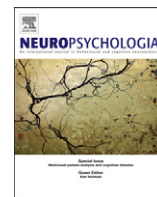


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Mental arithmetic activates analogic representations of internally generated sums

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ABSTRACT

The internal representation of numbers generated during calculation has received little attention. Much of the mathematics learning literature focuses on symbolic retrieval of math facts; in contrast, we critically test the hypothesis that internally generated numbers are represented analogically, using an approximate number system. In an fMRI study, the spontaneous processing of arithmetical expressions was tested. Participants passively viewed a sequence of double-digit addition expressions that summed to the same number. Adaptation was found in number-related regions in a fronto-parietal network. Following adaptation, arrays of dots were introduced, differing in their numerical distance from the sum of the addition expressions. Activation in voxels that showed adaptation to a repeated sum was also sensitive to the distance of the dot quantity from the sum. We conclude that participants exhibited adaptation to an internally generated number, that adapted representations were analogic in nature, and that these analogic representations may undergird arithmetic calculation.

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1. Introduction

Most of the research on the representation of numbers has utilized externally presented number stimuli like Arabic numerals, number words, or arrays of objects. However, when processing numbers in everyday life, people often have to generate numbers internally. For example, when calculating the tip to give a taxi driver in a cash exchange, a passenger might calculate precisely or estimate the amount to be paid. Either way, during the calculation process new numbers are mentally generated from the operands, and the mentally created numbers are typically not presented externally (e.g., as hand-drawn calculations). The process of mental calculation has generally been studied separately from the question of number representation. On one hand, studies on numerical representation focus on the nature of these representations, such as whether they preserve the quantity or size for which numbers stand (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza, Pinel, Le Bihan, & Dehaene, 2007), whether they are notation-dependant or -independent (Cohen Kadosh & Walsh, 2009), or whether they are holistic or componential (Dehaene, Dupoux, & Mehler, 1990; Reynvoet &

Brybaert, 1999). On the other hand, studies on math and arithmetic skills tend to focus on assessing strategies like mental calculation vs. fact retrieval (Delazer et al., 2005; Ischebeck, Zamarian, Egger, Schocke, & Delazer, 2007), or exact calculation vs. estimation (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Venkatraman, Ansari, & Chee, 2005). The present study combines these two lines of research and asks: what is the nature of the numerical representations that result from mental arithmetic? By testing the representation of numbers that are generated internally, as a result of solving arithmetic problem, we set up conditions that are less dependent on external notation. This arrangement can further our understanding of number representation in a way that has not yet been explored.

It has been suggested that humans use more than one numerical system when processing numbers. One distinction has been made between a language-independent system of number magnitude representation and a language-based system for stored tables and exact arithmetic knowledge (Campbell & Clark, 1988; Dehaene, 1992; Dehaene et al., 1999; Lemer, Dehaene, Spelke, & Cohen, 2003). For example, in a study with bilinguals, Dehaene et al. (1999) showed that the solving of arithmetic problems taught using precise calculation depended on the language in which they were taught, while the solving of problems taught using estimation strategies did not depend on the taught language. Precise vs. approximate calculation also resulted in the recruitment of different brain networks, with

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parietal regions more active during approximate calculation and left frontal regions more active during precise calculation (Dehaene et al., 1999). The authors concluded that estimation makes use of magnitude representations rather than language-dependent facts. Studies of numerical representation have also shown that when verbal number representations are unavailable (e.g., due to verbal interference), adults rely on a non-verbal, approximate numerical system (Cordes, Gelman, Gallistel, & Whalen, 2001; Frank, Fedorenko, Lai, Saxe, & Gibson, 2012; Whalen, Gallistel, & Gelman, 1999).

Numerical representations in the approximate magnitude system are said to be analogic, which means that representations preserve the quantity or size for which numbers stand (Dehaene, 1992; Gallistel & Gelman, 1992; McCloskey, 1992). This form of representation has been linked to a fronto-parietal network (Arsalidou & Taylor, 2011; Dehaene, 1992; Dehaene & Cohen, 1997; Ischebeck et al., 2006). Most of the regions included in this network are not exclusively sensitive to number processing; however, parts of the intra-parietal sulcus (IPS) have been more specifically associated with the analogic representation of numbers (Arsalidou & Taylor, 2011; Dehaene et al., 1996; Dehaene, Piazza, Pinel, & Cohen, 2003; Eger, Sterzer, Russ, Giarud, & Kleinschmidt, 2003). In a non-human primate study of numerical information processing, neurons in the IPS and in prefrontal cortex were found to be sensitive to a specific numerical value, exhibiting decreasing activation when the distance between the presented numerosity and the preferred numerosity for that neuron grew larger (Nieder & Miller, 2004). This pattern corresponds to the behavioral Distance Effect (Moyer & Landauer, 1967), which is the increase in reaction time as the distance between the to-be-compared numbers decreases. In an adaptation fMRI study in humans, a similar sensitivity to numerosity was found in the IPS (Piazza et al., 2004). In this study, participants passively observed a stream of dot collections with a similar numerosity but different shapes and spatial distributions. Deviants of other numerosities yielded larger activation the larger the distance between the adapted numerosity and the deviant (see also Ansari, Dhital, & Siong, 2006; Cantlon, Brannon, Carter, & Pelphrey, 2006). Piazza et al. (2004) used non-symbolic numerosities (arrays of dots) as their stimuli. However, in a later study, Piazza et al. (2007) showed that when adapting to non-symbolic numerosities, distance-sensitive dishabituation was observed with symbolic as well as non-symbolic deviants, and the same was found when adapting to symbolic numerosities in the form of Arabic numerals. The authors concluded that the adaptation was to the analogic representation of numbers that carries the meaning of quantity (but see Cohen Kadosh & Walsh, 2009, for an alternative interpretation).

