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Authors
Kanayet, Frank
Opfer, John
Cunningham, William

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Frank Kanayet (kanayet.1@osu.edu)
Department of Psychology, 255 Psychology Building
Columbus, OH 43206 USA

John Opfer (opfer.7@osu.edu)
Department of Psychology, 245 Psychology Building
Columbus, OH 43206 USA

William Cunningham (cunningham.417@osu.edu)
Department of Psychology, 100G Lazenby Hall
Columbus, OH 43206 USA

Abstract

In adult human brains, the horizontal segment of the intraparietal sulcus plays a large role in representing numeric magnitude. In children and non-human primates, however, frontal cortex may play a larger role. We hypothesized that there is a link between observed developmental changes in locus of representation (frontal to parietal) and type of representation used (logarithmic to linear). Participants were presented with number lines and asked to judge accuracy of linear, logarithmic, or log-linear placements. Consistent with hypotheses, event-related potentials generally revealed greatest parietal N1 amplitudes for linear placements and greatest frontal P3 amplitude for logarithmic placements. Additionally, effects of linear placements on cortical activity were moderated by numerical magnitude: parietal N1 amplitudes decreased with magnitude, whereas frontal P3 amplitudes increased with magnitude. These results suggest adults possess logarithmic and linear representations of number, and when logarithmic representations were elicited; there was greater involvement of frontal cortex.

Keywords: Numerical cognition; representation; brain imaging; event related potentials.

Introduction

Whether a pollster evaluating the sampling process for an election poll, a parishioner telling the time by counting the tolls of a church bell, or a child figuring out how much candy she had received on this Halloween versus a previous one, mental representations of numerical magnitude are important for projecting the future, monitoring the present, and learning from the past. Moreover, this ability to code our experiences numerically must scale consistently regardless of the shape, size, sensory modality or context in which particular numeric magnitudes are presented.

Two prominent brain areas have been implicated in humans' and other animals' representation of numerical magnitudes: the *prefrontal cortex* and the *horizontal segment of the intraparietal Sulcus* (HIPS). Most studies have shown that HIPS plays a major role in numeric representation, with magnitude coded in this area as an abstract, notation-independent representation (Dehaene, Piazza, Pinel, Cohen, 2003; Dehaene, Dehaene-Lambertz, & Cohen, 1998; Libertus, Woldroff & Brannon, 2007). However, comparative and developmental studies have found HIPS playing a less prominent role. For example, single cell recordings in monkeys (Nieder & Merten, 2007 & Nieder & Miller, 2004) and *f*MRI studies in children (Ansari et al. 2005; Ansari & Dhital, 2006; Cantlon, Brannon, Carter & Pelphrey, 2006; Cantlon et al., 2009) have shown stronger effects of numerical magnitude on prefrontal cortex than HIPS. Similarly, ERP studies with infants, have also found that nonsymbolic numeric processing generates activity in a parieto-prefrontal network (Izard, Dehaene-Lambertz & Dehaene, 2008; Libertus, Pruitt, Woldorff & Brannon, 2009).

To explain this developmental trend, we propose that: (1) at any given age, the brain represents numeric magnitudes using both a logarithmically-compressed code and a linear code, with the probability of a number being processed by the linear code increasing with age and experience; and (2) logarithmic-coding is predominantly processed in frontal areas, whereas linear coding is predominantly processed in parietal areas. Here we test an implication of this account, namely that large magnitude (low-frequency) numerals are more likely than small magnitude (high-frequency) numerals to be represented in frontal cortex, whereas the reverse is true of parietal cortex.

Development of Numeric Representations

The origin of our developmental hypothesis stems from behavioral studies on development of numeric representations (Booth & Siegler, 2006; Opfer & Siegler, 2007; Opfer & Thompson, 2008; Siegler & Opfer, 2003; Thompson & Opfer, 2008). In these studies, children and adults were asked to estimate the position of numbers on a blank line with the end-points labeled "0" and "100", "0" and "1000", or "0" and "10000". This estimation task is particularly revealing about cognitive representations of numeric value because it transparently reflects the ratio characteristics of the number system. Overall, younger children's estimates typically follow Fechner's Law and increase logarithmically with actual value, whereas older children's estimates increase linearly. At any given age, however, individual children use both logarithmic and linear representations of number, depending on numerical context. That is, for very large numeric contexts (e.g., on 0-1000 and 0-10000 number lines), children's estimates increase logarithmically; however, the same children will use linear representations when estimating the magnitudes of numbers for small numeric contexts (e.g., on 0-100 number lines). If our developmental hypothesis is correct, it should be possible to identify two different patterns in the brain that are consistent with the type of representation used, thereby providing neural correlates for the logarithmic-to-linear shift hypothesis.

