



HAL
open science

A rapid, objective and implicit measure of visual quantity discrimination

Mathieu Guillaume, Sandrine Mejias, Bruno Rossion, Milena Dzhelyova,
Christine Schiltz

► **To cite this version:**

Mathieu Guillaume, Sandrine Mejias, Bruno Rossion, Milena Dzhelyova, Christine Schiltz. A rapid, objective and implicit measure of visual quantity discrimination. *Neuropsychologia*, 2018, 111, pp.180 - 189. 10.1016/j.neuropsychologia.2018.01.044 . hal-01923007

HAL Id: hal-01923007

<https://hal.science/hal-01923007>

Submitted on 6 Mar 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Running Head: IMPLICIT MEASURE OF QUANTITY DISCRIMINATION

Title: A rapid, objective and implicit measure of visual quantity discrimination

Authors: Mathieu Guillaume¹, Sandrine Mejias², Bruno Rossion^{3,4}, Milena
Dzhelyova^{1,3}, and Christine Schiltz¹

¹ Cognitive Science and Assessment Institute (COSA), University of Luxembourg

² Sciences Cognitives et Sciences Affectives (SCALab), Université Lille 2, France

³ Institute of Research in Psychological Science, Institute of Neurosciences, Université
Catholique de Louvain, Belgium

⁴ Neurology Unit, Centre Hospitalier Universitaire (CHRU) de Nancy, France

Corresponding author: Mathieu Guillaume

mathieu.guillaume@uni.lu +352 46 66 44 9523

Address: Université du Luxembourg, Maison des Sciences Humaines

11, Porte des Sciences, L-4366 Esch-sur-Alzette

Manuscript Word Count: 7,359 (excluding abstract, footnotes, and references).

Keywords: Electroencephalography (EEG), Steady State Evoked Potential,

Numerical Cognition, Number Sense, Approximate Number System.

Abstract

There is evidence that accurate and rapid judgments of visual quantities form an essential component of human mathematical ability. However, explicit behavioural discrimination measures of visual quantities are readily contaminated both by variations in low-level physical parameters and higher order cognitive factors, while implicit measures often lack objectivity and sensitivity at the individual participant level. Here, with electrophysiological frequency tagging, we show discrimination differences between briefly presented visual quantities as low as a ratio of 1.4 (i.e., 14 vs. 10 elements). From this threshold, the neural discrimination response increases with parametrically increasing differences in ratio between visual quantities. Inter-individual variability in magnitude of the EEG response at this population threshold ratio predicts behavioural performance at an independent number comparison task. Overall, these findings indicate that visual quantities are perceptually discriminated automatically and rapidly (i.e., at a glance) within the occipital cortex. Given its high sensitivity, this paradigm could provide an implicit diagnostic neural marker of this process suitable for a wide range of fundamental and clinical applications.

Abstract Word Count: 167.

A rapid, objective and implicit measure of visual quantity discrimination

Typical human adults are thought to possess a *Number Sense*, an ability that allows them to represent and manipulate large numerical magnitudes (Dehaene, 1997). This numerical sense has been characterized as a cognitive system sensitive to scalar variability (Gallistel & Gelman, 2000; Platt & Johnson, 1971), the *Approximate Number System* (ANS). The ANS follows the Weber-Fechner law (Dehaene, 2003; but see Cantlon, Cordes, Libertus, & Brannon, 2009, for an alternative view), such that the value of the Weber fraction – the ratio between the amount just noticeably different from a magnitude and the magnitude itself (see Stevens, 1957; and Van Oeffelen & Vos, 1982) – is generally used to assess ANS acuity (Nieder & Miller, 2003; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Since the value of the Weber fraction predicts young adolescents' arithmetic performance throughout their scholarship (Halberda, Mazocco, & Feigenson, 2008), there is considerable scientific interest on the relation between ANS acuity and more elaborated numerical and mathematical skills (see Hyde, Berteletti, & Mou, 2016; but also Reynvoet & Sasanguie, 2016, for recent reviews).

Although a tight coupling between ANS acuity and mathematical ability has been reported in some studies (e.g., in children, Inglis, Attridge, Batchelor, & Gilmore, 2011; Mejias, Mussolin, Rousselle, Grégoire, & Noël, 2012; in adults, DeWind & Brannon, 2012; Nys, Ventura, Fernandes, Querido, Leybaert, & Content, 2013; see Chen & Li, 2014, for a meta-analysis), other studies failed to report such a relationship (e.g., Sasanguie, Göbel, Moll, Smets, & Reynvoet, 2013; Price, Palmer,

Battista, Ansari, 2012). This discrepancy has been attributed to ambiguities and difficulties in measuring ANS acuity (DeWind & Brannon, 2016; Gebuis, Cohen Kadosh, & Gevers, 2016; Norris & Castronovo, 2016; Szűcs, Nobes, Devine, Gabriel, & Gebuis, 2013). Indeed, the evaluation of the ANS is affected by non-numerical factors (Guillaume, Gevers, & Content, 2016; Leibovich, Al-Rubaiey Kadhim, & Ansari, 2017; Smets, Gebuis, Defever, & Reynvoet, 2014; Smets, Sasanguie, Szűcs, & Reynvoet, 2015; Smets, Moors, & Reynvoet, 2016), since there are inherent confounds between numerical magnitude and visual cues (such as the size of the elements or their total occupied area, see Gebuis & Reynvoet, 2012a; 2012b). This issue is particularly acute for non-symbolic comparison tasks when participants are explicitly instructed to judge two collections of elements. In these conditions, they are likely to make use of the available perceptual visual information to take their decision (Gebuis et al., 2016). Hence it is not surprising that inhibition and executive processes appear to have a large impact on numerical judgements (Cragg & Gilmore, 2014; Gilmore et al., 2013).

In light of these issues, implicit measures to assess ANS acuity have been developed, using functional magnetic resonance imaging (e.g., Ansari, Dhital, & Siong, 2006; Cantlon, Brannon, Carter, & Pelphrey, 2006; Piazza et al., 2004) or event-related potentials with electroencephalography (EEG, e.g., Fornaciai, Brannon, Woldorff, & Park, 2017; Gebuis & Reynvoet, 2013; Park, DeWind, Woldorff, & Brannon, 2016). Here we used EEG recording coupled with a Fast Periodic Visual Stimulation (FPVS) approach to provide a rapid (i.e., time-constrained), sensitive, objective and yet specific (i.e., minimizing biases)

measure of the ANS. This approach is based on the relatively old observation that the human brain synchronizes its activity to the periodic state of a flickering stimulus (Adrian & Matthews, 1934), leading to so-called Steady-State Visual Evoked Potentials (SSVEPs, Regan, 1977). Given its advantages in terms of sensitivity (i.e., high Signal-to-Noise ratio, SNR) and objectivity (i.e., measure at an experimentally-defined frequency, see Regan, 1989; and see Norcia, Appelbaum, Ales, Cottureau, & Rossion, 2015, for a review), it has recently been extended to complex visual stimuli, such as faces for instance, measuring sensitivity to changes of identity at specific periodic frequency rates (Rossion & Boremanse, 2011; Rossion, 2014).

To our knowledge, only two studies have applied a fast periodic visual stimulation approach in EEG in the domain of visual quantities. Libertus, Brannon, and Woldorff (2011) reported brain responses driven by rapid (i.e., 12.5 Hz) periodic numerical changes, these changes increasing between two ratios of numerical magnitudes. Interestingly, brain responses showed qualitatively similar increases for infants and adults. However, since the authors did not systematically manipulate non-numerical visual cues, the extent to which their recorded responses were affected by fluctuations within the irrelevant dimensions remains unknown. Most recently, Park (2017) reported specific brain responses to numerosity changes in visual dot displays changing in size, position and spacing at a faster rate of 8 Hz. The author was able to record neuronal synchronisation, over the medial occipital cortex, to periodic numerical variations (1 Hz), distinct from fluctuations within other dimensions. This paradigm achieved disentangling number from low-level visual cues, but it did

not allow the measurement of numerical discrimination thresholds. In the current study, we aimed at combining the contributions of both paradigms in controlling for visual cues and evaluating numerical discrimination threshold. Moreover, we optimized a number of methodological advantages of the FPVS-EEG approach (e.g., long time windows with high frequency resolution to increase SNR, baseline correction of EEG response, and quantification of the response through sums of harmonics; see e.g., Retter & Rossion, 2016) in order to obtain significant responses at the individual participant level, to relate to behavioural measures.

