectrum (1.2 Hz), and can therefore be dissociated from the neural response common to both faces and non-faces arising at the image presentation frequency (6 Hz). Every sequence began with a "ready?" message presented on a uniform grey background that invited participants to press the spacebar to initiate the sequence. Once launched, a central black fixation-cross appeared for between 1 to 5 seconds, after which the stimulation sequence (43.33 s) began. It actually consisted of a 1.67-second fade-in period, a 40-second period of interest (192 objects, 48 faces), and of a 1.67-second fade-out period. During the fade-in and fade-out, the maximal contrast of subsequent image cycles progressively ramped up and down respectively, so as to minimize blinks or artefacts elicited by the sudden appearance/disappearance of flickering stimuli. The fixation-cross remained superimposed on the images throughout the sequence. The participant's task was to fixate it and press the spacebar whenever it turned red. We used this orthogonal task to the image content in order to encourage a constant level of attention across the length of each sequence, and along the full experiment.

To examine how the response to this stimulation varied as a function of stimulus visibility and phenomenal experience, all participants completed 6 blocks in a fixed order in which image contrast increased progressively across the testing session. In this way, information gleaned by the participants during the high-contrast conditions (e.g., that the faces appear at regular intervals in the sequence) could not influence the response captured during the lowest contrast conditions. Each block contained 10 sequences at a given image contrast level: Block 1 (control) consisted of images at 0% contrast (i.e., dark grey squares flickering on a light grey background). Block 2 (critical) consisted of images at 0.5% contrast (determined at SESSION 1 as the subliminal threshold). Blocks 3 and 4 contained images at 1% and 1.5% contrast, respectively (intermediate conditions). Block 5 (supraliminal) consisted of images at 2% contrast (determined at SESSION 1 as the supraliminal threshold). The final block (control) contained images at full (100%) contrast. Additionally, we assessed participants' subjective impression of each sequence by collecting their responses on two visibility scales at the end of each SSVEP sequence, the goal being to compare their outputs. On the one hand, we adapted the classical PAS scale (qualitative visibility scale; Sandberg & Overgaard, 2015) for which we asked participants to judge whether among the grey square images they saw during the preceding sequence, they had (0) no impression of the stimuli ("you could not categorize any" – no experience), (1) brief glimpses of the stimuli ("you could categorize some of them" – brief glimpse), (2) an almost clear experience of the stimuli ("you could categorize almost all of them" – almost clear experience) or (3) a clear experience of the stimuli ("you could categorize all of them" – clear experience). On the other hand, they also had to estimate how many of the 240 images they just saw they felt they could categorize clearly (quantitative scale).

EEG recordings and analyses

We recorded scalp EEG using a 64-channel Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands). EEG analog signal was digitized at a 1024 Hz sampling rate. During recording setup, electrode offset was reduced to between ±50 μV for each individual electrode by softly abrading the underlying scalp with a blunt plastic needle and insulating the electrode tip with saline gel. Eye movements were monitored using 4 electrodes placed at the outer canthi of the eyes and above and below the right orbit.

EEG analyses were carried out using Letswave 6 (https://github.com/NOCIONS/letswave6) and custom scripts running on Matlab (The Mathworks). Continuous EEG data was first applied a band-pass filter between 0.1 and 100 Hz using a FFT band-pass filter, resampled to 250 Hz (linear interpolation), and segmented in 48-second epochs (from −2 seconds before stimulation to 2 seconds after the end of stimulation). Where necessary, noisy electrodes were then linearly interpolated using 2 immediately surrounding clean channels (performed for 13 participants, with a maximum of 4 interpolated channels per participant). These epochs were then re-referenced to a common reference computed using the average of all 64-scalp channels (excluding ocular channels). Epochs were then further segmented to contain an exact integer number of 1.2 Hz cycles beginning 2 seconds after the onset of the sequence (i.e., after the fade-in period, at the start of the proper sequence) until approximately 40 seconds after sequence onset (i.e., immediately before the fade-out period). For each participant, we created conditional averages for each of the 6 contrast levels (0%, 0.5%, 1%, 1.5%, 2% and 100%) and subjected the resulting averaged time series to Fast Fourier Transform (FFT), producing 6 frequency spectra (frequency resolution of 0.025 Hz) for each participant (one per condition). We also computed conditional grand-averages by averaging the FFT spectra for each condition across participants. In order to evaluate the magnitude of the effect across conditions and visualize it, two computations were performed on these files. On the one hand, grand-averaged FFT spectra were transformed into z-scores and computed as the difference between amplitude at the frequency of interest and the mean amplitude of 20 surrounding bins divided by the standard deviation of the 20 surrounding bins (10 on each side). On the other hand, both individual and grand-averaged FFT spectra were transformed into signal-to-noise (SNR) ratios and computed as the ratio between the amplitude at each frequency and the average of the 20 surrounding bins (for similar analyses see de Heering & Rossion, 2015; Liu-Shuang, Norcia, & Rossion, 2013; Jacques et al., 2016; Rossion et al., 2015). The size of the signal at a given frequency was then evaluated per condition on participants' signal-to-noise (SNR) ratios at each electrode both for the face and the image response in agreement with the results of the z-score analyse, which precisely determined the number of significant, consecutive and minimally involved harmonics across conditions (threshold at 3.09; $p < .001$, 1-tailed). Statistical tests include a repeated-measure ANOVA as well as one-sample and paired t-tests. Regions-of-interest (ROI) were defined as followed: Iz electrode for ROI 1, O2-PO4-PO8-P6 electrodes for ROI 2, O1-PO3-PO7-P7 electrodes for ROI 3, O2-PO8-P8-P10 for ROI 4 and O1-PO7-P7-P9 electrodes for ROI 5.

