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Original Article

Using parity cross-format adaptation to probe abstract number representation in the human brain

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It is debated whether there is an abstract, format-independent representation of number in the human brain, eg whether "four" shares a neural representation with "4." Most previous studies have used *magnitude* to investigate this question, despite potential confounds with relative quantity processing. This study used the numerical property of *parity*. Electroencephalogram recordings were collected from participants performing a fixation-cross task, while viewing 20-s sequences of alternating even and odd Arabic numerals presented at 7.5 Hz: responses to parity were selectively tagged at the asymmetry frequency of 3.75 Hz. Parity asymmetry responses emerged significantly over the occipito-temporal (OT) cortex, and were larger than control asymmetry responses to isolated physical stimulus differences, replicating a previous study. Following 20-s adaptation to cross-font even numerals, larger parity responses were recorded over the right OT cortex, further supporting distinct representations of even/odd numbers; there was no corresponding control adaptation effect. Interestingly, adaptation to even canonical dot stimuli also produced significantly larger parity asymmetry responses; adaptation to even number words trended non-significantly. These results are in line with parity being processed automatically, even across formats. More generally, they suggest that parity is a useful means for probing abstract representation of number in the human brain.

Keywords: Arabic numerals; conceptual adaptation; EEG frequency-tagging; format-independent; numerical cognition.

Introduction

Among colors, shapes, and words, numbers are one of the first concepts people are taught in modern, technologically advanced societies. While easy to be taken for granted, numbers are complex concepts, defined with many criteria: they refer symbolically to exact quantities, have cardinal and ordinal senses, are relational and operable, and transcend differences in format (see Núñez 2017). One current goal of neuroscience research in numerical cognition is to identify whether there is an abstract, format-independent, representation of number in the human brain. Format-independence is a key feature in some theoretical models of numerical cognition, such as the "abstract-code model," proposing a single form of internal numerical representation, complemented by a modular functional architecture (McCloskey et al. 1985; McCloskey et al. 1986). Yet in other models, such as the "triple-code model" (Dehaene 1992), format-independence is integrated as an abstract, analog magnitude representation, within a framework also containing format-dependent modules dedicated to cardinal mental representations of Arabic numerals and auditory number words. Yet other models, such as the "encoding-complex model" of format-specific number codes (Campbell and Clark 1988), question the existence of format-independent processing of number. Identifying the neural bases of abstract number representations would be informative for models of number processing, and conceptual processing more generally, as well as potentially influential for educational interventions to support mathematical learning.

Despite many neuroscience studies, it remains controversial whether or not the human brain contains a format-independent representation of number (eg a review in favor: Dehaene et al. 1998; a review against: Cohen Kadosh and Walsh 2009). In support of abstract number representations, there is little evidence of format-specific number processing areas, such as a "visual number form area," ie a brain region responding specifically to Arabic numerals (Amalric and Dehaene 2018; Merkley et al. 2019). Moreover, common brain responses have been reported with neuroimaging across symbolic numerical formats and modalities, eg visual Arabic numerals and auditory number words, and localized to the intraparietal cortex (eg Naccache and Dehaene 2001; Pinel et al. 2001; Dehaene et al. 2003; Eger et al. 2003). While other studies have replicated activation in the intraparietal cortex to number across formats, they are reticent to interpret their findings in terms of common, abstract representations based solely on voxel-sized response overlap, and often in light of common task demands; ie suggesting that similar cortical areas may be activated by internally distinct, format-specific representations, or reflect common task-related processing and demands (Le Clec'H et al. 2000; Vogel et al. 2017).

Investigations of abstract number representations have predominately been limited to the property of *magnitude*. While magnitude processing may be supported by abstract

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representations of number, it may also be influenced by associations with relative quantity processing of "numerosity," through large quantity discrimination or subitizing. For example, acalculic patients have been reported to have impairments in exact number processing, and yet still be able to derive approximate numerosity from symbolic numerals (Warrington 1982; Dehaene and Cohen 1991). Relative quantity processing need not rely on abstraction, as quantity information is already present in the physical properties of the stimulus (Gebuis and Reynvoet 2012). Common brain responses to magnitude have been reported with symbolic numbers and non-symbolic dot arrays (Temple and Posner 1998; Libertus et al. 2007; Piazza et al. 2007; Eger et al. 2009; but see Bulthé et al. 2014; meta-analysis: Escobar-Magariño et al. 2022), and symbolic numbers and continuous stimulus size (Schwarz and Heinze 1998; Kaufmann et al. 2005; Cohen Kadosh et al. 2007; Piazza et al. 2007; including in non-human primates: Tudusciuc and Nieder 2007), suggesting an integration of symbolic magnitude and non-symbolic quantity processing. While this may be evidence that an abstract conception of magnitude is accessed through non-symbolic representations, an alternative explanation is that responses to symbolic magnitude representations are not thoroughly abstract, but rather depend on associations with relative quantity processing.