Considering the representations used in mental calculation, fluency in math and arithmetic has traditionally been thought to mainly involve fact retrieval from memory (Pellegrino & Goldman, 1987; Resnick, 1983; Siegler, 1988). However, a number of recent findings suggest that mathematical performance can also be related to the precision of the analogic representations of numbers (Duncan et al. 2007; Halberda, Mazzocco, & Feigenson, 2008; Jordan, Glutting, & Ramineni, 2010; Jordan, Kaplan, Ramineni, & Locuniak, 2009; Locuniak & Jordan, 2008; Peters, Slovic, Västfjäll, & Mertz, 2008; Wilson et al. 2006). For example, Halberda et al. (2008) found that the precision of non-symbolic quantity representation in 14-year-olds correlated with their performance on symbolic math tests administered every year from kindergarten to sixth grade, even when lexical skills and general intelligence were taken into account. Similar results were obtained in a study that involved old and younger adults (Peters et al., 2008). Thus, it seems that fluency in math and arithmetic

problem solving is affected by the quality of analogic representations of quantities.

Studies of brain activity during engagement in arithmetic problem solving provide a potential window into the representational substrates of mathematical cognition. Although a number of studies have elucidated the brain regions that are involved in the processing of basic calculations (Dehaene et al., 1999; Delazer et al., 2003, 2004, 2005; Ischebeck et al., 2007; Ischebeck, Zamarian, Schocke, & Delazer, 2009; Venkatraman et al., 2005; Zamarian, Ischebeck, & Delazer, 2009), these studies were not designed to test the representational products of calculation. For instance, in agreement with the thesis that fluency in math is based on fact retrieval, in a series of studies, Delazer and colleagues (Delazer et al., 2003, 2004, 2005; Grabner et al., 2009; Ischebeck et al., 2007; Zamarian et al., 2009) demonstrated that algorithmic calculation, which characterizes complex and new arithmetic problem-solving, is associated with activation in bilateral IPS, while fact retrieval, which characterizes familiar problem-solving, is associated with activation in the left angular gyrus. The distinction between IPS and the angular gyrus was also associated with distinction between estimation and exact calculation (Stanescu-Cosson et al., 2000). Yet, contrary to these findings, Venkatraman et al. (2005) showed that the IPS was involved in the process of both exact and estimate calculation of single-digit addition problems.

In the present study, we extend beyond previous work, and test whether adaptation to quantities can take place when the actual to-be-adapted quantity is never presented. We use a passive viewing task, involving exposure to a series of symbolic addition expressions that sum to the same number. The resulting sum is never presented. Following an adaptation period, deviants are introduced amid the addition expressions. The deviants are arrays of dots, in which their quantities are varied to be larger, smaller, or exactly as the adapted sum. Adaptation by itself does not provide much information about the nature of the adapted representations. Thus, the choice of non-symbolic notation of the deviant stimuli serves to test whether the adaptation is to the analogic representations of quantities. The experimental questions are (1) whether representations of the arithmetical sum will exhibit adaptation, and (2) whether adaptation, if it exists, will be for the analogic representations of quantities.

2. Method

2.1. Participants

Forty participants (20 male) completed the experiment as part of a longer procedure that included fMRI and behavioral tests before and after training (reported elsewhere). Participants provided signed consent. For participating in the entire experiment, participants received \$230 in base pay, plus performance bonuses, for a mean total pay of \$317 (range of \$285 to \$346). All participants were college students or recent graduates, 18 to 25-years-of-age (mean age=20.87). Particularly, they were screened to be non-experts in math, as operationally defined by a math SAT¹ between 600 and 700 (mean=645, STD=32) and a major field of study outside of a math-connected discipline. Participants had to be right handed, with English as their first language, not taking any prescription psychotropic medications, and have no ferrous metal in the body.

2.2. Stimuli

Four standard sums were selected: two at the range of 30s (35 and 38) and two at the 50s (53 and 56). For each standard sum, a list of all possible addition expressions composed of two double-digit numbers was created (e.g., two samples for the sum 53 are: 24+29 and 18+35). The lists included between 14

¹ Math SAT is a general quantitative reasoning test used for selection into most universities in the US with a mean of approximately 500 and a maximum score of 800.

Table 1
Deviant quantities for each sum.

Deviant category	Ratio	Sum 35	Sum 38	Sum 53	Sum 56
Smaller—far	0.5	18	19	26	28
Smaller—intermediate	0.67	23	25	36	37
Smaller—close	0.8	28	30	43	45
Identical	1	35	38	53	56
Larger—close	1.25	44	48	66	70
Larger—intermediate	1.5	53	57	80	84
Larger—far	2	70	76	106	112

(for sum of 35) and 35 (for sum of 56) expressions. For each sum, seven sets of deviant stimuli were created. Following the results of Piazza et al. (2004), demonstrating the logarithmic nature of the distance effect, deviant numbers were selected to form a \log_2 scale to make the perceived difference between larger and smaller deviants for each standard sum equivalent. The deviants were dot displays in which the number of dots corresponded to one of seven ratios from the standard sum: 0.50, 0.67, 0.80, 1.00, 1.25, 1.50, and 2.00. Generally, deviants could contain a number of dots that were close (ratios of 0.80 and 1.25), intermediate (ratios of 0.67 and 1.50), or far (ratios of 0.50 and 2) from the quantity of the standard sum (ratio of 1.00), and could be larger or smaller than the sum quantity. The dots were presented in a random array on a 17 (horizontal) \times 12 (vertical) matrix at the center of the screen that created 204 possible locations. The matrix occupied 64% (width) \times 60% (height) of the screen. To control for non-numerical factors, such as overall area and contour, each dot was randomly selected to be large (1.72°), medium (1.33°), or small ($.95^\circ$). The deviant quantities for each sum are detailed in Table 1. All stimuli were presented as white figures on a black screen. The size of the numbers in the addition expressions was randomly selected from a range of font sizes from 16 to 28.