ACKNOWLEDGMENTS

This research has been funded by an ERC advanced grant (RADICAL) attributed to AC in 2013. AC is Research Director is Research Associate of the Fonds de la Recherche Scientifique – FNRS, Belgium. We would like to thank Genevieve Quek for earlier comments on the manuscript and Fabienne Chetail for writing the script used for SSVEP analyses.

COMPETING INTERESTS

The authors declare that no competing interests.

REFERENCES

Aru, J., Bachmann, T., Singer, W., & Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neurosci Biobehav Rev*, *36*(2), 737-46. doi: 10.1016/j.neubiorev.2011.12.003.

Blake, R., & Logothetis, N.K. (2002)? Visual competition. *Nat. Rev. Neurosci*, *3*, 13–21.

Boly, M., Seth, A.K., Wilke, M., Ingmundson, P., Baars, B., Laureys, S., Edelman, D.B., & Tsuchiya, N. (2013). Consciousness in humans and non-human animals: recent advances, and possible future directions. *Front. Psychol.*, *4*, 1–20.

Chalmers D. J. (2000). What is a neural correlate of consciousness?, in Neural Correlates of Consciousness: Empirical and Conceptual Questions, ed Metzinger T., editor. (Cambridge, MA: MIT Press), 17–39.

Crick, F., & Koch, C. (1990)? Towards a neurobiological theory of consciousness. *Semin. Neurosci.,* 2, 263–275.

De Graaf, T.A., Hsieh, P.J., & Sack, A. T. (2012). The 'correlates' in neural correlates of consciousness. *Neurosci Biobehav Rev.*, *36*,191-7. doi: 10.1016/j.neubiorev.2011.05.012.

Dehaene, S., & Changeux, J.P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*, 200–227.

Dehaene, S., Changeux, J.P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*, 204-211.

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition*, *79*, 1-37.

Dehaene, S., Sergent, C. & Changeux, J.P. (2003). A neural network model linking subjective reports and objective physiological data during conscious perception. *PNAS*, *100*, 8520-8525.

de Heering, A., & Rossion, B. (2015). Rapid categorization of natural face images in the infant right hemisphere. *eLife*, *4*:e06564. doi: 10.7554/eLife.06564.

DelCul, A., Baillet, S., & Dehaene, S. (2007). Brain Dynamics Underlying the Nonlinear Threshold for Access to Consciousness. *Plos Biology*, *5*, e260.

Einevoll, G.T., Kayser, C., Logothetis, N.K., & Panzeri, S. (2013). Modelling and analysis of local field potentials for studying the function of cortical circuits. *Nat. Rev. Neurosci.*, *14*, 770–785

Frässle, S., Sommer, J., Jansen, A., Naber, M., & Einhäuser, W. (2014). Binocular rivalry: frontal activity relates to introspection and action but not to perception. *J. Neuroscience*, *34*, 1738-1747.

Jacques, C., Retter, T.L., & Rossion, B. (2016). A single glance at natural face images generate larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. *Neuroimage*, *137*, 21-33. doi: 10.1016/j.neuroimage.2016.04.045.

King, J.R., Pescetelli, N., & Dehaene, S. (2016). Brain Mechanisms Underlying the Brief Maintenance of Seen and Unseen Sensory Information. *Neuron*, *92*, 1122-1134. doi: 10.1016/j.neuron.2016.10.051.

Koch, C., Massimini, M., Boly, M., & Tononi, G. (2016). Neural correlates of consciousness: progress and problems. *Nature Reviews*, *17*, 307-321.

Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends Cogn. Sci.*, *11*, 16–22.

Lamme, V.A.F. (2003). Why visual attention and awareness are different. *Trends Cogn. Sci.*, *7*, 12–18.

Lamme, V.A.F. (2010). How neuroscience will change our view on consciousness. *Cogn. Neurosci.*, *1*, 204-220.