Plausible candidates for these two different patterns of neural activation are provided by the developmental data showing a shift from prefrontal to parietal processing of numerical magnitude (Cantlon, et al., 2009; Rivera, Reiss, Eckert and Menon, 2005). More generally, evidence from perceptual learning has shown that complex conjunctive stimuli are processed by more posterior sites with gains in expertise, both within the visual cortex (Mukai et al., 2007) and between the prefrontal cortex and visual cortex (Eriksson, Larsson, Nyberg, 2008). As a result, information changes from being processed serially and with effort, to being processed in parallel and automatically. Possibly, the same is true for number representation, with the abstract representation that is needed for processing numeric magnitude regardless of shape, size, modality or context originally coming from the prefrontal cortex and gradually shifting to HIPS with gains in expertise.

Present Study

To test our hypothesis, we asked participants to judge whether a number had been accurately marked on a number line, and we evaluated the *Event-Related Potentials* (ERP) generated after participants saw number-line estimates that corresponded or not to a given numeral. By evaluating ERP components related to numeric estimation, we were able to test several predictions derived from our developmental hypothesis. Specifically, we were able to provide a novel test of whether subjects expected positions of numbers on number lines to increase linearly, logarithmically, both, or neither with numeric value, and we were able to test if the topography of those ERP components corresponded to our hypotheses.

Some ERP components can generate diagnostic data about representations of numerical magnitude, even before the subjects' response. Generally, targets that violate subjects' expectations elicit large P3 amplitudes (Donchin, 1981). Thus, numbers marked in non-linear positions would likely generate a higher P3 response than numbers marked in the linear position. Conversely, the N1 component is generally elicited when targets match the subject's orientation of attention (Luck, 2005; Folstein & Van Petten, 2008). Thus, numbers marked in the linear position would be expected to generate higher N1 responses than numbers marked in the non-linear position. Using this logic, ERP components are capable of early detection of both linear and non-linear representations of number. This provides an important test of our hypothesis because automatic, non-linear representations of number might occur in adults before they have time to provide formally correct, learned responses.

Method

Participants

Participants (N = 21, mean age = 20.5, 8 female) were recruited from an introductory psychology class and were awarded course credit for their participation in the experiment. Nineteen participants were right handed, and all had normal or corrected to normal vision.

Design and Procedure

Each problem presented a blank number line with a width of 255 pixels, labeled with '0' on the left end and '1000' on the right end. The numbers presented appeared on the top of the screen 192 pixels over the line (half point between the top of the screen and the number line). The numbers tested were 5, 78, 150, 606, 725 and 938. These numerosities were selected because they sample the whole length of the line and also maximize the discriminability between linear and logarithmic representations. All stimuli were presented in a dark and sound-attenuated room using DirecRT (Jarvis, 2006).

Participants were instructed to identify if the position of the hatch mark on a number line corresponded to the numeral presented by pressing one key if the position of the hatch mark were correct, and by pressing another if the position of the hatch mark were incorrect (keys were counterbalanced between participants).

At the beginning of each trial, the number line with the marked end points appeared and a fixation was placed where the target numerals were going to be shown for a period of 1 second. Next, the stimulus (i.e. the numeral) replaced the fixation for another 1-second interval. After this period, the hatch mark was placed either in the linear, logarithmic or log-linear position. Once the hatch mark was in place, participants had to decide if the mark was correctly placed and to press the appropriate key (no time limit was imposed on participants' responses). After the response, no feedback was provided and a 2000-ms intertrial stimulus interval (ISI) was used.

Participants were tested on three different sets of trials and the design of the study was all within subjects. Thus, on each block, participants encountered each of the six numerals compared to three possible hatch mark positions (linear, logarithmic, log-linear). The experiment consisted of 16 blocks and presentation of the trials was randomized within each block. This corresponds to a total of 288 trials (96 per trial type condition).