To achieve these goals, we used a specific version of the FPVS-EEG approach in which physically variable standard stimuli are presented at a fast periodic rate (e.g., at 10 Hz). Then, stimuli that deviate at the level of a high-level visual property are introduced in the sequence at a slower periodic rate (e.g., 1 out of 8 stimuli, at 1.25 Hz). Neural responses at the deviation rate in the EEG frequency domain emerge if and only if there is high-level visual discrimination of the deviant from the standard (e.g., face identities, Liu-Shuang, Norcia, & Rossion, 2014; facial expressions, Dzhelyova, Jacques, & Rossion, 2016; letters or words vs. pseudo-fonts, Lochy, Van Belle, & Rossion, 2015). This approach is highly sensitive to neural discrimination, and provides objective responses (i.e., at frequencies determined by the experimenter) without requiring explicit processing of the discrimination.

Here, in a FPVS-EEG design, we presented 45 seconds stimulation sequences to adult participants, during which the numerical ratio between a standard number

and the deviant was parametrically manipulated. Crucially, participants were not involved in any numerical explicit decision, leading to a bias-free measure of ANS. Additionally, low-level visual cues such as luminance or density were varied at random at each stimulation cycle, such that quantity was the only parameter periodically manipulated (see Figure 1). If this approach is sensitive to numerical processing, we expect EEG signal at the frequency of change of magnitude to increase when the ratio between the frequent and deviant stimuli increases. Besides, in a parametric design, EEG spectra should reveal the numerical threshold from which discrimination is successful (i.e., the smallest ratio in which a response to the deviant quantity was observed), and this EEG threshold can be directly compared to behavioural results obtained in explicit tasks (i.e., the Weber fraction).

Methods

Ethical considerations

We followed APA ethical standards to conduct the present study. The Ethic Review Panel from the University of Luxembourg approved the methodology and the implementation of the experiment before the start of data collection. The data reported in the present article were part of a larger EEG recording session that also evaluated language and symbol processing (which will be the focus of another manuscript) and that lasted 3 hours in total. Participants received 30 euros for their participation.

Participants

Twenty-five participants were recruited among undergraduate students at the University of Luxembourg. We excluded participants with any neurological or neuropsychological disorder, or any uncorrected visual impairment. To ascertain that no participant suffered from dyscalculia, we evaluated their arithmetic ability with the use of the Tempo Test Rekenen (De Vos, 1992), which is a timed pen-and-paper test (five minutes) consisting in arithmetic problems of increasing difficulty. All participants reached the inclusion criterion, which was 100 correct items out of 200, and were included into in the present study. However, one participant was excluded due to poor instruction compliance during EEG acquisition (too many movement artefacts). In the end, the data of twenty-four adult participants was considered (sixteen females). Mean age was 26 years (ranging from 21 to 35).

Material and Procedure

Experimental Setup.

Stimulus presentation and data collection were carried out with MATLAB (The MathWorks), using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, Pelli, Ingling, Murray, & Broussard, 2007; Pelli, 1997). The behavioural number comparison task and the EEG recording took place within a shielded room (in a Faraday cage, 2.88 m length, 2.29 m width, and 2.22 m height). The order of the tasks was counterbalanced across participants (13 participants started with the EEG measure, 11 with the behavioural paradigm). The latter were comfortably seated at a distance of 1 m from the display screen (a 24" LED monitor, 100 Hz refresh rate, 1 ms response time).

Number Comparison task.

Participants were instructed to determine as accurately and as fast as possible the more numerous of two dot arrays simultaneously displayed on two sides of a screen. Stimuli consisted of a multitude of plain dark blue dots on a light blue background¹. We created dot arrays following the methodology used by Piazza

¹ The RGB colour codes for the dots and the background were 003-037-082 and 188-185-255, respectively. As their colour was plain, the stimuli luminance and the brightness contrast were confounded with accumulated dot surfaces. We chose this colour combination to reduce as much as possible the brightness

and colleagues (2004). For half of the stimuli, the surface (i.e., the total area occupied by the dots) was manipulated as a function of the numerical magnitude and other visual parameters were left to vary at random; for the other half, the mean dot size was controlled whereas other visual cues randomly varied. We generated collections in pairs, and constantly maintained one collection to ten dots, varying the number within the other one, from ten to twenty-four dots with an increment of two. This manipulation led to eight different numerical ratios. We created twenty-four pairs per ratio, and every participant had thus to judge 192 trials.

To make their judgement, participants were instructed to press the left key on a keyboard with their left forefinger when they considered the more numerous collection to be on the left side, or alternatively to press the right key with their right forefinger when they judged that the right array was larger. Dots simultaneously appeared within two distinct dark blue circles that were continuously displayed at both sides of the screen. Each circle subtended a visual angle of $8^{\circ} 54'$. The onset of a central cross symbol primed participants for the apparition of the dot arrays 500 ms later. These were displayed for a maximal duration of 300 ms and were followed by a mask, which was composed

contrast as the latter induces retinal after-effects (Hochberg & Triebel, 1955).

The reduction of such after-effects was not specifically relevant for the numerical comparison task, but it was crucial for the Fast Periodic Visual Stimulation, during which dot arrays needed to be displayed for a very short period of time and without any following mask.

of colour changing pixels (at random, following the refresh rate) within both circles. The inter-stimulus interval was 500 ms, and the whole task lasted about seven minutes.

To index the performance throughout the numerical ratios, we computed the Weber fraction (w) by adjusting a Gaussian cumulative probability distribution function using nonlinear regression, based on the Levenberg-Marquardt-Fletcher nonlinear least square iterative method (see Halberda et al., 2008; Pica, Lemer, Izard, & Dehaene, 2004; for more detailed methodological considerations). The following mathematical expression was used to fit individual proportion correct responses as a function of ratios (r), based on the complementary error function $erfc(x)$. The parameter w in the equation is the Weber Fraction.

$$1 - \frac{1}{2} \operatorname{erfc} \left[\frac{1}{w} \sqrt{\frac{(r-1)^2}{2(r^2+1)}} \right]$$

Fast Periodic Visual Stimulation.

We used the same stimuli created for the number comparison task, although here only one array appeared at a time at the centre of the screen. In order to comply with the specificities of FPVS, we introduced two modifications to the stimuli. First, dot patches were presented without their surrounding circle, in order to minimize any irrelevant brain responses within the stimulation.

Second, to suppress the illusory impression of movement elicited by brief presentation of dots at different locations (see Heider & Simmel, 1944), we varied the identity of the elements, keeping the relation between manipulated

visual cues and numerical magnitudes the same than in the dot arrays (see Figure 1a). To do so, we created another set of square arrays based on the dot collections, in which every element consisted of the external square around each dot. Square and dot arrays were intermixed at random during sequences. We also introduced a random rotation (in steps of 1° up to 360°) to patches during their display in order to drastically increase the variety of the visual stimulation without affecting the relation between numerical and non-numerical information.

Participants were instructed to keep their gaze on the centre of the screen, where a blue diamond form was displayed. They were instructed that the diamond would change colour from blue to red during the sequences (the change was not periodic and occurred six to eight times), and that they should press a key on a button switch with their right forefinger when they detected the change. They were told that geometrical forms would appear on the screen background, and they were explicitly told to restrain orienting their gaze towards forms, and to try not to figure out what they were.

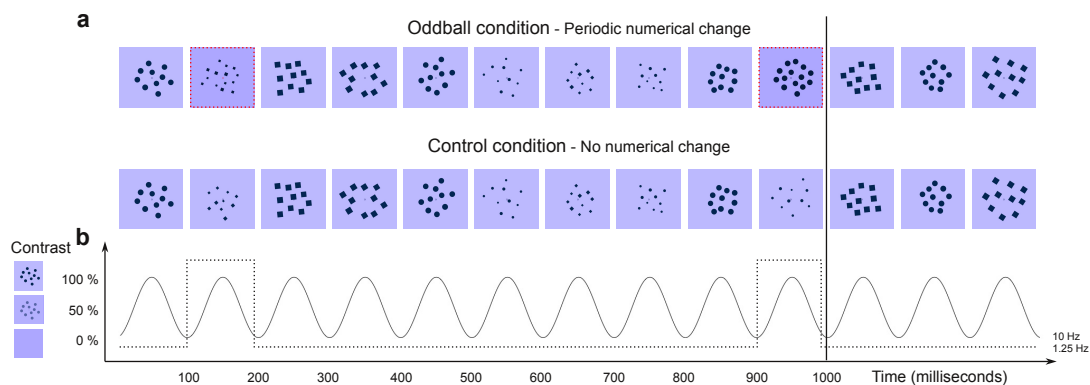


Figure 1. Illustration of the experimental design. (A) During 45 s sessions, geometrical forms are sequentially presented at a fast rate (10 Hz). In all experimental conditions, one rare number (fourteen in the illustration, highlighted with a surrounding red dotted line) was periodically displayed, one every eight stimuli (1.25 Hz), among a frequent number (ten), whereas in a control condition, no numerical changes occurred. (B) The onset and the offset of the stimuli followed a sinusoidal contrast stimulation (from blank to full luminance) at 10 Hz. Note that the deviant frequency, 1.25 Hz, is embedded with the base frequency, 10 Hz.