Here, we target the property of *parity*, ie whether numbers are categorized as even or odd, to investigate abstract number representation. Parity is an abstract numerical concept, orthogonal to magnitude/relative quantity processing, and has been explicitly studied in a relatively small number of studies (eg in behavioral experiments with a parity task: Hines 1990; Dehaene et al. 1993; Berch et al. 1999; or in the context of mathematical equations: eg Krueger 1986; Lochy et al. 2000). Yet there is some evidence that parity is extracted *automatically* from symbolic number representations and can be used to *implicitly* tap into number representations. Multidimensional scaling of similarity judgments of the Arabic numerals 0–9 led to clustering for parity (cross-format in Shepard et al. 1975; in children as well as adults: Miller and Gelman 1983). In a behavioral study by Reynvoet et al. (2002), participants performing a parity task on target Arabic numerals responded faster with masked, 57-ms primes that were parity-congruent, even when the primes were presented as written number words. This cross-format priming was replicated in a similarly designed study, in which the primes were reported not to be consciously identified (43-ms primes; and including electroencephalogram (EEG) responses: Fabre and Lemaire 2005). Recently, two studies reported EEG responses discriminating even and odd Arabic numerals while participants performed a non-numerical task regarding brief changes of a fixation cross (Guillaume et al. 2020; Retter et al. 2024).

In line with these previous studies, we predicted that (i) neural responses to parity could be measured automatically to Arabic numerals, without participants being asked to attend to parity or to perform a numerical task. To investigate parity responses, we used an EEG frequency-tagging symmetry/asymmetry paradigm as in Retter et al. (2024), in which alternating even and odd Arabic numerals enables the selective tagging of parity responses at the *asymmetry* frequency, while generic responses to visual stimuli occur at the *symmetry* frequency. To control for physical stimulus confounds, we compared the parity asymmetry responses to those to non-conceptual groups of numbers (Guillaume et al. 2020; Retter et al. 2024). Further, we tested (ii) whether adaptation to one category of numbers (eg even numbers) would increase the amplitude of asymmetry responses distinguishing even and odd (or non-conceptual control) categories. To this end, one category of numbers was presented repeatedly, with a different Arabic numeral stimulus set, in an initial adaptation sequence phase (as for adaptation to motion or face perception, eg: Tyler and Kaitz 1977; Ales and Norcia 2009; Gwinn et al. 2021). If asymmetry responses are increased after adaptation (but not following adaptation to non-conceptually grouped numbers), this would further support the existence of automatically activated distinct representations of even and odd numbers. Moreover, we tested (iii) whether adaptation to one parity category represented with different numerical formats, canonical dot representations or written number words, would also produce an adaptation effect on the parity responses measured with the same Arabic numeral sequences. Increased asymmetry responses to parity after adaptation with numbers having a different format would support an abstract, format-independent nature of the underlying number representations. In this way, we used parity to search for evidence of an abstract representation of number in the human cortex, transcending changes in format, and independent of magnitude.

Methods

Participants

The participants consisted of 20 human adults, recruited from a university community for a 1.5–2 hour experiment with remunerated compensation (a 20-euro voucher). All reported normal or corrected-to-normal vision, no neurological disease or learning disability, and German as the language of mathematics acquisition. Each participant was tested in an individual session following signed, informed consent, with testing procedures approved by the Ethical Review Panel of the University of Luxembourg (ERP 20–057), and consistent with the Code of Ethics of the World Medical Association (2013 Declaration of Helsinki). The data of two participants were rejected due to referencing errors during EEG setup, ie gel bridges between the common mode sense (CMS) electrode and one or two neighboring electrodes. The data of three participants, tested consecutively, were excluded due to an abnormal amount of high-frequency noise visible during recording. The age of the remaining sample ranged from 19 to 28 years old ($M = 22.1$; $SE = 0.67$); two participants identified as male, and 13 as female; and two participants reported being left-handed, and 13 as right-handed.