2.3. Procedure

The general design followed the design used by Piazza et al. (2004, 2007). The task was divided into two runs, 5 min and 28 s each. Each run started with a white fixation cross presented at the center of the screen, which remained visible throughout. Each run was further divided into two blocks, one from each range of stimuli (30s and 50s). Alternating between the two ranges ensured that a new adaptation process started in each block. Using two different ranges also allowed us to explore possible differences in the population of neurons that process each range (Eger et al., 2009). In each block, 150 stimuli were presented; about 14 of them were deviants. Stimuli were presented for 300 ms at a constant rate of one every 1000 ms. Each block started with an adaptation period of fifty addition expressions that all summed to the same number (35, 38, 53, or 56), followed by 100 trials that could be either standard (addition expression that is summed to the same number) or deviant (array of dots). At least five and at most nine standard stimuli separated one deviant from the next. A block ended with a 12 s break. The addition expressions appeared at one of twelve possible locations 7.5° around the fixation cross. Participants were instructed to pay attention to the expressions on the screen but make no response. They were told that after the experiment is over they would be asked some questions about what they had seen. Participants were not informed about the dots stimuli.

The experiment reported was part of a larger study that included a comparison between experimental and control groups before and after training. The complete study consisted of nine one-hour sessions and included pre and post behavioral tests (sessions 1 and 9), pre and post fMRI scans (sessions 2 and 8), and five training sessions (sessions 3–7). The behavioral tests included the following tasks: Math Fact Retrieval, Number Comparison, Multi-Digit Arithmetic Fluency, Dots Comparison, and Complex Math. The scans included two additional tasks (conducted before the reported task): an fMRI version of the training task, and another adaptation task that tested tuning curves of symbolic numerals. The results of the other tasks, as well as results of the post-scan, are reported elsewhere. The Institutional Review Board (IRB) of the University of Pittsburgh approved the reported procedure.

2.4. fMRI parameters

Scanning was performed on a 3.0 T Siemens Magnetom Allegra head-only research scanner. An FDA approved research head coil was used for all of the scans. Stimulus presentation was controlled using “E-prime” software (Schneider, Eschman, & Zuccolotto, 2002).

Functional scans were obtained using a standard EPI pulse sequence. Thirty-eight 3.2 mm thick oblique slices were obtained during the functional scans. Acquisition parameters used in this study were: TR=2000 ms, TE=25 ms, flip angle= 70° , with a field of view of 205 mm. These parameters gave us coverage of temporal lobe structures as well as full coverage of the parietal lobe. T1-weighted anatomical images were acquired with a magnetization prepared rapid gradient echo sequence (repetition time TR=1540 ms; echo time=3.04 ms; image matrix= 256^2 ; voxel size=1 mm \times 1 mm \times 1 mm; 192 slices).

The Analysis of Functional Neuroimages (Afn) package was used to preprocess and analyze the data (Cox, 1996). Data were pre-processed with the following steps: (1) motion correction by registering all volumes with the third volume, as well as alignment of all functional volumes for each individual to his/her anatomy and transforming the anatomy to standard space (NN27); (2) spatial smoothing using a 5.5 mm full-width at half-maximum Gaussian kernel; (3) scaling signal for each voxel to mean of 100. Next, functional data were concatenated across the two runs and analyzed with a general linear model (3dDeconvolve). Regressors for the model included two regressors for a linear decrease during the first 50 s of each block (one for each range), as well as time onsets for each deviant type (seven ratios for each range: 30s and 50s) which were modeled with gamma model (GAM, by Afn). The baseline activity was modeled by linear, quadratic, and cubic trends, six motion estimates, and a time series from two foci in the ventricles (Windischberger et al., 2002). Group activation was analyzed with one-sample *t*-test of beta coefficients generated in the single-subject deconvolution process, and a Monte Carlo simulation was used to correct for multiple comparisons.

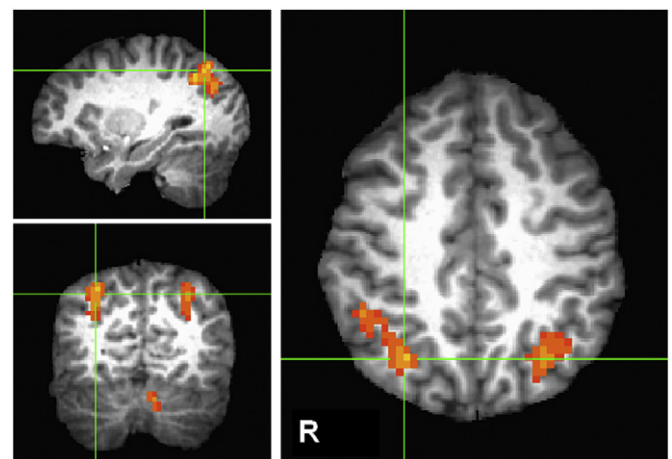


Fig. 1. Parietal regions showing a significant (corrected $p < .01$, based upon a corrected alpha level of $p < .00005$ and a cluster extent of eight or more voxels) linear decrease during the adaptation periods (first 50 s of each block), collapsed across 30s and 50s adaptation ranges. Talairach coordinates of crosshair: $x=29$, $y=-63$, $z=41$.

Table 2

Coordinates of peak activation within clusters that survived an alpha threshold of $p < .01$ (corrected, based upon an uncorrected alpha level of $p < .00005$ and a cluster extent of eight or more voxels) for a linear decrease of activation during the adaptation period, collapsed across the 30s and the 50s adaptation ranges. The peaks within the clusters were defined as local maxima separated by at least four voxels.

Cluster location	Peak coordinates (Brodmann area, if applicable)	<i>t</i> value	Cluster size
Right parietal cortex	28, -65, 44 (BA 7)	6.41	157
	43, -50, 38 (BA 40)	5.90	
	29, -55, 35 (~BA 39)	6.53	
	32, -67, 29	6.46	
Left parietal cortex	-38, -56, 44 (BA 40)	5.66	120
	-28, -61, 35 (BA 39)	6.90	
Right middle frontal gyrus	47, 32, 26 (BA 46)	7.26	56
Right precentral gyrus	47, 2, 35 (BA 6)	5.45	39
Left inferior frontal gyrus	-40, 8, 29 (BA 9)	5.86	19
Right medial cerebellum	8, -64, -25	6.61	14
Left medial cerebellum	-7, -64, -25	5.79	24

3. Results

3.1. Adaptation analysis

Data from the adaptation period were used to determine whether adaptation occurs in response to repeated representation of an internally generated quantity. We searched for regions where activity decreased linearly during the first 50 s of each block. Significant adaptation effects were found in seven regions: the right and left parietal lobules (shown in Fig. 1), the right middle frontal gyrus, the right precentral gyrus, the left inferior frontal gyrus, and the right and left medial cerebellum (see Table 2).