Stimulus presentation followed a sinusoidal contrast modulation from 0 to 100% (see Figure 1b), as in previous FPVS-EEG studies (Rossion & Boremanse, 2011; Liu-Shuang et al., 2014). The base frequency rate was 10 Hz, which means that the sinusoidal contrast peaked ten times per second. In other words, ten different stimuli were displayed during one second (the onset and the offset of one array lasted 100 ms). In a control condition, arrays always containing ten elements were displayed during the sequence. The number of geometrical form was thus exactly the same, although the visual cues randomly varied from item to item, thus at every cycle, throughout the sequence (see Figure 1a). Critically, in the experimental conditions, a periodic variation was introduced within the sequence: every eight item (1.25 Hz), the number of elements changed (see Supplementary Material). We manipulated the numerical ratio between the standard number and the deviant, creating seven experimental conditions in which the same ratios were used than the ones from the numerical comparison task (i.e., 1.2, 1.4, 1.6, 1.8, 2.0, 2.2, 2.4). The deviant number was always the same during a condition.

Stimulation sequences lasted 49 seconds, including 45 seconds of stimulation and 2 seconds of fade in and fade out. We repeated the control condition and every experimental conditions four times, for a total of thirty-two sequences. When visual inspection of the EEG during acquisition led to the detection of obvious artefacts (e.g., offsets of the electrodes larger than 40mV), the experimenter excluded and reran the noisy sequence. This procedure was rare and only occurred six times out of the whole 768 sequences across our twenty-four participants (less than 1% of the sequences).

EEG acquisition.

EEG data was acquired at 1024 Hz using a 128-channel BioSemi ActiveTwo system (BioSemi B. V., Amsterdam, The Netherlands). The electrodes were positioned on the cap according to the standard 10-20 system locations (for exact position coordinates, see <http://www.biosemi.com>). Two additional electrodes, the Common Mode Sense (CMS) active electrode and the Driven Right Leg (DRL) passive electrode, were respectively used as reference and ground electrodes. Offsets of the electrodes, referenced to the CMS, were held below 40 mV. We monitored eye movements with four flat-type electrodes; two were placed above and below participant's right eye, the other two were positioned lateral to the external canthi.

EEG analysis.

EEG analyses were carried out using the toolbox Letswave 6 (<http://nocions.webnode.com/letswave>) running on MATLAB 2016 (The Mathworks). Additional statistical analyses were conducted with the lme4

package (Bates, Maechler, Bolker, Walker, 2015) on R (R Core Team, 2016). All data files were downsampled from 1024 Hz to 512 Hz to reduce data processing time. We used a 4-order band-pass Butterworth filter (0.1 to 100 Hz), and then re-referenced the data to the common average. Channels were not interpolated. We did not correct the EEG spectra for ocular movements, since frequency-domain EEG responses of interest in these conditions fall in tiny frequency bins that are largely immune to artefacts (Regan, 1989; Rossion, 2014). EEG recordings were then segmented from stimulation onset (excluding the fade in) until 44 s (440 stimulus onsets, 22,528 data points at 512 Hz), as this was the value that contained the most complete 1.25 Hz cycles within the stimulation (55 cycles). We averaged the four repetitions of the same condition in the time domain for each participant, and we then applied a Fast Fourier Transformation (FFT) to these segments. Amplitude spectra were extracted for all 128 channels with a frequency resolution (the size of the frequency bins) of 0.022 Hz. Three indices were then computed, in line with previous FPVS-EEG studies.

We calculated the SNR for the whole frequency spectrum, as the ratio between the amplitude at each frequency and the amplitude average of the twenty surrounding bins (ten at each side, excluding the immediately adjacent bins and the two most extreme values amongst the twenty bins, see Dzhelyova et al., 2016; Liu-Shuang et al. 2014). SNR was averaged for each condition across individual participants and was used for data visualization that allowed general peak detection. The noise level within this measure is centred on one, so that a clear and definite peak above one indicates a specific neuronal response at the given frequency.

To assess general topography as a function of the condition, we computed the Sums of the Baseline-corrected Amplitudes (SBA) of the deviant harmonics (i.e., 1.25 Hz, 2.50 Hz, 3.75 Hz, etc., up to the highest harmonics within all conditions in which we recorded a significant response, see Retter & Rossion, 2016).

Baseline-corrected amplitudes were obtained by subtracting the mean amplitude of the twenty surrounding bins to each bin (excluding the immediately adjacent bins and the two most extreme values, see Liu-Shuang et al. 2014). It should be noted that baseline-corrected amplitudes are centred on zero and can be positive or negative, so that the addition of amplitudes of random frequency bins will statistically tend to add zero. The SBA is expressed in microvolt and can thus be used to quantify the signal (Dzhelyova & Rossion, 2014; Retter & Rossion, 2016). If different from zero, the SBA value indicates that the electrode recorded a specific response. To assess whether the response of interest was affected by the numerical ratio, we averaged electrodes in different Regions of Interest (ROIs). Electrodes were pooled following Liu-Shuang and colleagues (Figure 3 C, 2014). Due to the general topography of our results (see Figure 3), we only considered EEG activity within the whole posterior scalp. We present the results recorded from four ROIs: one medial occipital region encompassing Oz, O1, O2, and three occipito-parietal regions (left, high medial, and right areas)². We averaged the SBA from all electrodes in each ROI, and we averaged the data at the group level.

² The complete list of the averaged electrodes in BioSemi standard 128 channels layout is the following: *Medial Occipital*, A13, A14, A15, A22, A23, A24, A25, A26, A27, and A28; *Medial Occipito-Parietal*, A5, A7, A17, A18, A19, A20, A21, A30,

Finally, to assess inter-individual brain response across the conditions, we cropped all FFT spectra around the response of interest (1.25 Hz and the subsequent harmonics until the highest harmonic giving a significant response), surrounded by its neighbouring frequency bins. We then summed all spectra and applied a Z score transformation to each bin as a function of its surrounding twenty bins (ten at each side). This manipulation provides a Z score, for twenty-one frequency bins: the central bin corresponding to the response of interest (signal), and all other bins representing the noise level. If there is no significant response, there is a one-in-twenty-one chance (less than 5%) for EEG activity from the central bin to be stronger than activity at all the surrounding bins, and thus there is less than 5% chance that its associated Z score would be greater than 1.64 ($p < .05$, one-tailed, testing signal > noise level).

A31, A32, and B4; *Left Occipito-parietal*, A8, A9, A10, A11, A12, A16, D29, D30, D31, and D32; *Right Occipito-parietal*, A29, B5, B6, B7, B8, B9, B10, B11, B12, and B13. Please refer to <http://www.biosemi.com> for the exact location of the electrodes.

Results

Number Comparison Task

Overall, participants were able to determine the larger of the two dot arrays with a mean accuracy of 91.95%, 95 % Confidence Interval (CI) [91.11, 92.79], and they produced the correct result on average in 593 ms, 95% CI [581, 606]³.

Numerical ratio affected performance, with accuracy rates ranging from 68.11%, 95% CI [64.29, 71.94], to 98.78%, 95% CI [97.88, 99.68] (Figure 2), and correct response times (RTs) ranging from 754 ms, 95% CI [699, 809] to 521 ms, 95% CI [506, 536], for the closest and the most distant ratio, respectively. We analysed the effect of numerical ratio on performance with linear mixed effects models: we constructed a full model with the numerical ratio and the position (i.e., left or right) of the correct response as fixed effects (without interactive form), and with participants and items as random factors. We used a logistic regression to model accuracy. We inspected the residual plots for latency models to ascertain that there were no obvious deviations from homoscedasticity or normality. To assess the significance of each factor contribution, we compared this model to two reduced models without the effect in question using chi-squares tests on the log-likelihood values. For both accuracy and RTs, the full model fitted better

³ It should be noted that we only considered responses during the ratio 1.0 condition (i.e., 10 vs. 10) as an illustration of general performance, which is depicted in Figure 2 (we randomly assigned one response amongst the two choices as the correct answer). We excluded the results from this condition in all statistical analyses and restricted our dataset from ratio 1.2 to ratio 2.4.

than the reduced model without numerical ratio, respectively $\chi^2(1) = 327.67$, $p < .001$, and $\chi^2(1) = 71.46$, $p < .001$, whereas the first did not fit significantly better than the reduced model without position, $\chi^2(1) = 3.43$, $p = .063$, and $\chi^2(1) = 1.78$, $p = .181$. As expected, we replicated the numerical ratio effect; the more distant the magnitudes, the better the performance. The position of the larger array had no impact. The mean value of w was 0.213, 95% CI [0.199, 0.228].