Stimuli and conditions

The stimuli consisted of sets of numbers from 2–9. In the parity experiment, groups of even and odd numbers were contrasted (2,4,6,8 vs. 3,5,7,9), and in the control experiment, groups of non-conceptual numbers were contrasted (2,3,6,7 vs. 4,5,8,9; as in Retter et al. 2024). The control was used to provide a relative measure of visual response differences across number groups, without differences in parity and being approximately matched for magnitude (group 1: 2 even numbers; mean: 4.5; group 2: 2 even numbers: mean: 6.5). These visual response differences across number groups may account for asymmetry responses in the control condition, even without adaptation: the asymmetry responses in the parity condition are also predicted to be impacted by similar visual response differences. To identify a conceptual response to parity, we therefore tested whether parity asymmetry response amplitudes were larger than asymmetry amplitudes in the visual control condition. In a previous study (Retter et al. 2024), parity EEG asymmetry amplitudes were larger than responses to two control conditions only for a 20 *drawn* stimulus set. The 20 *drawn* stimulus set (made freely available in Retter et al. 2024b) was therefore used in the main testing sequences here. Briefly,

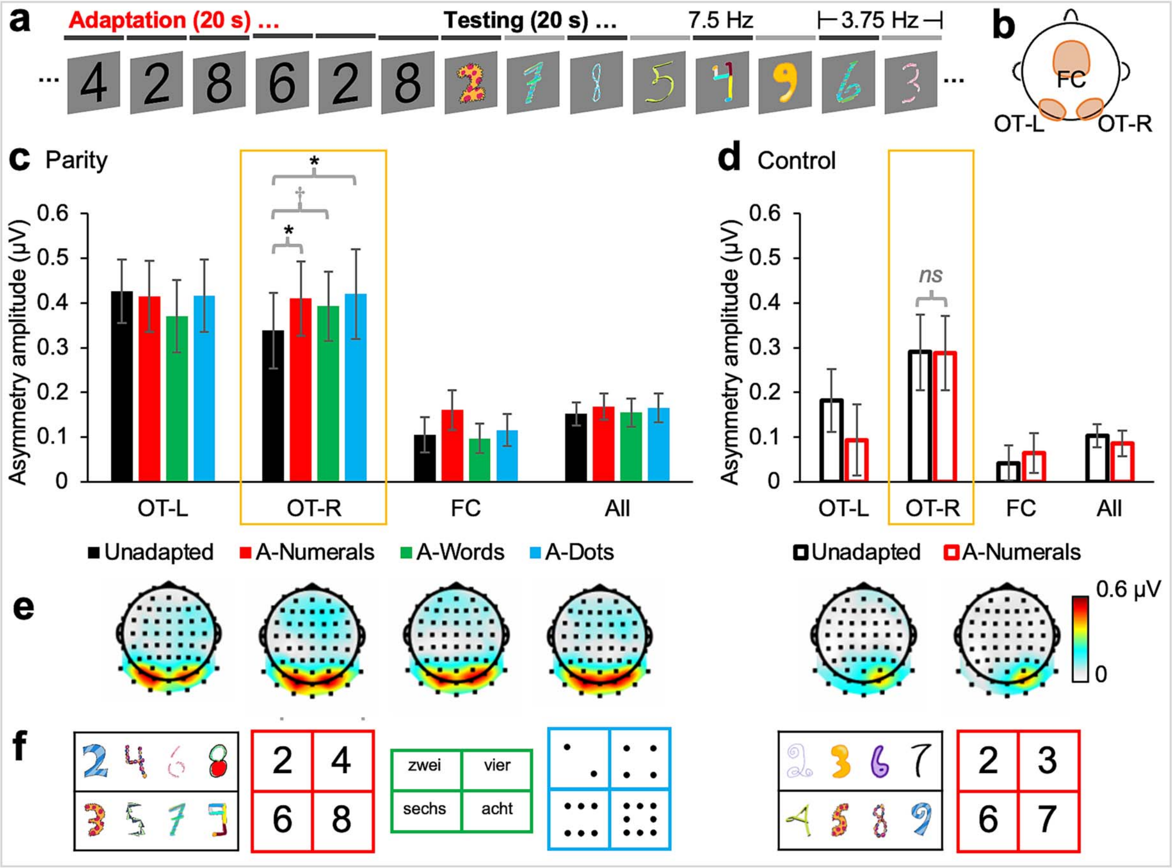

Figure 1. Experimental design and asymmetry results. (a) Trial structure, illustrated for the A-numerals condition of the parity experiment: An even-adaptation sequence is immediately followed by a testing sequence in which even and odd numerals are alternated, defining the 3.75 Hz asymmetry tag for parity. (b) Scalp regions drawn on a topographical map: OT-L, OT-R, and FC. Group-level parity (c) and non-conceptual control (d) asymmetry response amplitudes at 3.75 Hz and its specific harmonics (1F + 3F + 5F, baseline-corrected). Error bars indicate ±1 SE of the mean across participants. Responses are plotted at the regions indicated in panel b, and at the mean of all 68 channels (all). Response differences from the unadapted condition at the OT-R region (yellow box highlight) are indicated as follows: Significant, $P < 0.05$ (*); $P < 0.1$ (†); $P > 0.1$ (ns). (e) The corresponding scalp topographies, to a common scale; condition names as indicated above. (f) Examples of stimuli per condition: All conditions utilized the colored numerals as used in the unadapted conditions for the testing sequence part; for the unadapted conditions, the top and bottom rows define the contrasted (asymmetry) groups within each experiment (parity and control). The stimuli for the adapting sequence part are additionally illustrated for each condition (ie A-numerals, A-words, A-dots for the parity experiment and A-numerals for the control experiment).

this stimulus set consisted of 20, diverse exemplar types applied to each numeral, hand-drawn in color on a tablet (eg see Fig. 1).