Given past literature that has implicated parietal cortex with analogic representation, we first focused on the two parietal regions identified by the group analysis. The entire volumes of the parietal clusters were used as masks for further analysis. Following the procedure reported by Piazza et al. (2004, 2007), within each parietal region we isolated, for each participant, the voxel with the largest adaptation effect for each range. As mentioned, a secondary purpose for using two ranges was to examine a possible difference in the population of neurons that process each range. To address this question, we used a MANOVA approach to determine whether the anatomical distribution of peak adaptation effects in each hemisphere varied across the 30s vs. 50s adaptation ranges. No significant differences were found (see Appendix A.1).

Fig. 2 shows the averaged time course of the Blood Oxygenation Level Dependent (BOLD) signal during the adaptation period, averaged across blocks and participants, for each of the selected voxels. Activation increased following the onset of the block, attained its peak around 12 s (6 TRs) after the stimuli onset, and then decreased linearly to a minimum at the end of the adaptation period. The activation was higher for a range in the voxel that better adapted to that range.

To determine whether the adaptation effect varied across the two hemispheres or adapted ranges, the signal changes (calculated as raw BOLD value in each TR minus the value in the first TR) at the peak of the response to the new sum for each block (TRs 5–9) were compared to the signal change values at the end of the adaptation period (TRs 21–25), with Hemisphere (Left vs. Right), Preferred Range (30s vs. 50s), Presented Range (30s vs. 50s), and Phase (peak vs. end), as factors (see shaded areas, Fig. 2). As expected, the effect of Phase was significant with activation significantly higher at the Peak than the End of the adaptation period: $F(1, 32)=41.01$, $MSE=.000$, $p<.0001$, $\eta_p^2=.56$. The overall signal change in the left hemisphere was significantly larger than the signal change in the right hemisphere, $F(1, 32)=6.75$, $MSE=.000$, $p<.02$, $\eta_p^2=.17$, indicating that the initial presentation of each new sum generated a more robust Peak response in the left hemisphere. However, the variable of Hemisphere did not interact with any other variable, implying that representations in the two hemispheres adapted to the two ranges in a similar manner. No main effects were found for Preferred Range ($F(1, 32)=1.54$, $MSE=.000$, $p=.22$) or Presented Range ($F<1$), suggesting that the adaptation process to the two ranges was also similar. However, the interaction of Preferred Range and Presented Range was significant: $F(1, 32)=9.4$, $MSE=.000$, $p<.005$, $\eta_p^2=.23$; and so was the three-way interaction between Preferred Range, Presented Range, and Phase: $F(1, 32)=77.78$, $MSE=.000$, $p<.0001$, $\eta_p^2=.71$. The two-way interaction reflected a Preferredness Effect, such that overall signal change was larger for a presented range at its preferred voxel. The three-way interaction showed a larger Phase effect (i.e., the difference between Peak and End) in the preferred voxel for each range (see shaded areas in Fig. 2). This interaction shows that the range that was ideal for a voxel showed higher peak activation but also lower activation at the end of the adaptation period. This is to say that the Preferredness effect includes both higher responsiveness and a steeper rate of

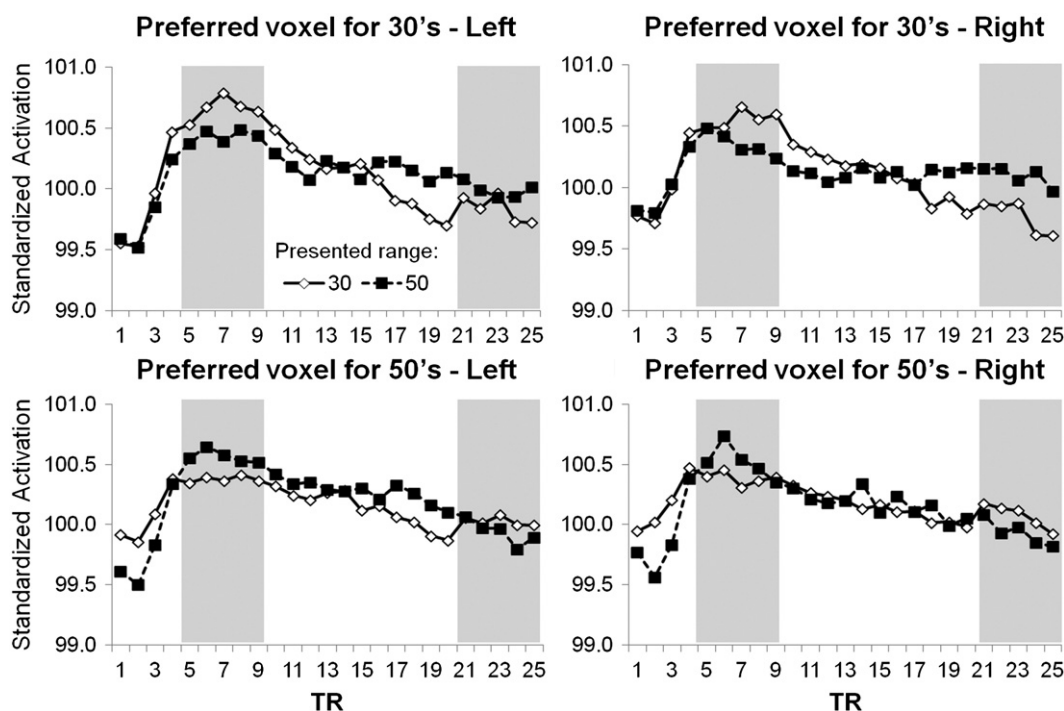


Fig. 2. The time course of the BOLD signal during the adaptation period, averaged across blocks, in the voxels that were selected for each participant to show the largest adaptation effect (increase followed by linear decrease during the first 50 s of each block). Left panels display activation of voxels from the left hemisphere; right panels display voxels from right hemisphere; top panels display preferred voxels for 30s; and bottom panels display preferred voxels for 50s. Shaded areas denote the Peak and End phases used in the ANOVA.

adaptation (see additional comparisons concerning the different ranges in [Appendix A.2](#)). Since the voxels were selected according to the linear decrease they exhibited to one of the ranges, these results can be simply explained in terms of a statistical selection bias, although it is also possible that they reflect an underlying neural organization that is sensitive to different magnitude ranges.