ERP Recording Procedure After attaining informed consent from participants, a NuAmps quick cap with 32 Ag/AgCl electrodes (Compumedics Neuroscan, El Paso, TX, USA) was placed on their heads to record their brain activity. Linked ears served as reference during recording. Before the beginning of the experiment, impedances were held below 40 kΩ[1]. The electroencephalogram (EEG) was amplified with an A/D conversion rate of 1000 and a gain of 250mV. Finally, a recording low-pass filter of 300Hz was used.

Before analysis of the data, the raw EEG data were processed offline using BESA (Version 5.2). Raw data were re-referenced to an average of all electrodes and a digital 0.1 to 30Hz bandpass filter was used. Also, artifact correction (Berg & Scherg, 1994) was used to reduce ocular artifacts and blinks. After artifact correction, an artifact rejection procedure (tailored to each individual) was conducted. After this process, 7 participants – who had less than 85% of the trials accepted – were removed from further analyses. ERP epochs (-200ms to 1000ms) were created for the three trial types (i.e. linear, logarithmic and log-linear), and for hatch mark number size (i.e. hatch marks that corresponded to small numbers and large numbers).

Results

Behavioral Results

Number comparison is typically characterized by effects of distance and size on speed and accuracy of judgments (Moyer & Landauer, 1967). We obtained similar results for judgments of number line placements. Consistent with distance effects, log-linear trials, which were closer to the correct (linear) placements than logarithmic ones, required more time to solve and resulted in the lowest accuracy rates. Consistent with size effects, judging the location of large numbers (i.e. larger than 500) on the number line required more time than judging the location of small numbers (i.e. smaller than 500), with accuracy also being lower for placement of large numbers compared to small numbers. Finally, there was evidence of interactive effects of size and trial type, with larger effects of trial type for small numbers ($\omega^2 = .54$) than for large numbers ($\omega^2 = .32$) on reaction times. This interaction is interesting because it suggests that representations of small numeric magnitudes are more strongly linear and non-logarithmic than representations of large numeric magnitudes, leading to less discriminability between trial types for the large magnitudes.

A potential problem with accuracy measures, such as those reported above is that they can fail to detect systematic response biases. To address this issue, we conducted d' analyses. Because performance of participants was near ceiling, hits and false alarm rates were corrected. Specifically, hit rates were constructed by the formula (hits + 1)/(total trials + 2), and false alarm rates were constructed by the formula (false alarms + 1)/(total trials + 2).

As predicted by the size effect, discriminability between the linear, and the logarithmic and log-linear trials declined with numeric size (see Figure 1). This result was confirmed by a one-way repeated measures ANOVA ($F(5,100) = 36.83$, $p < .001$, $\omega^2 = 0.59$). An alternative explanation of this result is that it is due to the distance between the linear and logarithmic trials not being constant throughout the whole range of numbers. Thus, it is possible that the reason why discrimination decreases for the numbers 725 and 938 is because the distances between the linear and logarithmic trials decrease too. To test this alternative hypothesis, we performed a planned comparison between two numbers that differ in size but that have the same distance between the linear and logarithmic hatch mark positions (5 and 725). As predicted by the size effect, even though the distance between the linear and logarithmic trials is equal for these two numbers, discriminability was significantly smaller for 725 ($d' = 2.25$, $SD = 0.78$) than for 5($d' = 3.04$, $SD = 0.56$; $p < .001$).

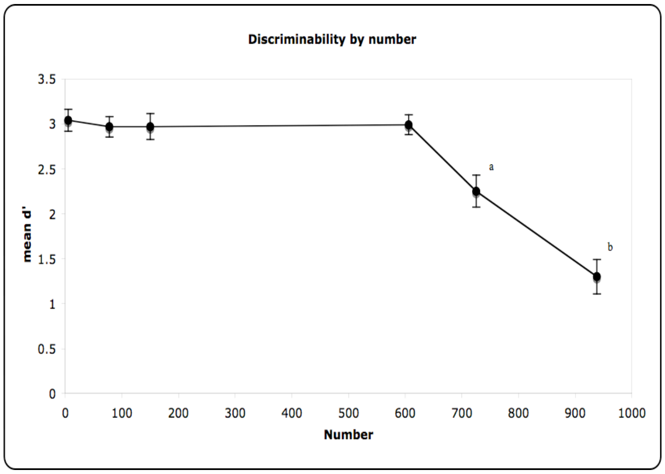

Figure 1: Mean d prime values for each numeral (+ SE). (a) and (b) represent significant differences at $p < .05$..