There were six conditions tested in this study, four of which comprised the parity experiment: (i) one without adaptation (*Unadapted*); and three following adaptation to the group of even numbers (2,4,6,8) across different formats: (ii) numerals (*A-Numerals*); (iii) words (*A-Words*); and (iv) dots (*A-Dots*). The two remaining conditions comprised the control experiment, measuring visual response differences to non-conceptual numbers: (v) without adaptation (*Unadapted Control*) and (vi) following adaptation to one non-conceptual number group (2,3,6,7; *A-Numerals Control*). The 20 *drawn* stimulus set was always used in the testing sequences: in the unadapted condition, only this stimuli set was used. To limit the impact of physical stimulus features on adapted responses, and to enable cross-format investigations, different stimulus sets were used during the adaptation sequence parts. In the adapt to numerals (A-Numerals and A-Numerals Control) conditions, the stimuli were Arabic numerals in black, Arial font. In the adapt to words (A-Words) condition, the stimuli were number words in German (zwei, vier, sechs, and acht), in black, Arial font. In the adapt to dots (A-Dots) condition, the stimuli were black dots in a canonical, die- or domino-like configuration, to enable rapid perception of quantity (Fig. 1f).

Stimuli were sized to a height of ~360 pixels, not including a transparent background; the Arial numerals and number words were sized on average, in order to preserve natural variance of the font. The stimuli were presented one at a time, centrally, on a uniform, mid-level gray (123/255) screen. Stimuli were presented with custom software running over Java (Oracle, USA), with a Dell S2419HGF (USA) monitor with a refresh rate of 120 Hz, and a Dell (USA) PC with a Geforce 1050 (Nvidia, USA) graphics card. Participants were seated at a 1 m viewing distance from the screen, so that stimuli subtended ~1.9° of vertical visual angle.

Paradigm and procedure

As in Retter et al. (2024), neural responses to parity were recorded with electroencephalogram (EEG), using a frequency-tagging (Regan 1989; Norcia et al. 2015) symmetry/asymmetry paradigm (Tyler and Kaitz 1977; Victor and Zemon 1985). Stimuli were presented at 7.5 Hz in 20-s testing sequences. A 62.5% squarewave contrast modulation was used to present the stimuli, such that for each 133-ms stimulation cycle a stimulus was presented for

83 ms and there was a 50 ms inter-stimulus-interval. Stimulus size was varied randomly at each presentation cycle, from within 80–120% of the original in 10% increments, to reduce exact image repetitions (Dzhelyova and Rossion 2014). The two groups of stimuli (again, 2,4,6,8 vs. 3,5,7,9 for the parity experiment; 2,3,6,7 vs. 4,5,8,9 for the control experiment) were alternated throughout presentation, defining a 3.75 Hz (ie 7.5 Hz/2) "asymmetry" frequency tag, reflecting differences in the responses to the two number groups, in addition to the 7.5 Hz "symmetry" frequency tag of responses common to the two stimulus groups, ie general responses to the visual stimulus presentation. All analyses were performed on the asymmetry responses, the primary responses of interest, although symmetry responses are also reported.

For the adaptation conditions, the 20-s testing sequences were immediately preceded by a 20-s adaptation sequence, consisting of only even numbers for the parity experiment, and 2,3,6,7 for the control experiment, presented at 7.5 Hz (eg as applied to symmetry/asymmetry studies on motion direction perception: Tyler and Kaitz 1977; Ales and Norcia 2009; and face perception: Retter and Rossion 2016, 2017; Gwinn et al. 2021). Adaptation to one stimulus group (eg leftward motion) is used to enhance potential asymmetry responses, possibly by decreasing the response amplitude or latency selectively to that stimulus type (and therefore, eg enhancing the contrast between adapted leftward motion and unadapted rightward motion: see Fig. 2 of Ales and Norcia 2009). In some cases, asymmetry responses are only predicted to be present following adaptation (eg Ales and Norcia 2009; David et al. 2024), but in other cases, such as here, asymmetry responses are predicted to be present even without adaptation, due to conceptual and physical stimulus differences across small stimulus groups: asymmetry responses are predicted to increase following (conceptual) adaptation (Retter et al. 2024).