To summarize, activation in voxels selected according to their linear decrease during adaptation period was sensitive to the adapted range. The lack of significant differences between the two ranges (30s and 50s) suggests that the adaptation process was equally effective in the different ranges. Thus, it seems that participants were adapted to the sums of addition expressions but the range of the repeated sum did not affect the observed results.

3.2. Deviants analysis

After confirming that adaptation to sums indeed took place, we proceed to investigate the nature of the adapted representations. We therefore examined the response of the voxels, selected according to their pattern of activation during the adaptation period, to the deviant dot stimuli that were introduced following each adaptation period. For each of the four voxels from each individual (one for each range and each hemisphere), the beta coefficients of the gamma model for each ratio-deviant were extracted. Thus, this analysis involved data that were temporally independent from the data used for voxel selection. Moreover, the adaptation was for symbolic presentations of addition expressions, while the deviants were non-symbolic arrays of dots.

The analysis included four within-subject variables: Hemisphere (2) \times Preferred Range (2) \times Presented Range (2) \times Ratio (7). Importantly, the deviant responses across the seven ratios formed a quadratic pattern: $F(1, 32)=20.96$, $MSE=.313$, $p<.0001$, $\eta_p^2=.4$. That is, a distance effect was observed: the further the quantity of dots was from the adapted sum, the higher the deviant response. The variable of Ratio did not interact with any other variable (in most cases: $F < 1$), indicating that the distance effect observed for a range that was ideal for a voxel was not significantly different from the distance effect for the other range, in both hemispheres. No difference was found between hemispheres and the variable of Hemisphere did not interact with any other variable. The variables of Preferred Range and Presented Range showed no main effects ($F_s < 1$), but the interaction between the two variables, indicating the Preferredness effect, was significant, $F(1, 32)=14.43$, $MSE=.18$, $p<.001$, $\eta_p^2=.31$: the conditions in which the voxel that was best adapted to a specific range and then presented with deviants within this range showed smaller beta coefficients (mean: .04) than the conditions in which that voxel was presented with deviants from the other range (mean: .12), which might be a result of less adaptation to this range. As mentioned above, however, the Preferredness effect did not interact with the distance effect. [Fig. 3](#) shows the pattern of the distance effect in each of the preferred range and presented range conditions (averaged across hemispheres). The main effect of Ratio across all condition is shown in the top-left panel of [Fig. 4](#).

To examine whether the parietal regions are uniquely sensitive to the distance effect, a similar analysis was conducted on deviant data extracted from the frontal and cerebellar ROIs that also exhibited significant adaptation effects in the whole-brain analysis ([Table 2](#)). As in the parietal regions, the individual voxels were selected using the adaptation period data from each participant. A distance effect, measured as a quadratic function of Ratio, was found in the right middle frontal gyrus, right precentral

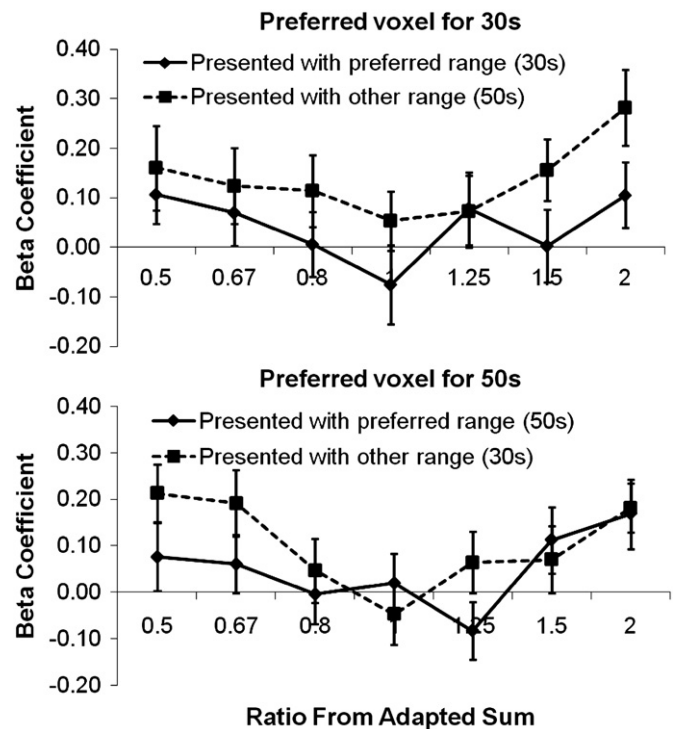


Fig. 3. The consistent pattern of beta coefficients at the different conditions of preferred range and presented range, as a function of the ratio of deviants from the adapted sum, at the parietal regions, collapsed across hemispheres. The significance of the distance effect, as a quadratic pattern, was: $p < .05$ for all conditions except for Preferred-30 s-Presented-30 s ($p=.1$).

gyrus, and bilateral cerebellum ($p < .05$, $\eta_p^2 < .34$; see [Table B.1](#) and full details in [Appendix B](#)). In the left inferior frontal gyrus, the quadratic function of Ratio was only marginally significant ($p=.07$). The interaction between Preferred Range and Presented Range, which indicates the Preferredness effect, was not significant at any of the non-parietal regions ($p_s > .19$), nor were the interactions of Ratio with any of the other variables. Although a quadratic function of ratios was demonstrated in most non-parietal regions, testing the difference of each ratio from the adapted quantity (i.e., ratio 1), at the four regions showing the distance effect, revealed a significant difference only for the ratio of 2 ($p < 0.05$). In contrast, in the parietal regions, ratios of .5, .67, and 2 differed significantly from the ratio of 1 ($p < .05$) and the ratio of 1.5 was marginally significant ($p=.09$). Thus, a greater distance was required to achieve a significant dishabituation response to the dot displays in the non-parietal than in the parietal regions.