Electrophysiological Results

To understand the temporal characterization of the number line estimation task, average waveforms were computed for the three experimental trials (i.e. linear, logarithmic, log-linear). Additionally, these waveforms were averaged into four different electrode sites with the purpose of reducing experiment-wise error caused by computing multiple statistical comparisons. The frontal left (FL) electrode site was computed by averaging the electrodes FP1, F3, F7, FC3, and FC7. The frontal right (FR) electrode site was computed by averaging the electrodes FP2, F4, F8, FC4, FC8. The parietal left (PL) electrode site was computed by averaging the electrodes CP3, TP7, P3, P7. The parietal right (PR) electrode site was computed by averaging the electrodes CP4, TP8, P4, P8.

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[1] Although the impedance threshold for accepting a participant was 40 kΩ, in reality most of the electrodes achieved impedances of 10 to 15 kΩ.

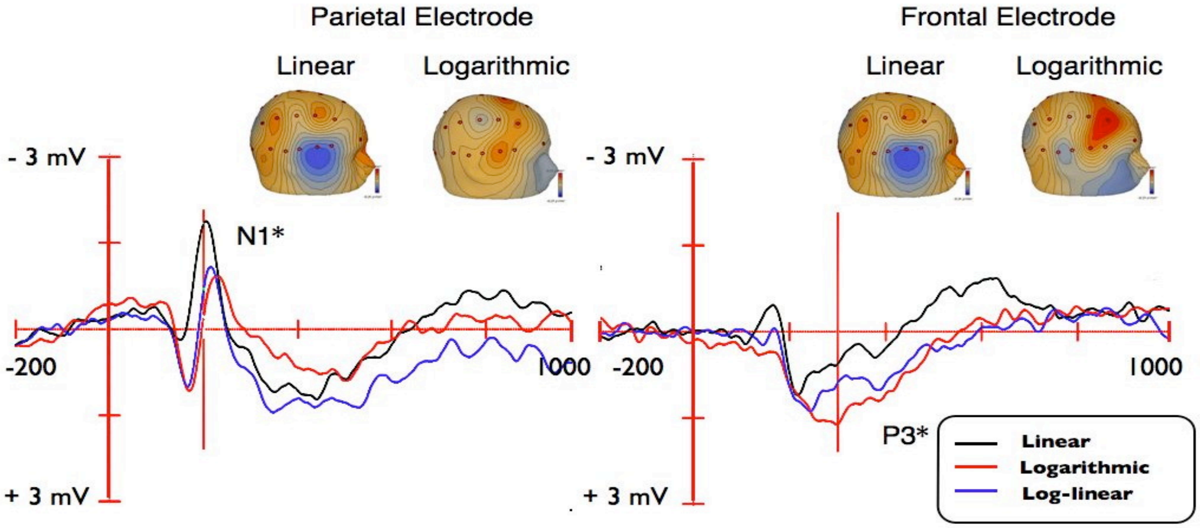

Figure 2: Top: Current source density topographies for linear and logarithmic trial types at 200 ms (left) and at 300 ms (right). Bottom: N1 (140-240 ms) and P3 (260-700 ms) ERP components for linear, logarithmic, and log-linear trials for parietal (left) and frontal (right) electrode sites.

Visual inspection of the waveforms is consistent with the main hypothesis from the study (see Figure 2). First, linear trials generated a greater N1 peak than both the logarithmic and log-linear trials, especially in parietal electrode sites. Moreover, at frontal electrode sites, the logarithmic trials generated a greater P3 peak than the log-linear trials, and in turn, the log-linear trials generated a greater P3 peak than the linear trials. These effects suggest that even before the behavioral response is effectuated, there is a strong recognition of the linear placements of numbers followed by a signal of surprise related to the logarithmic and log-linear placements of numbers.