In the Unadapted Parity and Unadapted Control conditions, the adaptation time was filled with the regular sequence structure (ie alternating number groups), so that all trials were of the same total duration. The full trial structure was as follows: (i) 1–2 s of a fixation cross alone (to remain superimposed throughout subsequent stimulus presentation); (ii) the 20-s adaptation or regular stimulation sequence; (iii) the 20-s testing sequence; (iv) 1–2 s of the fixation cross alone. Per condition, there were eight trial repetitions, leading to a total of 2.7 minutes of the testing sequence part, encompassing 600 stimulus alternation events. The trials of all conditions were shown in a fully randomized order, re-randomized for each participant. In total, the experimental testing lasted ~45 minutes.

Participants were naïve to the parity manipulation: they were informed only that numbers would appear on the screen, and their task was to pay attention to those numbers while maintaining fixation on the centrally-presented, superimposed fixation cross. Participants' task was to press on the space bar as rapidly and accurately as possible each time that they detected occasional, brief (250 ms) luminance changes of the fixation cross, from dark gray to off-white (minimum of 0.75 s between luminance events; six randomly-spaced events per trial).

EEG acquisition and analysis

The EEG acquisition and analysis were similar to that in Retter et al. 2024 (as well as Retter and Rossion 2016, 2017; Gwinn et al. 2021). Briefly, and noting any differences: the EEG was acquired at a sampling rate of 512 Hz, with a BioSemi, ActiveTwo system, containing 68 active recording electrodes in the standard 10/20 locations; the standard 64, and additionally PO9, I1, I2, and PO10 (BioSemi B.V., Amsterdam, Netherlands; https://www.biosemi.com/).

The analysis software LetsWave 6 (https://www.letswave.org/) was used, running over Matlab R2019b (MathWorks, USA). Data pre-processing included a fourth-order Butterworth band-pass filter at 0.1–80 Hz; removal of a single ICA component related to muscular artifacts from eye movements for one participant blinking > 0.2 times/s during the stimulation sequences (across all participants: M = 0.03 blinks/s; SD = 0.07 blinks/s). Noisy channels for each participant, defined by having multiple deflections beyond $\pm 100\ \mu$V, were replaced with linear interpolation of neighboring channels (M = 1.0 channels interpolated; range = 0–3). Data were re-referenced to the average of all channels, and the 20-s stimulation sequences were cropped to an integer number of 3.75 Hz cycles (75 cycles per sequence = 20.0 s = 10,240 sampling bins). Sequence repetitions were averaged by condition, and a fast Fourier transform was used to transform the data into frequency-domain normalized amplitude and phase spectra.

The asymmetry responses to 3.75 Hz stimulation were measured in the amplitude spectra at 3.75 Hz, and two higher, specific harmonics at 11.25 and 18.75 Hz (ie excluding even, symmetry harmonic responses); the symmetry responses were measured at 7.5 Hz and five higher harmonics, up to 45 Hz (as in Retter et al. 2024: in that study, these harmonics were selected according to a significance threshold; see also Retter et al. 2021). The harmonics were summed separately for the asymmetry and symmetry responses (Retter and Rossion 2016; Retter et al. 2021). The region-of-interest (ROI) was defined as four left and four corresponding right occipito-temporal (OT) channels (as in Retter et al. 2024); although statistical analyses were restricted to this ROI, for a more comprehensive report, responses were also described over a fronto-central (FC) region, consisting of eight channels: F1, Fz, F2, FC1, FCz, FC2, C1, Cz, and C2, and the average of all 68 EEG channels (eg see Fabre and Lemaire 2005; Guillaume et al. 2020). A baseline of 16 frequency bins, centered around the target frequency bin of interest, was used as a measure of relative baseline noise. For response amplitude measurement, the mean baseline amplitude was subtracted from that of the target frequency, following removal of the minimum and maximum noise bins; for response significance, a z-score was computed relative to the 16-bin baseline.

Three predictions were tested with the asymmetry response amplitudes, the first of which was a replication of Retter et al. 2024: (i) that asymmetry responses are significantly present to parity without adaptation, and that these asymmetry responses to parity are larger than to control number groups. In order to closely replicate that study, responses were analyzed over the bilateral OT region, and response significance within each condition was evaluated with z-scores, as described above. To compare unadapted parity and control asymmetry response amplitudes, a paired-samples t-test was used, one-tailed with the prediction that parity would produce larger asymmetry responses than the control.