3.3. Distance effect at the group level

An additional voxel-wise analysis was done at the group level, to look for regions that showed a distance effect of deviants from the adapted sum without *a priori* constraints on their locus. This analysis also permitted a comparison between the activation maps related to adaptation to those related to the distance effect for the deviants from the adaptive sum. Five clusters exhibiting a significant distance effect were identified (corrected $p < .05$, based upon an uncorrected alpha of $p < 0.01$ and a cluster extent of 60 or more voxels) (see [Table 3](#)). Two of these clusters overlapped with significant right frontal and parietal clusters identified through the group analysis of adaptation effects (see [Fig. 5](#)), indicating that the adaptation and distance effects arise from shared neural tissue, despite differences in numerical

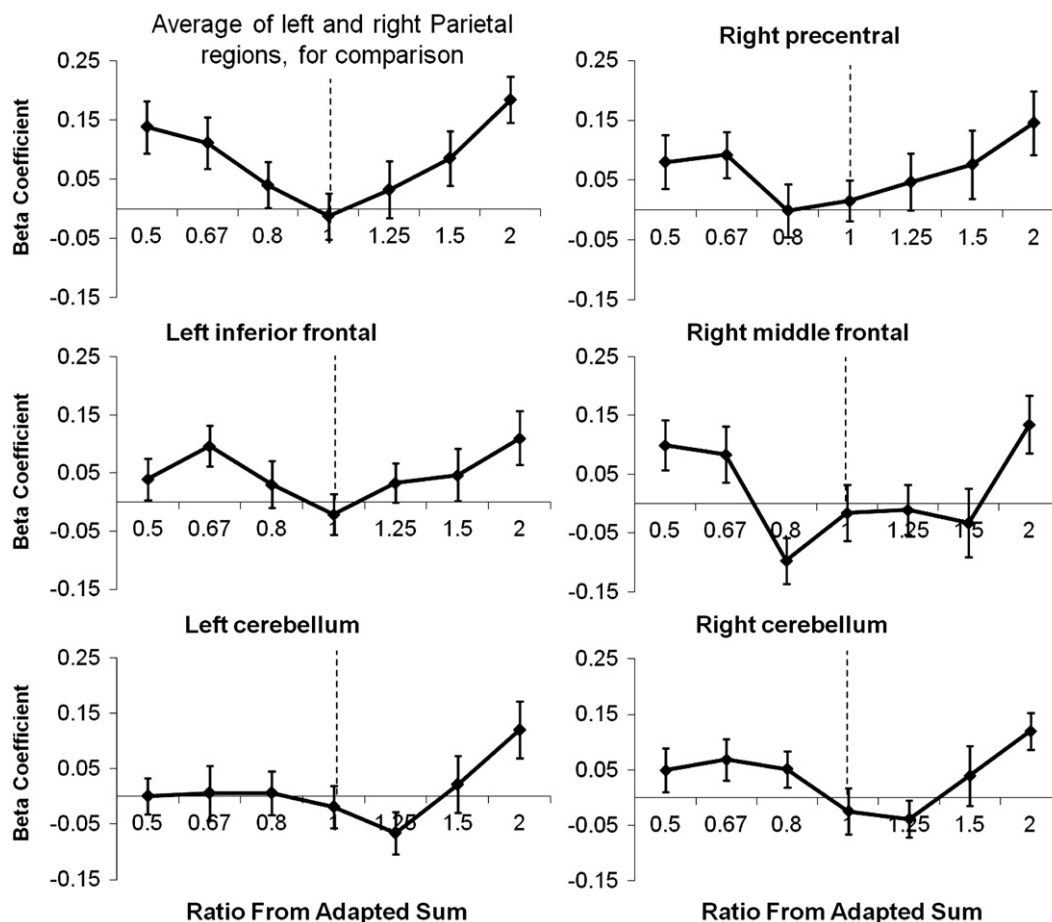


Fig. 4. Beta coefficients as a function of the ratio of deviants from the adapted sum (collapsed across preferred and presented ranges) in the non-parietal regions. The average of left and right parietal regions is presented in the top-left panel, for comparison. The dashed line in Ratio 1 denotes the position of the expected lowest beta coefficient.

Table 3

Coordinates of peak activation and cluster size that survived an alpha threshold of $p < .05$ (corrected, based upon an uncorrected alpha level of $p < .01$ and a cluster extent of 60 or more voxels) for the distance effect during deviants periods, collapsed across the 30s and the 50s adaptation ranges. Asterisks mark clusters that overlapped with a cluster identified in the group analysis of adaptation effects (Table 2).

Cluster location	Peak coordinates (Brodmann area)	Cluster size
Right parietal cortex*	41, -43, 56 (BA 40) 26, -61, 26 (BA 7 and 19)	82 163
Right middle frontal/precentral gyrus*	32, -10, 59 (BA 6) 41, 2, 29 (BA 6)	72 81
Left precentral/middle frontal gyrus	-31, 5, 53 (BA 6)	77
Right fusiform gyrus	38, -37, -13 (BA 37)	109
Left fusiform/middle temporal gyrus	-52, -52, -7 (BA 37)	73

notation. No overlap was found for the remaining three clusters, which localized to the left dorsal precentral gyrus and bilateral fusiform gyri. Activation in these regions may be due to notation-specific numerical processing or to non-numeric differences across the dot displays. No overlap was observed in the left parietal cortex, which showed the adaptation effect, because the distance effect in this region did not survive the statistical threshold for significance in the group analysis.