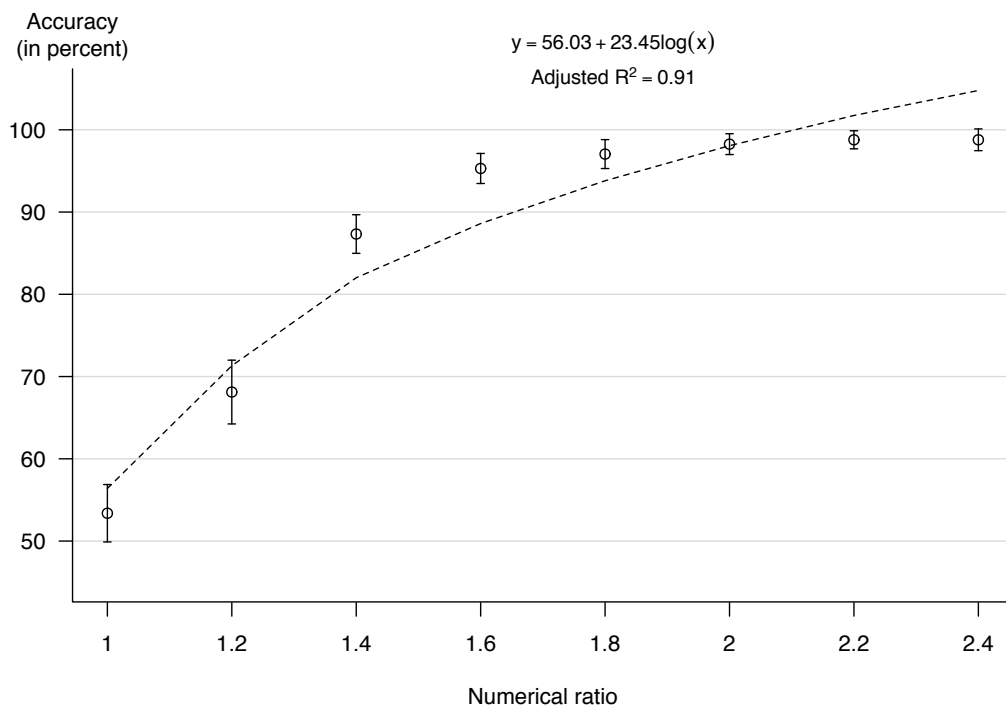


Figure 2. Average accuracy in the numerical comparison task (per cent) as a function of the numerical ratio between the two dot arrays. Vertical lines depict 95% confidence intervals. The dashed line represents the best logarithmic fit of the data (adjusted $R^2 = .91$).

Fast Periodic Visual Stimulation in EEG

Instruction compliance.

On average, participants took 674 ms ($SD = 118$ ms) to respond to the colour change that affected the fixation diamond. Misses were rare, occurring in less than one percent of the trials. No participants failed to detect the change more than once during a 45 second session. Such high detection rate indicates that participants followed the instruction and kept their gaze on the centre of the screen during EEG acquisition. Although three participants reported detecting some numerical changes at the end of the experiment, no participant reported noticing the periodicity of these changes when interrogated.

Signal-to-Noise Ratio.

Figure 3 depicts the SNR of the EEG spectrum recorded on Oz in every condition, averaged for all participants. SNR peaked at 10 Hz (and its harmonics) in every condition. This is expected since these responses reflect the visual contrast between the background and the dots induced by the periodic onset of the stimuli.

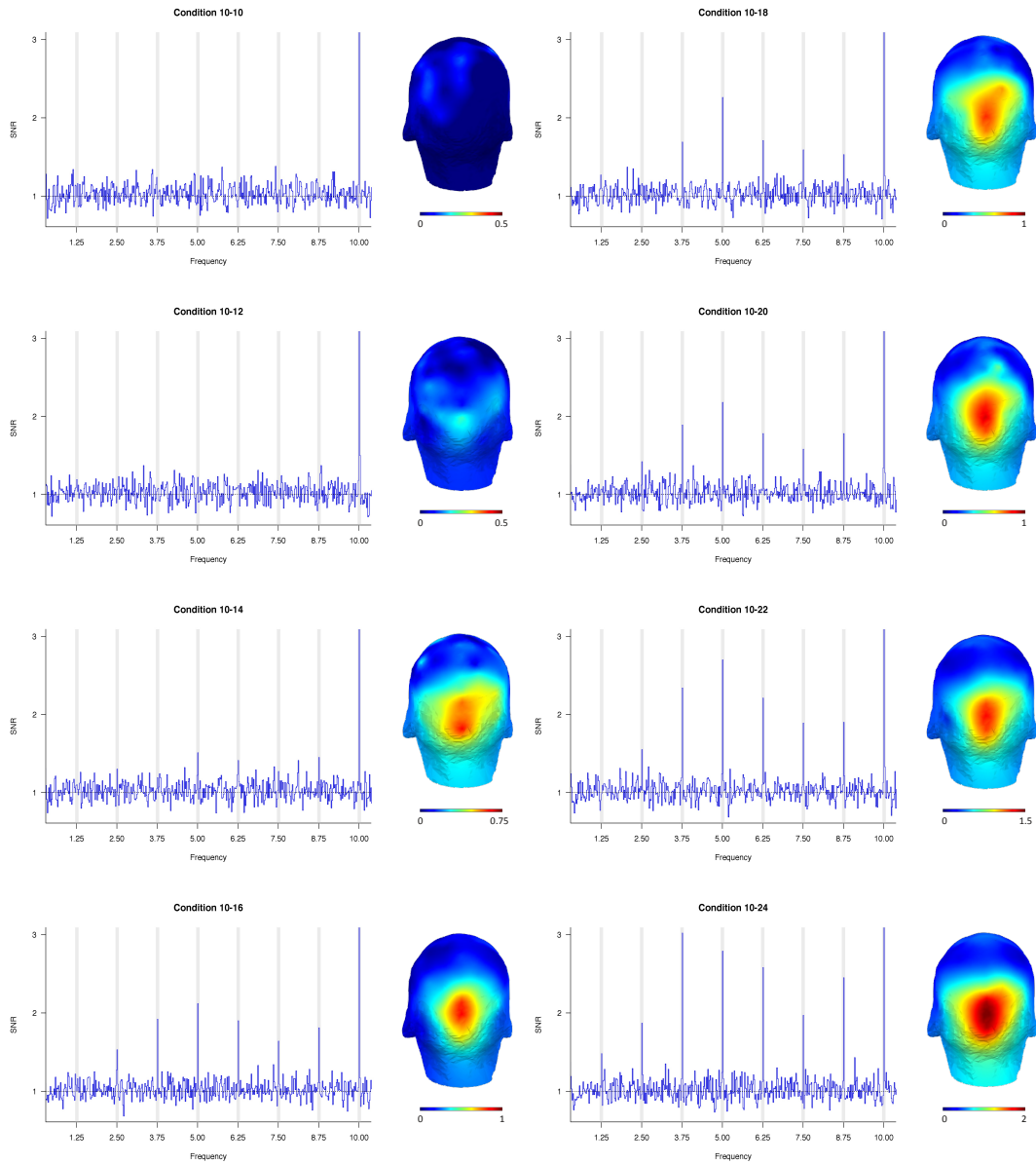


Figure 3. Specific brain responses to numerical ratios. The figure depicts the grand-averaged spectra (displayed from 1 to 11Hz) over the occipital electrode Oz for every condition. The deviant frequency bin (1.25 Hz) and its harmonics are highlighted in grey. Note that the eighth harmonic corresponds to the base frequency rate (10 Hz). Topographical maps of the grand-averaged data show the Sums of the Baseline-Corrected Amplitudes (μV) for the periodic response up to the eighteenth harmonics (from 1.25 to 22.5 Hz, excluding 10 and 20 Hz). Topographical scales are displayed as a function of the maximum value in each condition.

More importantly for the purpose of the study, there was a very clear EEG response at 1.25 Hz and its harmonics in all conditions associated with a numerical ratio equal to or greater than 1.4 (see Figure 3). The SNR seemed to progressively increase with increasing numerical ratio. Critically, since the periodicity of the deviant response was only related to numerical changes, this response thus reflected implicit visual discrimination of the numerical quantities. We did not observe any peaks above noise level in the control condition (i.e., 10 vs. 10, no numerical changes) nor in sequences with a numerical ratio of 1.2 (i.e., 10 vs. 12). The highest SNR responses (excluding the base frequency rate) were observed on the third, the fourth and the fifth harmonics in the conditions with a numerical ratio greater than 1.4. We observed clear peaks up to the eighteenth harmonics (i.e., 22.5 Hz) in the condition with the largest numerical change (i.e., 10 vs. 24). The eighteenth harmonic was the highest harmonic at which we recorded significant response to the deviant within all our conditions.

Quantifications (Sums of the Baseline-Corrected Amplitudes).

To generate the topography of the cerebral responses specific to the numerical discrimination, we summed the baseline-corrected amplitudes of the target frequency (1.25 Hz) and its harmonics up to the eighteenth (i.e., the highest harmonic with significant response, based on SNR analyses). Responses at harmonics of the base rate frequency (i.e., 10 and 20 Hz) were excluded from the sum to avoid contamination of the data. We computed SBA per participant and for every condition, and then we averaged the responses at the inter-individual level.