Two additional predictions were specific to this study: (ii) that adaptation to one group of numbers leads to increased asymmetry responses in the parity experiment but not for the control; and (iii) that adaptation to even numerals, number words, and dots all lead to increased asymmetry responses in the parity experiment. The right OT ROI was used to probe for an adaptation effect to parity, as right-lateralized parity responses were reported previously (Retter et al. 2024; see also Fabre and Lemaire 2005; Guillaume et al. 2020). To compare parity responses to control responses, a repeated-measures ANOVA was applied, with within-participants factors of *Experiment* (2 levels: Parity; Control), and *Adaptation* (2 levels: A-Numerals; Unadapted). To investigate whether there was a difference across conditions in the Parity experiment, a one-way ANOVA with the factor *Condition* was applied (4 levels: Unadapted; A-Numerals; A-Dots; A-Words). To directly compare the unadapted to adapted conditions, one-tailed (predicting a larger asymmetry response following adaptation) paired-samples t-tests were planned for the Unadapted condition vs. each the A-Numerals, A-Dots, and A-Words conditions in the parity experiment, and the Unadapted Control condition vs. the A-Numerals Control condition in the control experiment. P-values were uncorrected for multiple comparisons, given the different numbers of comparisons used to test the three main hypotheses, and different numbers of parity and control experiment conditions.

Results

This study measured EEG frequency-tagged asymmetry responses, reflecting differences between two alternating groups of Arabic numerals, in order to test three predictions: (i) that responses to parity can be measured automatically, without adaptation; and that these parity responses are larger in amplitude than arbitrary, control number grouping responses (in replication of Retter et al. 2024); (ii) that adaptation to one group of numbers, eg even numbers, leads to increased response amplitude for parity but not for the control; and (iii) that adaptation to even Arabic numerals, canonical dot number representations, and number words, all lead to increased responses to parity with Arabic numeral presentations. Responses were analyzed in the frequency-domain, following baseline-corrected harmonic summation (for visualization of original amplitude spectra: Fig. S1; for symmetry responses: Fig. S2).

Firstly, significant asymmetry responses (at 3.75 Hz and its specific harmonics) were found over the bilateral OT cortex to parity (2,4,6,8 vs. 3,5,7,9) without adaptation, $Z = 17.9$, $P < 0.001$, as predicted. There were also significant asymmetry responses in all other parity and control experiment conditions (Table S1a; scalp topographies in Fig. 1e; for the symmetry responses to stimulus presentation at 7.5 Hz and its harmonics: Table S1b; Fig. S2), indicating that physical stimulus differences across numeral groups were sufficient to elicit neural asymmetry responses. Then, unadapted asymmetry response amplitudes to parity (Fig. 1c) were compared to those to the control (2,3,6,7 vs. 4,5,8,9; Fig. 1d). As predicted, there was a significantly larger asymmetry response to parity ($M = 0.38\ \mu V$; $SE = 0.069\ \mu V$) than to the control ($M = 0.24\ \mu V$; $SE = 0.028\ \mu V$) over the bilateral OT region, $t_{14} = 2.38$, $P = 0.016$, $d = 0.61$ (see full black bars vs. black contour bars for OT-L and OT-R in Fig. 1). The unadapted response to parity was 62% larger than that to the unadapted control condition, potentially indicating an increase above physically-driven asymmetry amplitude due to additional conceptual parity discrimination.

In regard to the second prediction, concerning adaptation effects, there was a significant increase in asymmetry response amplitude following adaptation to even numerals in the parity experiment over the right OT cortex, $t_{14} = 1.93$, $P = 0.037$, $d = 0.50$ (see yellow highlight box in Fig. 1c). In addition, the asymmetry response observed over the FC region of $0.055\ \mu V$ revealed a 1.5 times increase in amplitude (Fig. 1c). In the control experiment, there was not a significant increase in asymmetry response amplitude over the right OT cortex following adaptation, $t_{14} = 0.05$, $P = 0.48$, $d = 0.01$ (see yellow highlight box in Fig. 1d), and no indication of a substantial increase at other scalp regions (Fig. 1d). Despite a large effect size, the interaction of *Experiment (Parity; Control)* and *Adaptation,* $F_{1,14} = 2.33$, $P = 0.15$, $\eta_p^2 = 0.14$, over the right occipito-temporal (OT-R) cortex, was not significant, which would have more robustly supported the prediction of an adaptation effect only in the parity experiment.

Thirdly, regarding cross-format adaptation in the parity experiment, the amplitude was lowest in the unadapted condition as predicted, although the differences were modest: the response was only ∼1.2 times larger in the three adapted than in the unadapted condition, ranging from a voltage difference of 0.054–0.081 μV (Fig. 1c). When comparing these four conditions (ie three adapted and one unadapted), there was a medium effect size, but not significance, for *Condition* of parity asymmetry responses over the right OT cortex, $F_{3,42} = 1.78$, $P = 0.17$, $\eta_p^2 = 0.11$, although this may relate to similar amplitudes in the three adapted conditions (see colored bars vs. unadapted black bar in yellow highlight box in Fig. 1c). There was also not a significant effect of *Condition,* and small effect size, for the three latter conditions tested alone, $F_{2,28} = 0.28$, $P = 0.76$, $\eta_p^2 = 0.02$. As described above, the comparison of unadapted to adapted numerals was already performed in testing the second prediction, with a significantly larger amplitude for adapting to numerals reported at the right OT region ($t_{14} = 1.93$, $P = 0.037$, $d = 0.50$). Additional planned comparisons of the unadapted asymmetry response with the remaining two adapted conditions at the right OT region showed non-significantly higher asymmetry amplitudes for the adapted responses to words, $t_{14} = 1.42$, $P = 0.088$, $d = 0.37$, with a small-to-medium effect size, and significantly higher asymmetry amplitudes for the adapted responses to dots, $t_{14} = 1.84$, $P = 0.044$, $d = 0.47$, with a medium effect size.