4. Discussion

In the present study we tested whether adaptation to quantities can take place when the actual to-be-adapted quantity is never presented. The standard stimuli, to which adaptation was tested, were addition expressions composed of two double-digit numbers. The specific addends in the expressions rarely repeated, thus, any numerically-related adaptation response should be only to the one repeated aspect in the stimuli, namely, the sum of the two addends. An important strength of the present study is the separation between the data according to which voxels were selected for analysis (linear decrease during adaptation period), and the data according to which activation in these voxels was evaluated (sensitivity to the distance of the number of dots actually presented, from the adapted sum). Thus, deviant stimuli differ from adaptation stimuli both qualitatively and temporally.

During the adaptation period, an increase followed by a linear decrease of activation was observed in brain regions known to be part of the fronto-parietal network that supports processing of numerical information. Importantly, the region that has been recognized as mainly associated with the analogic representation of numbers – the IPS (Dehaene, 1992) – exhibited the largest adaptation effect, in both left and right hemispheres. The presence of an adaptation effect by itself does not directly test the nature of the adapted representations. For instance, one could claim that adaptation could have been to the repeated addition expressions per se: just the fact that numbers were presented

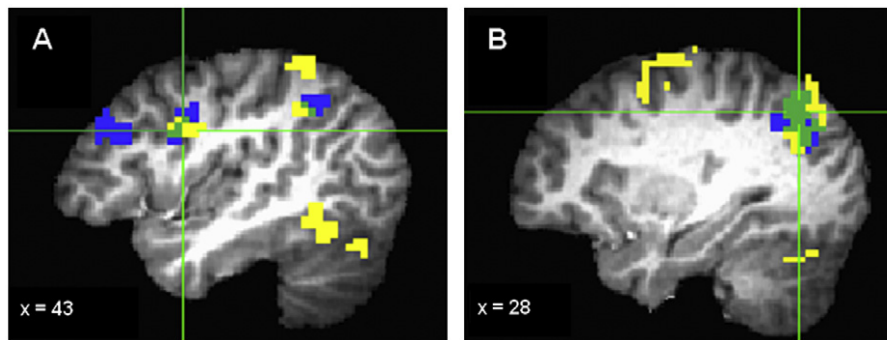


Fig. 5. Overlap of group clusters of adaptation to addition expressions and sensitivity to distance in frontal cortex (A) and parietal cortex (B). Blue: linear decrease during adaptation period ($p=.00005$); yellow: distance effect from the sum ($p=.01$); green: overlap. Talairach coordinates of crosshair in panel A: $x=43, y=3, z=27$; and in panel B: $x=28, y=-66, z=38$.

could have triggered the increase of activation in number-sensitive regions, and the fact that more numbers were introduced could ultimately have caused adaptation to “seeing numbers”. However, the results from the deviant analysis provide more direct evidence about the representational source of the adaptation effect. If adaptation was merely to “seeing addition expressions”, no distance effect would have been expected for deviant stimuli and certainly not one centered on the sum. Since distance of deviants was measured in respect to the adapted sum, any sensitivity of the recovery from adaptation to distance from the sum would imply that adaptation was to that sum and not to the mere presentation of addition expressions.

A distance effect from the adapted sum was observed in voxels selected according to the adaptation effect they showed at the first part of each block. It is worth noting that similar effects were observed for deviants larger or smaller than the adapted sum, thus, a greater activity in response to more distant deviants cannot be attributed to the overall number of dots. Also, since the analyzed voxels were selected according to the adaptation function they showed, the probability that these voxels show a distance effect by mere chance is low. The finding that voxels that showed adaptation to addition expressions also showed a distance effect to dot deviants provides evidence for the type of representations that were adapted in response to the addition expressions. Since deviant stimuli were composed of non-symbolic dot collections, it can be said that the mental representations that were internally generated and adapted during the adaptation period were analogic representations of the sums' quantities. Piazza et al. (2007) have already shown across-notation recovery from adaptation, through the actual presentation of Arabic numbers and dot quantities. In the present study however, the to-be-adapted number was not shown. The distance effect, in this case, indicates that the sums were calculated – either automatically or intentionally – each time an addition expression was briefly presented; otherwise, no adaptation to the sum would take place. In view of these facts, the adaptation found for the analogic representations of numbers in the present study was to numbers generated internally by participants.

The distance effect in the IPS, shown in Fig. 3, was centered on the actual sum (ratio of 1) in three out of four conditions. This result should be considered in light of previous finding showing a systematic underestimation of the number of dots in a given display (Izard & Dehaene, 2008). Underestimating the number of dots should have resulted in the distance effect shifted to the right (to larger ratios), given that participants would have perceived the larger number of dots as the actual sum. This was actually the case for voxels preferring the 50s when deviants for

sums in the 50s were presented. The other three conditions did not show such a shift, which could be a result of one or both of the following reasons. First, underestimation might be attributed to the response selection stage and therefore may not exist in passive view; and second, the sums might have been underestimated too. Regarding the second option, some studies have suggested the existence of an Operational Momentum: a bias toward larger outcome values for addition and smaller values for subtraction problems (Knops, Viarouge, & Dehaene, 2009; Lindemann & Tira, 2011; Pinhas & Fischer, 2008). Yet, only small to no operational momentum was found for symbolic addition expressions using double-digit operands (Knops et al., 2009), and when carry problems are included (as was the case in the current study) this can eliminate the effect altogether (Lindemann & Tira, 2011). Thus, we assume that the operational momentum should not have had an effect in the current study.

A whole brain analysis, searching for sensitivity to distance from the adapted sum, revealed a distance effect mainly in right fronto-parietal regions. A similar asymmetry between hemispheres was reported by Piazza et al. (2007), who found a smaller distance effect in left IPS when the adaptation was to symbolic stimuli and the deviants were non-symbolic stimuli (see also: Ansari, 2007; Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007; Cohen Kadosh, Cohen Kadosh, Schuhmann, et al., 2007; Piazza, Mechelli, Price, & Butterworth, 2006; Piazza, Pinel, Le Bihan, & Dehaene, 2007). Ansari (2007) suggested that the left IPS is specialized for symbolic representations of quantity. In line with this view, Piazza et al. (2006) demonstrated that processing approximate numerosity correlates with increased activity of a right lateralized fronto-parietal cortical network, while exact counting correlates with additional left regions. Since it is reasonable to assume that, in the present study, the brief presentation of adaptation and deviant stimuli alike gave rise only to approximation of numerosity, the asymmetry found in the present study further supports the conclusions of Ansari (2007) and Piazza et al. (2006). It is important to note, however, that although not significant at the group level brain analysis, a distance effect was observed in the voxels selected from the left parietal regions according to their adaptation response. Thus, the lack of group level significance might indicate larger individual variability in the location of the distance effect in left regions, compared with right regions. The overlap between distance-sensitive and adaptation-sensitive voxels in the group level once again confirmed the claim that the two analyses are associated: about a third of the voxels in right parietal and frontal regions that were adapted to the sums also overlapped with those that showed sensitivity to the distance of a non-symbolic quantity of dots from the adapted sum.