General scalp topography.

The scalp topographies for each condition are depicted in Figure 3. We did not find any 1.25 Hz response at the scalp level for the control condition nor for the smallest numerical ratio. However, we consistently recorded the strongest peaks in other conditions in posterior regions, centred on the medial occipital electrodes.

Effect of numerical ratio.

The mean value of the SBA within the whole posterior scalp (the four ROI taken together) was 0.25 μV , 95% CI [0.19, 0.30]. Mean SBA values were 0.54 μV [0.44, 0.64] for the medial occipital region, 0.23 μV [0.17, 0.28] for the central occipito-parietal region, 0.22 μV [0.17, 0.28] for the left occipito-parietal area, and 0.27 μV [0.21, 0.33], for the right occipito-parietal region. Using mixed effects linear modelling, we constructed a full model with the numerical ratio and the cerebral regions as fixed predictors of the SBA (without interactive form), and with participants as random factor. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. We compared this model to two reduced models without the predictor in question using chi-squares tests on the log-likelihood values. The full model fitted better than both reduced models, $\chi^2(1) = 89.01$, $p < .001$, and $\chi^2(4) = 224.65$, $p < .001$, respectively without numerical ratio and without cerebral regions. This means that the response due to the periodic change of numerical quantities was significantly affected by both the numerical ratio and by the location of the electrodes. The signal indeed peaked within the medial occipital region.

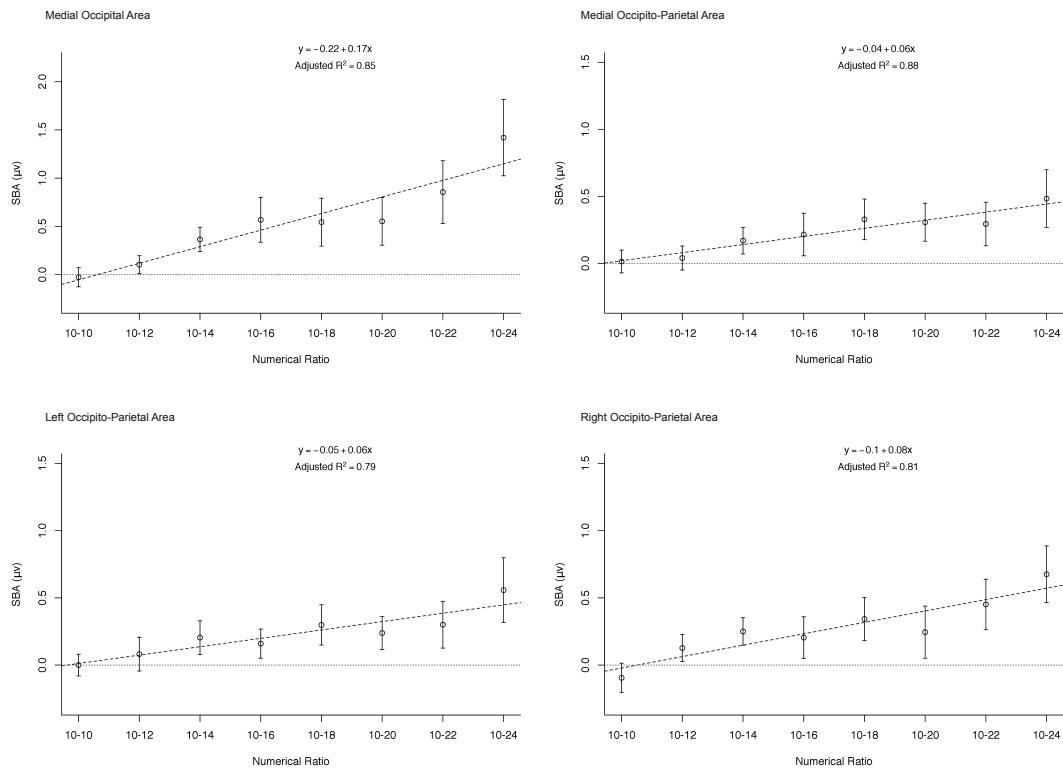


Figure 4. Sums of the Baseline-Corrected Amplitudes (μV) for every numerical condition, averaged across the participants. The SBAs are displayed for the Medial Occipital region (upper left), the Medial Occipito-Parietal region (upper right), the Left Occipito-Parietal region (bottom left), and the Right Occipito-Parietal region (bottom right). Vertical lines depict 95% confidence intervals. The dashed lines represent the best linear fit of the data.

A closer look at the data depicted in Figure 4 revealed that there was no signal above the noise level in the control condition and the condition with the closest numerical ratio (10-12). Strikingly, we observed a positive linear trend in all ROIs (with an adjusted explained variance ranging from .79 to .88), indicating that the strength of the response increased with the numerical ratio. Over the whole posterior scalp, this positive linear trend had an adjusted explained variance of .78. The analyses conducted on the SBA thus corroborated our previous analyses; we did not find any evidence for numerical discrimination

with a ratio less than 1.4 in the EEG spectra, but we did observe supportive evidence that dot arrays were discriminated from ratio 1.4 onward, and that the neuronal discrimination was proportionally related to the numerical ratio.

Individual analyses.

Individual spectra.

Next, we conducted individual analyses to test whether the numerical quantity change was found in all or the majority of individuals, ensuring that outliers did not drive our group-level data and assessing the sensitivity of our approach. For each participant and for every condition, we computed the amplitudes, in Z score, for twenty-one frequency bins with the central bin corresponding to the numeracy change. Figure 5 illustrates the pattern of signals around the deviant response for each participant when discriminating 14 from 10 (ratio 1.4). We show here the amplitudes from this condition since it was the condition with the smallest ratio in which we recorded a significant response at the group level. Strikingly, this numerical ratio was also the first in which participants were able to achieve high performance levels (87.32% accuracy) during the number comparison task. Rather than reporting results from the same electrode for all participants, we selected for each individual the signals from the electrode on which we recorded the largest amplitude within our defined ROIs. The largest response was observed in medial occipital areas (Oz, O2, POz) for fifteen out of twenty-four participants.

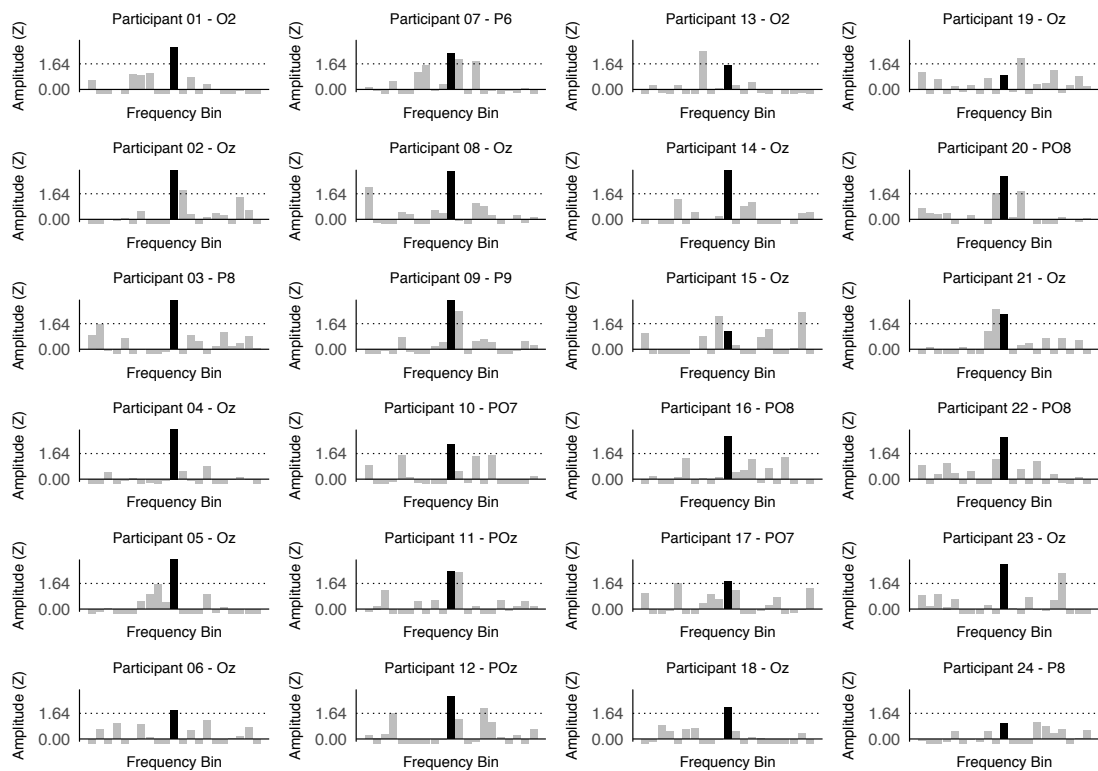


Figure 5. Individual EEG responses (in the frequency domain) to the numerical change with a ratio of 1.4. The best responding electrode from posterior regions (within our four ROI) was chosen for each participant. Amplitudes are expressed in Z-score, so that a value higher than 1.64 represents a significant response. The EEG spectra are centred at the frequency bin corresponding to the periodic response (summed up to 22.5 Hz, excluding 10 and 20 Hz). Twenty neighbouring bins that represent the noise level surround this bin. All participants (except #13, #15, #19, and #24) showed a specific response to the deviant frequency.