To test these effects statistically, a 3-way (trial type: linear, logarithmic, log-linear x electrode site: FL, FR, PL, PR x component: N1, P3) repeated-measures ANOVA was conducted on the mean amplitudes calculated for the N1 and P3 time windows. All reported p-values are Greenhouse-Geisser corrected for violations of sphericity assumptions. Results indicated a significant component x electrode interaction, ($F(3,39) = 8.37$, $p < .001$, $\eta^2 = 0.39$). This effect is largely due to a larger N1 component in parietal sites compared to frontal sites. Furthermore, as expected, a trial type x electrode x component interaction was significant ($F(6,78) = 3.85$, $p = .033$, $\eta^2 = 0.23$). This interaction was due to different simple main effects of trial type at the N1 component for the PL ($F(2,26) = 8.07$, $p = .003$, $\omega^2 = 0.25$) and PR ($F(2,26) = 14.81$, $p < .001$, $\omega^2 = 0.40$) electrode sites versus simple main effects of trial type at the P3 component for the FR ($F(2,26) = 4.69$, $p = .048$, $\omega^2 = 0.16$) and PL ($F(2,26) = 18.25$, $p < .001$, $\omega^2 = 0.45$) electrode sites.

To explore this more closely, we computed average waveforms for the correct linear trials with hatch marks that corresponded to small numbers (i.e. 5, 78, 150) and to large numbers (i.e. 606, 725, 938). As can be seen in Figure 3, compared to small numbers, large numbers generated smaller N1 peaks at parietal electrode sites and larger P3 peaks at frontal electrode sites. This pattern of results indicates that small numbers were expected to appear in the linear position, whereas large numbers were not. Thus, even though participants made the correct response for both types of numbers, the brain shows evidence that large numbers and small numbers are processed differently.

To test these results statistically, we conducted a 3-way (Condition: small numbers, large numbers x Electrode: FL, FR, PL, PR x Component: N1, P3) repeated measures ANOVA. Results showed a significant electrode x component interaction ($F(3,39) = 9.14$, $p < .001$, $\eta^2 = 0.41$). This effect is largely due to a change in polarity from the N1 to the P3 components in parietal electrodes. Moreover, as expected there was a significant trial condition x electrode x component interaction ($F(3,39) = 8.05$, $p < .001$, $\eta^2 = 0.38$). Post-hoc analysis revealed that when hatch marks were positioned linearly, a greater N1 component at the PR electrode site ($F(1,13) = 5.67$, $p = .033$, $\omega^2 = 0.14$) was elicited by small numbers than by large numbers. Also, at the FL electrode site, linearly positioned hatch marks elicited a greater P3 component ($F(1,13) = 6.31$, $p = .026$, $\omega^2 = 0.16$) for large numbers than for small numbers.

DISCUSSION

We aimed to provide a temporal characterization of brain activity evoked by representations of numeric magnitudes. This characterization supported two conclusions: (1) the adult brain continues to represent numeric magnitudes using both a logarithmically-compressed code and a linear code, with the probability of a number being processed by the linear code decreasing with numeric magnitude (and thus frequency and prior experience); and (2) that logarithmic-coding is predominantly processed in frontal areas, whereas