Lamme, V.A.F., & Roelfsema, P.R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci*, *23*, 571-9.

Lau, H. C., & Passingham, R.E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *PNAS*, *103*, 18763–18768.

Liu-Shuang, J., Norcia, T., & Rossion, B. (2013). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia*, *52*, 57-72.

Navajas, J., Ahmadi, M., & Quiroga, R.Q. (2013). Uncovering the mechanisms of conscious face perception: a single-trial study of the N170 responses. *The Journal of Neuroscience*, *33*, 1337-1343.

Norcia, A.M., Appelbaum, L.G., Ales, J.M., Cottereau, B.R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of Vision*, *15*, 4-4.

Odegaard, B., Knight, R.T. & Lau, H. (2017). Should a Few Null Findings Falsify Prefrontal Theories of Conscious Perception? *The Journal of Neuroscience*, *37*, 9593–9602.

Peters, M.A.K., Kentridge, R.W., Philips, I., & Block, N. (2017). Does unconscious perception really exist? Continuing the ASSC20 debate. *Neuroscience of Consciousness*, *3*: nix015.

Pitts, M.A., Padwal, J., Fennelly, D., Martínez, A., & Hillyard, S.A. (2014). Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness. *Neuroimage*, *101*, 337–350.

Pollen, D.A. (1999). On the neural correlates of visual perception. *Cereb. Cortex*, *9*, 4–19.

Quek, G.L., & Rossion, B. (2017). Category-selective human brain processes elicited in fast periodic visual stimulation streams are immune to temporal predictability. Neuropsychologia. doi: 10.1016/j.neuropsychologia.2017.08.010.

Quek, G.L., Liu-Shuang, J., Goffaux, V., Rossion, B. (2018). Ultra-coarse, single glance face detection in a dynamic visual stream. *NeuroImage*, *176*, 465-476.

Ramsøy, T., & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenol. Cogn. Sci.*, *3*, 1–23.

Regan, D. (1989). Human brain electrophysiology: evoked potentials and evoked magnetic fields in science and medicine. Amsterdam: Elsevier.

Retter, T.L., & Rossion, B. (2016). Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, *91*, 9-28.

Rossion, B., Torfs, C., Jacques, C., & Liu-Shuang, J. (2015). Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain. *Journal of Vision*, *15*, doi: 10.1167/15.1.18.

Sandberg, K., Timmermans, B., Overgaard, M., & Cleeremans, A. (2010). Measuring consciousness: Is one measure better than the other? *Consciousness & Cognition*, *19*, 1069-1978.

Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience*, *8*, 1391-1400.

Soto, D., Mäntylä, T., Silvanto, J. (2011). Working memory without consciousness. *Current Biology*, *21*, R912.

Soto, D., & Silvanto, J. (2014). Reappraising the relationship between working memory and conscious awareness. *Trends Cogn. Sci.*, *18*, 520–525.

Srinivasan, R., Russell, D.P., Edelman, G.M., & Tononi, G. (1999). Increased Synchronization of Neuromagnetic Responses during Conscious Perception. *The Journal of Neuroscience*, *19*, 5435–5448.

Supèr, H., Spekreijse, H., & Lamme, V.A. (2001) Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nat. Neurosci.*, *4*, 304–310.

Sutoyo, D., & Srinivasan, R. (2009). Nonlinear SSVEP responses are sensitive to the perceptual binding of visual hemifields during conventional 'eye' rivalry and interocular 'percept' rivalry. *Brain Res.*, *1251*, 245-55. doi: 10.1016/j.brainres.2008.09.086.

Tononi, G., Srinivasan, R., Russell, D.P., & Edelman, G.M. (1998) Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *PNAS*, *95*, 3198 –3203.

Tsuchiya, N., & Koch, C. (2014). On the relationship between consciousness and attention. In *The Cognitive Neurosciences* (Gazzaniga, M.S., ed.), pp. 839–853, MIT Press.

Tsuchiya, N., Wilke, M., Frässle, S., & Lamme, V.A.F. (2015). No-Report Paradigms: Extracting the True Neural Correlates of Consciousness. *Trends Cogn Sci.*, *19*, 757-770. doi: 10.1016/j.tics.2015.10.002.

Wilke, M., Logothetis, N.K., & Leopold, D.A. (2003) Generalized flash suppression of salient visual targets. *Neuron*, *39*, 1043–1052.

Wilke, M., Mueller, K.M., & Leopold, D.A. (2009) Neural activity in the visual thalamus reflects perceptual suppression. *Proc. Natl. Acad. Sci. U.S.A.*, *106*, 9465–9470.

Zhang, P., Jamison, K., Engel, S., He, B., & He, S. (2011). Binocular rivalry requires visual attention. Neuron, *71*, 362-369.

FIGURES