In this condition, and despite the very low number of 45 seconds stimulation sequences in each condition (i.e., four), twenty-one out of twenty-four participants showed a clear peak at the central bin of interest (Figure 5). All these responses were greater than the Z criterion value of 1.64 (i.e., significant at an alpha error level of 5 %). These data confirmed that the group-level effect was neither driven by a few outlier participants nor biased by the levels of the surrounding frequency bins.

Relationship with numerical comparison.

Based on the latter observation, we conducted correlational analyses to test whether the response amplitude was related to the behavioural performance measured in the number comparison task across individuals. In the previous section, we restricted our analyses of the EEG spectra to one electrode by participant in only one condition. Here, we correlated the value of the Weber fraction (from the numerical comparison task) to an index of the cerebral response beyond a single electrode, taking into consideration all numerical ratios. In order to obtain this index, we summed up to the eighteenth harmonic (excluding 10 and 20 Hz) the average EEG spectra within the ROIs, and we computed the Z score of the brain response to the target 1.25 Hz frequency for each ratio. We then fitted a linear regression to predict the EEG response as a function of the numerical ratio. Finally, we extracted the standardized coefficient relative to the numerical ratio (i.e., the slope) for every participant. This coefficient was then used as an index of neural sensitivity to numerical ratios in the correlation analysis.

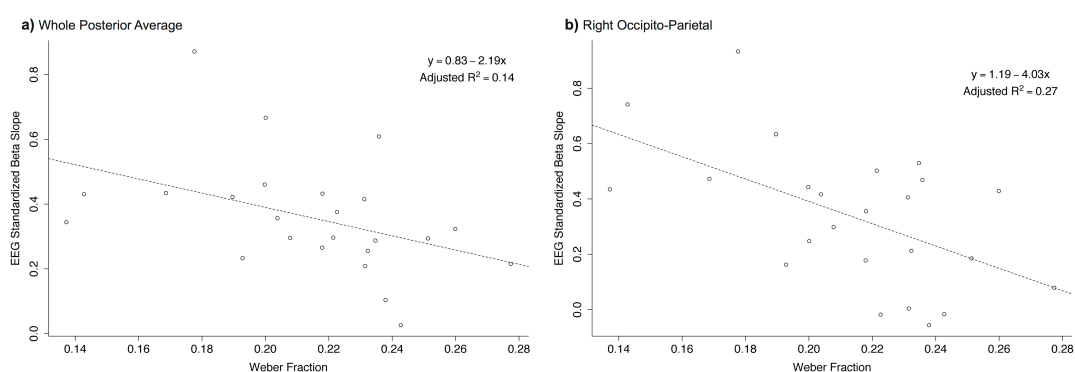


Figure 6. Scatter plots of the relation between the value of the Weber Fraction (from the numerical comparison task) and the Standardized (β) coefficient of the slope predicting EEG

response to the numerical change, (A) within the whole posterior scalp (41 electrodes), on the left, and (B) within the right Occipito-parietal area (10 electrodes), on the right. The dashed lines depict the best linear fit of the data for each region (adjusted $R^2 = .14$ and $.27$).

Pearson's correlation coefficient between the two variables was at $-.21$, 95% CI $[-.56, .20]$, $N = 24$, in the medial occipital area; at $-.25$, 95% CI $[-.59, .16]$ in the central occipito-parietal region; at $-.26$, 95% CI $[-.60, .15]$ in the left occipito-parietal area; and at $-.55$, 95% CI $[-.78, -.19]$ in the right occipito-parietal region. Across the whole posterior scalp (i.e., the four ROIs together, which comprises 41 electrodes), the correlation coefficient was at $-.42$, 95% CI $[-.70, -.02]$. The scatter plots in Figure 6 depict the relation within the two significant ROIs: the whole posterior scalp, and the right occipito-parietal region. We computed a linear regression that supported the reliability of the relation, with adjusted R^2 of $.14$ and $.27$ respectively. Visual inspection of the residual plots did not reveal any obvious deviations from homoscedasticity or normality, and the Bonferonni outlier test (Fox & Weisberg, 2011) did not detect any influential value on the regression. Note that lower w indexes better accuracy (less imprecision), so that better performance in the behavioural task was in fact related to a steeper slope of the EEG signal of interest.

Discussion

Although there is considerable scientific interest in ANS acuity due to its relationship to mathematical ability, its measure is challenging and limited by confounded low-level factors in explicit behavioural tasks. Many cognitive

processes influence the outcome of such tasks, preventing a fair assessment and comparison of ANS acuity across individuals at different developmental stages, within typical and atypical populations. Here, by recording neural synchronization to a deviant number in a fast periodic stream of non-symbolic displays, we provide an implicit and specific (i.e., minimizing low-level confounds) measure of ANS acuity in typical human adults. This measure is objective, occurring at an experimentally defined frequency of 1.25 Hz in our paradigm, and highly sensitive, being obtained in a few minutes of recording (4 repetitions of 45 seconds by ratio) for all individuals tested. ANS acuity, here of 1.4 (i.e., 10 vs. 14), was determined using parametrically increasing numerical ratios between the common stimuli, presented at 10 Hz, and the deviations of quantities occurring at 1.25 Hz.

Previous studies evaluated number sensitivity with implicit measures during passive viewing tasks (e.g., Ansari et al., 2006; Cantlon et al., 2006; Libertus et al., 2011; Park, 2017; Piazza et al., 2004). These measures have the advantage of being independent from executive functions or other higher-order cognitive processes (Gilmore et al., 2013), in contrast to behavioural designs typically used to measure ANS acuity (e.g., DeWind & Brannon, 2016). Here the use of an orthogonal non-periodic implicit task in our study ensured that the EEG response recorded at the frequency of interest was not elicited by any active – or goal-driven – processing of the dot arrays. A response obtained in these conditions implies that the cognitive processes underlying the discrimination of number are largely automatic, a core characteristic of the ANS (Dehaene, 1997). Hence it is particularly suitable to measure the ANS in human observers.

Despite the limitations of an explicit behavioural paradigm, our data revealed similarities between EEG and behavioural responses. There was indeed a significant correlation between participants' Weber fractions in the numerical comparison task and their slope predicting EEG response to the different numerical ratios. In behaviour, the largest increase in performance was found between 1.2 and 1.4 numerical ratios. In EEG, the first significant response *emerged* at the 1.4 ratio. Hence, our study provides a conservative discrimination *threshold*, i.e. a ratio at which the response becomes significant because it is recorded in response to a sufficiently high proportion of trials (i.e., invariant). Future studies could even refine this threshold and discriminate among different individuals, by concentrating on a range of smaller ratios between 1.1 and 1.5.

However, there were also noticeable differences between EEG and behaviour. For instance, we did not record significant EEG synchronisation to the deviant number for the smallest ratio (i.e., 1.2) whereas in behaviour, average performance is higher than chance level even at the lowest ratio of 1.2. While this may be taken as an increased sensitivity of the behavioural measure during the active task, it is more likely to be due to the successful use of confounded visual cues in a subset of items to solve the pairwise discrimination involved in the behavioural task (Gebuis et al., 2016). Moreover, since behavioural performance was already close to ceiling at a numerical ratio of 1.4 (the threshold determined in EEG), the behavioural paradigm was unable to capture any increase beyond that threshold. In contrast, beyond 1.4, the magnitude of

brain responses to deviant numerosities increased further, in proportion to the numerical ratio between the standard and the rare number, such that progressively larger numerical ratios induced progressively stronger EEG responses. This pattern can be explained by the Weber-Fechner law, reflecting another typical signature of the ANS (Dehaene, 2003) captured with our FPVS-EEG approach.

In both the behavioural and the EEG experiment we manipulated the extensive and the intense visual parameters confounded with number (i.e., respectively, the surface and the mean size) according to the method used by Piazza et al. (2004). Our FPVS method was designed to counteract the bias of behavioural Weber fraction measures (DeWind & Brannon, 2016; Guillaume et al., 2016; Norris & Castronovo, 2016; Smets et al., 2014; Szűcs et al., 2013) by presenting all non-numerical visual cues (e.g., geometric form, size, density) at random, so that visual information greatly differed from item to item, even within the standard number (Figure 1a). Critically, these non-numerical parameters changes were non-periodic. In a given sequence, although non-numerical dimensions might show spectral peaks at some of our frequencies of interest, the only parameter that was systematically and constantly tagged at the frequencies of interest (e.g., 1.25 Hz and its harmonics) was the number of elements (see Supplementary Material). Due to the nature of our analyses (i.e., considering all harmonics up to the eighteenth), such influence from the visual cues should be

minimized in comparison to the constant spectral power of the numerical dimension⁴.