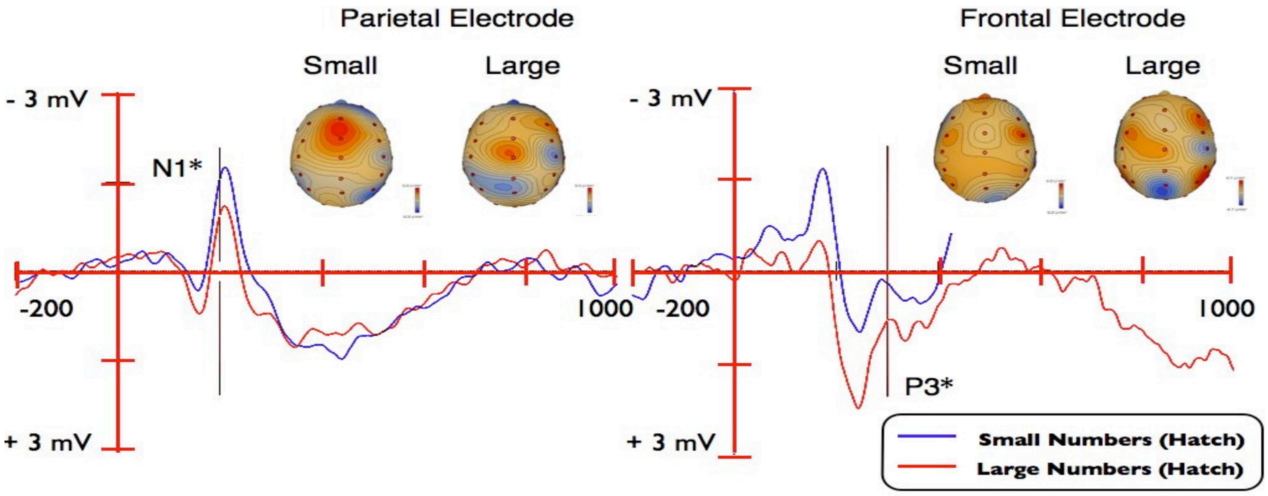

Figure 3: Top: Current source density topographies for correct linear trials divided into small and large numbers at 200 ms (left) and at 300 ms (right). Bottom: N1 (140-240 ms) and P3 (260-700 ms) ERP components for correct linear trials divided into small and large numbers for parietal (left) and frontal (right) electrode sites

linear coding is predominantly processed in parietal areas. These findings are important because they are consistent with our proposed explanation for a key finding in the developmental neuroscience of number representation. Namely, that although it has been found that HIPS is crucial for numeric processing (Dehaene, et al., 2003), studies that test children, have found a greater involvement of the prefrontal cortex (Ansari et al. 2005; Ansari & Dhital, 2006; Cantlon, et al., 2006; Cantlon, et al., 2009; Rivera, Reiss, Eckert and Menon, 2005).

Evidence supporting our first conclusion comes from several findings from this study. Behavioral results indicate that both linear and non-linear positions of numbers were judged as correct, with probability of non-linear positions being judged as correct increasing as numbers increased in size. Electrophysiological results were consistent with this behavioral finding. Small numbers shown in the linear position generated a greater N1 peak than did large numbers shown in the linear position. Similarly, large numbers shown in the linear position generated a greater P3 peak than did smaller numbers. Moreover, these electrophysiological findings held even when subjects' behavior correctly identified locations as linear. Thus, neither behavioral nor electrophysiological results are consistent with the idea that numbers are solely represented linearly or solely non-linearly.

Evidence supporting our second conclusion comes solely from electrophysiological data. As indicated by the N1 component, smaller numbers were more easily identified than large numbers, and this identification was predominantly found in parietal sites (Dehaene, 1996; Libertus et al., 2007). On the other hand, linear trials that corresponded to larger numbers (that are less entrenched) generated a greater surprise response (as indicated by the P3 component) in frontal electrode sites. Likewise, the results for the discrimination between linear and logarithmic conditions showed that the significant N1 component for linear trials was located in parietal electrodes, while the P3 component for logarithmic trials was located in frontal electrodes.

An alternative hypothesis that could explain the role of prefrontal cortex is that it could be signaling general attentional demands or processes of response selection that become more active for more difficult tasks. However, using habituation paradigms, Cantlon and her collaborators have found greater activity in the prefrontal cortex of children for numeric processing (Cantlon et al., 2006; Cantlon et al., 2009). Therefore, this finding rules out the response selection hypothesis because there was no response needed, and brings doubts about the attentional demands hypothesis because there should not be significant differences in attentional demands between the number and the control tasks used. Furthermore, in our analysis, large numbers have smaller discrepancies between the linear and logarithmic trials. Therefore, if this hypothesis were correct we would expect smaller P3 amplitudes for them. Instead, we found that large numbers elicited larger frontal P3 amplitudes.

In conclusion, this is the first study to provide neural evidence for competing representations of numerical magnitude. By using an ERP paradigm with a number line estimation task, we were able to investigate numeric processing both before participants had reached a final decision about magnitude and a behavior was executed. This paradigm led to the novel finding that not all numbers are represented as linearly positioned on the number line, despite the fact that participants' judgments are very linear at the behavioral level. In this way, our findings are consistent with a novel developmental proposal that can integrate apparently contradictory results regarding the neural representation of numeric magnitude.

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