Discussion

A neural response to parity, at the asymmetry rate of 3.75 Hz and its specific harmonics, was recorded without adaptation, even when participants were not instructed to attend to the numerical stimuli or to perform a numerical task (instead, the task was to detect fixation-cross luminance changes). Importantly, this asymmetry response to parity exceeded that of a control condition with two non-conceptual groups of numerals, replicating Retter et al. (2024) (Fig. 1). An automatic response to parity, without an explicit parity (or even numerical) task, is in line with some previous studies (Shepard et al. 1975; Miller and Gelman 1983; Reynvoet et al. 2002; Fabre and Lemaire 2005; Guillaume et al. 2020; Retter et al. 2024; Retter and Schiltz 2025); although there have been few studies investigating the neural bases of parity representations, in contrast to the attention given to magnitude representations (eg reviews on magnitude: Sokolowski et al. 2017; Cohen Kadosh et al. 2008). While we propose that parity was processed automatically, we did not explicitly ask participants whether they were aware of the parity manipulation in some sequences. However, we think this was unlikely: in a recent study presenting numbers with probabilistic parity-color associations, only a few participants reported being explicitly aware of this manipulation (Retter and Schiltz 2025). Moreover, with fast stimulus presentation in frequency-tagging, participants consistently report being unaware of the regularities in stimulus presentation (eg in the periodicity of face presentation: Retter et al. 2020).

Significant asymmetry responses were also recorded without adaptation to the control condition of non-conceptual Arabic numeral groups, suggesting that physical stimulus differences across small sets of numerals (eg in shape) are non-negligible

(Fig. 1d; Table S1a). Indeed, due to their distinctive physical differences, Arabic numerals can be identified accurately and rapidly (Cohen 2009; Starrfelt and Behrmann 2011; for decoding human brain responses to Arabic numeral shapes, see: Eger et al. 2009; Bulthé et al. 2014; Appelhoff et al. 2022). However, the responses to the control condition here were of significantly lower amplitude than those to parity, replicating the previous study by Retter et al. (2024); as well as that of Guillaume et al. (2020), although the latter study was limited by comparing only half the trial repetitions for the control condition). Here, the parity asymmetry response of 0.38 μV was 1.6 times larger than to the control of 0.24 μV over the OT cortex; in an earlier experiment, a parity asymmetry response of 0.36 μV was 2.0 times larger than to the control of 0.18 μV over the same region (Retter et al. 2024). The impact of physical stimulus features may have been limited here by using a diverse stimulus set with 20 styled exemplars per numeral (Retter et al. 2024b) and varying image size (from 80% to 120% of the original) at each presentation. Although conceptual responses to parity might not simply be additive to visual responses, higher response amplitudes to parity than to physical stimulus differences alone provides evidence in support of a conceptual response to parity.

To our knowledge, this is the first study to investigate neural responses discriminating even and odd numbers following adaptation (although adaptation has been applied extensively to investigate magnitude representations; for a review: Soltész and Szűcs 2014). Within-format, cross-font adaptation to four, even Arabic numerals increased the asymmetry response amplitude to even and odd numerals over the right OT (and FC) cortex for the parity condition (Fig. 1c). This finding is in line with a generic representation of even numbers, as the numbers 2, 4, 6, and 8 were adapted together, as well as suggests that the present results may go beyond differences between even and odd numerals in terms of physical stimulus features, since different stimulus sets were used in the adapting and testing phases here (adapting: black Arial font; testing: colorful hand-drawn stimuli). A slight amplitude increase following adaptation was also evident in the symmetry responses, perhaps related to the change in stimulus set, but was much lower than for the asymmetry responses: eg there was a 21% asymmetry response increase over the right OT cortex following adaptation to numerals (Fig. 1c), but only a corresponding 7% symmetry response increase (Fig. S2a). Importantly, adaptation to a group of four, non-conceptual Arabic numerals did not produce such an adaptation effect in the control condition (Fig. 1d), although the interaction between experiment and adaptation was not significant, albeit with a large effect size.