Neural synchronisation to the numerical deviation was recorded over posterior regions, centred on the medial occipital electrodes (electrode Oz). This scalp topography is typical of SSVEP studies with simple visual stimuli in general (see Norcia et al., 2015 for review), and is also similar to topographies reported in previous SSVEP studies measuring responses to numerical quantities (Libertus et al., 2011, in adults; Park, 2017). Medial occipital BOLD responses to non-symbolic magnitudes were also described in fMRI studies displaying stimuli for very short time periods (less than 100ms, Bulthé, De Smedt, Op de Beeck, 2014; Eger, Pinel, Dehaene, Kleinschmidt, 2015; for similar EEG results see also Park, 2016). This posterior location contrasts with the hypothesis that analogue magnitude processing takes place in the vicinity of the intraparietal cortex (Cantlon et al., 2006; Nieder, & Dehaene, 2009; Piazza et al., 2004). It also differs from the occipito-temporal responses that are systematically observed in FPVS studies investigating high-level visual processing with words (left hemispheric

⁴ It should be noted that we considered in our analyses the averaged brain responses from four different sequences. Yet we cannot totally exclude that averaging distinct non-periodic sequences led to the periodical emergence of some non-numerical cues in the averaged signal, which might have affected the specificity of our averaged EEG responses. Future studies should assess whether periodic averaged properties of non-periodic sequences affect averaged brain responses.

dominance in Lochy et al., 2015) or faces (right hemispheric dominance in e.g., Dzhelyova et al., 2016; Liu-Shuang et al., 2014; Rossion & Boremanse, 2011). In light of the above-mentioned findings, it is very likely that the medial occipital position of EEG synchronisation reflects the nature of the numerical stimulus itself and indicates that number was discriminated at an early stage of processing, possibly within the primary visual cortex.

Most studies do not focus on this occipital response related to the discrimination of quantities and have suggested that it is only related to the basic processing of the visual information (e.g., Bulthé et al., 2014) or that is induced by feedback from higher parietal regions, in a top-down relationship (Eger et al., 2015).

However, Roggeman, Santens, Fias, and Verguts (2011) found increasing activity within the occipital regions with increasing numerosity, independently of any attentional processes, and suggested that this occipital activity underlies an automatic, low-level mapping to a cognitive “location” which is driven by the stimulus itself. This proposal is consistent with Dehaene and Changeux’s (1993) view that neurons from the visual system create an intermediate topographical map of the location of each object, regardless of its size. In the same vein, Park and colleagues (2016) also hypothesised that early occipital processing during number discrimination is related to the individuation of all the items composing a visual scene, which *in fine* corresponds to distilling the numerical information of the stimulus. This interpretation is in line with the description of neurons within the primary visual cortex that are specifically sensitive to the discontinuity of the contrast intensities and thus can be directly linked to the individuation process (Marr, 1976). In other words, it could be argued that

number is a distinct visual dimension. Indeed it has recently been suggested that number is a topologically invariant characteristic of visual scenes (Kluth & Zetzsche, 2016), a framework that could also account for the report that humans universally and spontaneously seem to extract numerical information (Ferrigno, Jara-Ettinger, Piantadosi, & Cantlon, 2017). More generally, and although our approach with fast stimulation does not provide unambiguous time-domain information, our results are in line with the view that quantities are decoded in the visual cortex (Burr & Ross, 2008; see also Stoianov & Zorzi, 2012), at least by V2 or V3 (Fornaciai et al., 2017). Such early processing of the discrete visual dimension is the cognitive basis on which more elaborate number notions will be constructed in the higher-level abstract parietal regions (Nieder & Dehaene, 2009). Incidentally, the numerical sensitivity recorded within the right occipito-parietal area correlated the strongest with the Weber fraction. It might thus be the connection between the visual cortex and higher-level numerical areas alongside the occipito-parietal processing stream (Roggeman et al., 2011) that is crucial for our numerical intuition, but this proposal will need to be probed in future studies.

In summary, we provide evidence with an original FPVS-EEG approach for objective, sensitive, and automatic discrimination of briefly presented numerosities over the medial occipital cortex. Critically, the magnitude of an individual's EEG response to deviant number predicts behavioural performance at an independent numerical comparison task. Taken together these findings indicate that numerical magnitude is automatically extracted very early in the visual system. The present frequency-tagging EEG paradigm provides an implicit

neuronal marker for this process and contributes a tool to fundamental and clinical investigations of the human number sense.

Acknowledgments

This work is supported by the Fonds national de la Recherche Luxembourg (INTER/FNRS/15/11015111/Face perception/Christine Schiltz), and a PDR T.0207.16 FNRS for a collaborative work between Luxemburg and Belgium. The authors are grateful to Alexandre Poncin and the HIWI students for their help during data collection, and to Pierre Henneaux for invaluable theoretical advices in signal processing. The authors declare no conflict of interest.

Author contributions

Conception: M.G., S.M., B.R., C.S., Experiment Design: M.G., S.M., C.S., Data Collection: M.G., Data analysis: M.G., M.D.; Drafting Manuscript: M.G.; Critical Revision: S.M., B.R., M.D., C.S.

References

Adrian, E. D., & Matthews, B. H. (1934). The Berger rhythm: potential changes from the occipital lobes in man. *Brain*, *57*(4), 355–385.

- Ansari, D., Dhital, B., & Siong, S. C. (2006). Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Research, 1067*(1), 181–188.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48.
- Brainard, D. H. (1997). The Psychophysics Toolbox, *Spatial Vision, 10*, 433–436.
- Bulthé, J., De Smedt, B., & Op de Beeck, H. P. (2014). Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. *NeuroImage, 87*, 311–322.
- Burr, D., & Ross, J. (2008). A Visual Sense of Number. *Current Biology, 18*(6), 425–428.
- Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional Imaging of Numerical Processing in Adults and 4-y-Old Children. *PLoS Biology, 4*(5), e125.
- Cantlon, J. F., Cordes, S., Libertus, M. E., & Brannon, E. M. (2009). Comment on “Log or linear? Distinct intuitions of the number scale in Western and Amazonian indigene cultures.” *Science, 323*(5910), 38b–38b.
- Chen, Q., & Li, J. (2014). Association between individual differences in non-symbolic number acuity and math performance: A meta-analysis. *Acta Psychologica, 148*, 163–172.
- Cragg, L., & Gilmore, C. (2014). Skills underlying mathematics: The role of executive function in the development of mathematics proficiency. *Trends in Neuroscience and Education, 3*(2), 63–68.
- Dehaene, S. (1997). *The Number Sense*. New York: Oxford University Press.

- Dehaene, S. (2003). The neural basis of the Weber–Fechner law: a logarithmic mental number line. *Trends in Cognitive Sciences*, 7(4), 145–147.
- Dehaene, S., & Changeux, J.-P. (1993). Development of elementary numerical abilities: A neural model. *Journal of Cognitive Neuroscience*, 5(4), 390–407.
- DeWind, N. K., & Brannon, E. M. (2012). Malleability of the approximate number system: effects of feedback and training. *Frontiers in Human Neuroscience*, 6, 1-10.
- DeWind, N. K., & Brannon, E. M. (2016). Significant Inter-Test Reliability across Approximate Number System Assessments. *Frontiers in Psychology*, 7, 1-10.
- De Vos, T. (1992). *Test voor het vaststellen van het rekenvaardigheidsniveau der elementaire bewerkingen (automatisering) voor het basis en voortgezet onderwijs: Handleiding [Test to determine the mathematics ability level for elementary operations (automatization) in primary and secondary education: Manual]*. Nijmegen, the Netherlands: Berkhout.
- Dzhelyova, M., Jacques, C., & Rossion, B. (2016). At a Single Glance: Fast Periodic Visual Stimulation Uncovers the Spatio-Temporal Dynamics of Brief Facial Expression Changes in the Human Brain. *Cerebral Cortex*, 1-18. doi: 10.1093/cercor/bhw223
- Dzhelyova, M., & Rossion, B. (2014). Supra-additive contribution of shape and surface information to individual face discrimination as revealed by fast periodic visual stimulation. *Journal of Vision*, 14(14, 15), 1–14.
- Eger, E., Pinel, P., Dehaene, S., & Kleinschmidt, A. (2015). Spatially Invariant Coding of Numerical Information in Functionally Defined Subregions of Human Parietal Cortex. *Cerebral Cortex*, 25(5), 1319–1329.

- Ferrigno, S., Jara-Ettinger, J., Piantadosi, S. T., & Cantlon, J. F. (2017). Universal and uniquely human factors in spontaneous number perception. *Nature Communications*, *8*, 13968.
- Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression*, Second Edition, Sage.
- Fornaciai, M., Brannon, E. M., Woldorff, M. G., & Park, J. (2017). Numerosity processing in early visual cortex. *NeuroImage*, *157*, 429–438.
- Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*, *4*(2), 59–65.
- Gebuis, T., Cohen Kadosh, R., & Gevers, W. (2016). Sensory-integration system rather than approximate number system underlies numerosity processing: A critical review. *Acta Psychologica*, *171*, 17–35.
- Gebuis, T., & Reynvoet, B. (2012a). Continuous visual properties explain neural responses to nonsymbolic number: The neural correlates of nonsymbolic number. *Psychophysiology*, *49*(11), 1649–1659.
- Gebuis, T., & Reynvoet, B. (2012b). The Role of Visual Information in Numerosity Estimation. *PLoS ONE*, *7*(5), e37426.
- Gebuis, T., & Reynvoet, B. (2013). The neural mechanisms underlying passive and active processing of numerosity. *NeuroImage*, *70*, 301–307.
- Gilmore, C., Attridge, N., Clayton, S., Cragg, L., Johnson, S., Marlow, N., ... Inglis, M. (2013). Individual Differences in Inhibitory Control, Not Non-Verbal Number Acuity, Correlate with Mathematics Achievement. *PLoS ONE*, *8*(6), e67374.
- Guillaume, M., Gevers, W., & Content, A. (2016). Assessing the Approximate Number System: no relation between numerical comparison and estimation tasks. *Psychological Research*, *80*(2), 248-258.

- Halberda, J., Mazocco, M. M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, *455*(7213), 665–668.
- Heider, F., & Simmel, M. (1944). Changing form to avoid movement illusion: An experimental study of apparent behavior. *The American Journal of Psychology*, *57*(2), 243–259.
- Hochberg, J. E., & Triebel, W. (1955). Figural after-effects with colored stimuli. *The American Journal of Psychology*, *68*(1), 133–135.
- Hyde, D. C., Berteletti, I., & Mou, Y. (2016). Approximate numerical abilities and mathematics : Insights from correlational and experimental training studies. In M. Capeletti, W. Fias (Eds.). *Progress in Brain Research* Vol. 227 (pp. 335–351). Amsterdam: Elsevier.
- Inglis, M., Attridge, N., Batchelor, S., & Gilmore, C. (2011). Non-verbal number acuity correlates with symbolic mathematics achievement: But only in children. *Psychonomic Bulletin & Review*, *18*(6), 1222–1229.
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3? *Perception*, *36* (14), 1-16.
- Kluth, T., & Zetsche, C. (2016). Numerosity as a topological invariant. *Journal of Vision*, *16*(3), 30–30.
- Leibovich, T., Al-Rubaiey Kadhim, S., & Ansari, D. (2017). Beyond comparison: The influence of physical size on number estimation is modulated by notation, range and spatial arrangement. *Acta Psychologica*, *175*, 33–41.
- Libertus, M. E., Brannon, E. M., & Woldorff, M. G. (2011). Parallels in Stimulus-Driven Oscillatory Brain Responses to Numerosity Changes in Adults and Seven-Month-Old Infants. *Developmental Neuropsychology*, *36*(6), 651–667.

- Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia*, *52*, 57–72.
- Lochy, A., Van Belle, G., & Rossion, B. (2015). A robust index of lexical representation in the left occipito-temporal cortex as evidenced by EEG responses to fast periodic visual stimulation. *Neuropsychologia*, *66*, 18–31.
- Marr, D. (1976). Early processing of visual information. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *275*(942), 483-519.
- Mejias, S., Mussolin, C., Rousselle, L., Grégoire, J., & Noël, M.-P. (2012). Numerical and nonnumerical estimation in children with and without mathematical learning disabilities. *Child Neuropsychology*, *18*(6), 550–575.
- Nieder, A., & Dehaene, S. (2009). Representation of Number in the Brain. *Annual Review of Neuroscience*, *32*(1), 185–208.
- Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude: Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron*, *37*, 149–157.
- Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottureau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of Vision*, *15*(6), 1-46.
- Norris, J. E., & Castronovo, J. (2016). Dot Display Affects Approximate Number System Acuity and Relationships with Mathematical Achievement and Inhibitory Control. *PLOS ONE*, *11*(5), e0155543.
- Nys, J., Ventura, P., Fernandes, T., Querido, L., Leybaert, J., & Content, A. (2013). Does math education modify the approximate number system? A

comparison of schooled and unschooled adults. *Trends in Neuroscience and Education*, 2(1), 13–22.

Park, J. (2017). A neural basis for the visual sense of number and its development: A steady-state visual evoked potential study in children and adults. *Developmental Cognitive Neuroscience*.

<https://doi.org/10.1016/j.dcn.2017.02.011>

Park, J., DeWind, N. K., Woldorff, M. G., & Brannon, E. M. (2016). Rapid and Direct Encoding of Numerosity in the Visual Stream. *Cerebral Cortex*, 26(2), 748–763.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, 44(3), 547–555.

Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and Approximate Arithmetic in an Amazonian Indigene Group. *Science*, 306(5695), 499–503.

Platt, J. R., & Johnson, D. M. (1971). Localization of position within a homogeneous behavior chain: Effects of error contingencies. *Learning and Motivation*, 2, 386–414.

Price, G. R., Palmer, D., Battista, C., & Ansari, D. (2012). Nonsymbolic numerical magnitude comparison: Reliability and validity of different task variants and outcome measures, and their relationship to arithmetic achievement in adults. *Acta Psychologica*, 140(1), 50–57.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL

<https://www.R-project.org/>.

- Retter, T. L., & Rossion, B. (2016). Visual adaptation provides objective electrophysiological evidence of facial identity discrimination. *Cortex*, *80*, 35–50.
- Regan, D. (1977). Steady-state evoked potentials. *Journal of Optical Society of America*, *67*(11), 1475–1489.
- Regan, D. (1989). *Human brain electrophysiology: evoked potentials and evoked magnetic fields in science and medicine*. Elsevier, New York
- Reynvoet, B., & Sasanguie, D. (2016). The Symbol Grounding Problem Revisited: A Thorough Evaluation of the ANS Mapping Account and the Proposal of an Alternative Account Based on Symbol–Symbol Associations. *Frontiers in Psychology*, *7*. <https://doi.org/10.3389/fpsyg.2016.01581>
- Roggeman, C., Santens, S., Fias, W., & Verguts, T. (2011). Stages of Nonsymbolic Number Processing in Occipitoparietal Cortex Disentangled by fMRI Adaptation. *Journal of Neuroscience*, *31*(19), 7168–7173.
- Rossion, B. (2014). Understanding face perception by means of human electrophysiology. *Trends in Cognitive Sciences*, *18*, 310–318.
- Rossion, B., & Boremanse, A. (2011). Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *Journal of Vision*, *11*(2), 16–16.
- Sasanguie, D., Göbel, S. M., Moll, K., Smets, K., & Reynvoet, B. (2013). Approximate number sense, symbolic number processing, or number–space mappings: What underlies mathematics achievement? *Journal of Experimental Child Psychology*, *114*(3), 418–431.

- Smets, K., Gebuis, T., Defever, E., & Reynvoet, B. (2014). Concurrent validity of approximate number sense tasks in adults and children. *Acta Psychologica, 150*, 120–128.
- Smets, K., Sasanguie, D., Szűcs, D., & Reynvoet, B. (2015). The effect of different methods to construct non-symbolic stimuli in numerosity estimation and comparison. *Journal of Cognitive Psychology, 27*(3), 310–325.
- Smets, K., Moors, P., & Reynvoet, B. (2016). Effects of Presentation Type and Visual Control in Numerosity Discrimination: Implications for Number Processing? *Frontiers in Psychology, 7*:66, doi: 10.3389/fpsyg.2016.00066
- Stevens, S. S. (1957). On the psychophysical law. *Psychological Review, 64*(3), 153.
- Stoianov, I., & Zorzi, M. (2012). Emergence of a “visual number sense” in hierarchical generative models. *Nature Neuroscience, 15*(2), 194–196.
- Szűcs, D., Nobes, A., Devine, A., Gabriel, F. C., & Gebuis, T. (2013). Visual stimulus parameters seriously compromise the measurement of approximate number system acuity and comparative effects between adults and children. *Frontiers in Psychology, 4*, 1-12. doi: 10.3389/fpsyg.2013.00444
- Van Oeffelen, M. P., & Vos, P. G. (1982). A probabilistic model for the discrimination of visual number. *Perception & Psychophysics, 32*(2), 163–170.