Most similarly, in a previous study of Fabre and Lemaire (2005), an EEG response to parity was reported as an effect of priming congruency. Larger amplitude deflections to target numerals and written number words were reported for parity-incongruent than parity-congruent written word primes, at the N400 component over central and parietal regions. While in that experiment, participants performed a parity task on the target stimuli, in the present experiment participants performed an orthogonal non-numerical task (as in Guillaume et al. 2020; Retter et al. 2024). Using neural measures, such as EEG, to study numerical processing has the advantage that a numerical task is not required, which reduces distracting factors, such as the comprehension of (the language of) instruction and test anxiety and enables extension of the same paradigm to young children and infants. Adaptation to parity could provide an interesting tool for future studies, eg for using fMRI to localize parity responses, as markers of number representations, in the (human) brain.

Following adaptation to even numbers, we predicted that the responses to even numbers would be affected, eg selectively decreased or delayed, and this would enhance the differences in the responses to even vs. odd numbers, ie to parity. However, the responses specific to even numbers and odd numbers could not be distinguished in the frequency domain, given that they were presented at the same frequency (in alternation, leading to the 3.75 Hz asymmetry tag). In an attempt to distinguish even- and odd-specific responses, we turned to a relative phase model (developed in Gwinn et al. 2021). The results of this additional analysis suggested that without adaptation the response to even numbers was smaller than that to odd numbers, but a similar difference was present between the responses to the two non-conceptual sets of numbers in the control experiment. In contrast, following adaptation, the difference in the responses to even and odd numbers appeared to be enhanced through an increase in the response to unadapted odd numbers (Fig. S3), while no such changes were observed in the control condition. Given the imprecision of this model with very short (133-ms) response cycles, and high levels of variability across participants (eg see Fig. 6 of Retter and Rossion 2016), the adaptation mechanisms still remain unclear, and warrant further investigation in future studies.

Increased parity responses to Arabic numerals over the right OT cortex were also observed when presenting even canonical dot images during the adaptation phase (Fig. 1c), revealing cross-format adaptation. Although large dot displays may be processed in terms of inexact, relative quantities, ie non-symbolically (eg Núñez 2017; Liu et al. 2018), the canonical dot stimuli used here are thought to be processed symbolically, as exact quantities, like for dice and dominoes (eg see Venkatraman et al. 2005). There was a small-to-moderate effect in the predicted direction of adapting to even written number words, although it did not reach significance ($P = 0.088$, $d = 0.37$) (We also observed a corresponding effect of 0.06 μV in the *opposite* direction over the left OT cortex.). An adaptation effect for canonical dot stimuli, and a small trend for written word stimuli, suggests that there may be a generic, abstract representation of parity in the human brain. Especially if supported in future studies, identifying an abstract representation of number would inform the neural bases of number processing, and conceptual understanding more generally. For example, in the triple code model, parity is processed directly only from Arabic numeral representations (Dehaene 1992; Dehaene et al. 1993). According to this model, one would thus expect an automatic adaptation effect only for numerals, but not words or dots, which is not consistent with the present results.

Finally, evidence towards an abstract neural representation of number does not imply that number representations cannot have some differences due to input format (eg with EEG: Plodowski et al. 2003; Liang et al. 2012). In addition to early differences in early perceptual processing, format likely also affects high-level, conceptual neural representations of number. For example, the neural representations of written number words may be molded by their associations with the language system and verbal reasoning (eg Wagner et al. 2015; Bugden et al. 2021), while the representations of Arabic numerals may be shaped by their associations with visual ordering and mathematical reasoning (eg Dehaene 1992; Habermann et al. 2020). In other words, the key question is not whether there are any differences in conceptual neural representations of numbers across formats (Cohen Kadosh and Walsh 2009), but whether there is an abstract representation of number common to all formats. For example, here a hint of an increased amplitude over the FC cortex following adaptation was only observed following adaptation to numerals, not dots or number words, but a difference in the response presentation does not exclude the possibility of a common abstract representation. We propose that using parity to probe abstract representations of number in the human brain, in addition to magnitude representations, is a promising avenue for future research on this key question.

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Author contributions

Talia L. Retter (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Supervision, Validation, Visualization, Writing—original draft, Writing—review & editing), Henning Lütje (Conceptualization, Data curation, Investigation, Methodology, Writing—review & editing), Christine Schiltz (Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing—review & editing).

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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Data and code availability

Arabic numeral stimuli are freely available here: https://doi.org/10.5061/dryad.1zcrjdg13.

Disclaimer

No artificial intelligence was used in the generation of this manuscript.

Ethics

Each participant was tested in an individual session following signed, informed consent, with testing procedures approved by the Ethical Review Panel of the University of Luxembourg (ERP 20-057), and consistent with the Code of Ethics of the World Medical Association (2013 Declaration of Helsinki).

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