The distance-sensitive result was found, to a lesser extent, in the voxels that were selected according to their adaptation function in frontal and cerebellar regions. Frontal regions were also reported to exhibit a distance effect in the study by Piazza et al. (2007), where shifts between notations were introduced. The authors suggested that the frontal sensitivity was a result of awareness to distance that was reached due to the large distance from the adapted number that was easily noticed. The finding of frontal number-sensitive regions is also consistent with Nieder and Miller's (2004) report on monkey's processing of numbers. According to their report, neurons in both parietal and frontal areas are sensitive to the distance of the presented number from the preferred number of the neurons, but the parietal activity is earlier than the frontal activity. Nieder and Miller concluded that signals from the parietal regions feed forward to frontal regions. Frontal sensitivity to distance in the present study is interesting, given that the deviants were highly distinguished from adaptation stimuli in their notation. One could expect that high awareness of the deviants' different notation might overshadow the fine variability between deviants (i.e., the distance of number of dots from the adapted sum). The distance effect found in right frontal regions suggests that participants might have been, at least to some extent, aware of the relation of the deviants to the sums. This awareness could have been a consequence of behavioral tests, which were given to participants on the day previous to the scan. Two tests included deciding whether a presented number was larger or smaller than a standard number. One task involved symbolic numerals (double-digit numbers) and the other involved non-symbolic arrays of dots. These tests could have raised awareness to the relation between standard adaptation stimuli and deviants in the adaptation task.

No previous study has reported the cerebellar nodule to be involved in number-related or calculation-related tasks (Arsalidou & Taylor, 2011), possibly due to poor anatomical coverage of this brain region. The role of the cerebellum in these tasks should be further examined.

Another aspect of the present study is the use of double-digit numbers for the sums as well as for the addends in the addition expressions. The lack of explicit instructions to calculate the sum of the addition expressions, together with the very short presentation time of the complex expressions, suggest that any calculation that took place was not entirely intentional. There is some evidence for the automatic calculation of sums, as long as the addends are single-digits numbers. For instance, the automatic addition effect (Lefevre, Bisanz, & Mrkonjic, 1988) and the associative effect (Winkelman & Schmidt, 1974) are assumed to be the result of automatic retrieval of "math facts" for single-digit problems. However, no automatic retrieval is expected for expressions involving double-digit numbers given that these participants did not have stored facts for these expressions. With no memory traces to rely on and given adequate time, sums at the ranges of 30s and 50s could be precisely calculated either by means of retrieving math facts of the tens and units of the addition expression, or by calculating the sums using some kind of an algorithm. However, in the present study, each addition expression was presented for 300 ms, which is a very short time for either strategy. With not enough time to use a deliberate strategy, and no memory traces to be retrieved, we suggest that the sums in the present study were calculated automatically by means of estimation.

Estimation has been specifically associated with the IPS and more generally with the fronto-parietal network (Dehaene et al., 1999; Stanescu-Cosson et al., 2000), which is the network said to process numbers meaningfully and is also the network that showed adaptation in the present study. Delazer et al. (2003), and Ischebeck et al. (2007, 2006) showed that when solving untrained arithmetic problems, the fronto-parietal network was activated, and that following training of new or complex arithmetic procedures, a training-related shift was observed from IPS and frontal regions to the left angular gyrus (Delazer et al., 2003; Ischebeck et al., 2007, 2006), which is a region associated with math fact retrieval (Dehaene, 1992). In the present study, the repetition of addition expressions was minimized to avoid the formation of memory traces. It is important to note that in the current study, the angular gyrus was found to be sensitive to neither the adaptation (measured as linear decrease during the first 50 s of the block) nor to the distance of deviants from the adapted sum. The lack of sensitivity of the angular gyrus provides support for the claim that adaptation was to the product of an estimation calculation and not to stored facts that might have been used to solve it.

Our findings add to the converging evidence showing that fluency in math cannot be attributed to fast and efficient retrieval of math facts stored in long-term memory in every condition. Correlations between math and arithmetic abilities and the quality of analogic numerical representation have been shown in past studies (Duncan et al., 2007; Halberda, et al., 2008; Jordan et al., 2010, 2009; Locuniak & Jordan, 2008; Peters, et al., 2008; Wilson et al., 2006). We now show a direct link between calculation and analogic representation of quantity, by demonstrating that the spontaneous calculation of double-digit arithmetic expressions activates abstract analogic representations of quantity.

To summarize, the present study shows that mere presentation of addition expressions can drive adaptation to the sums of the expressions. This finding illustrates that internally generated sums behave similarly to external stimuli, such as visual displays of Arabic numerals and dot quantities, as in Piazza et al. (2007). The fact that adapted regions were sensitive to the distance of dots stimuli from the adapted sum suggests that the generated sum corresponded to the analogic approximate representation of the sum's quantity. Finally, the conditions applied in the study (brief presentation, double-digit number addends, no explicit instructions) suggest that calculation of the sum of two double-digit numbers – at least approximately – can be accomplished spontaneously based on meaningful analogic representations. This conclusion supports the notion that the addition procedure is automatic (Ric & Muller, 2012) and challenges previous conclusions that have emphasized the importance of symbolic fact retrieval, associating automatic calculations (Delazer et al., 2003; Ischebeck et al., 2007, 2006) and fluency in math (Pellegrino & Goldman, 1987; Resnick, 1983; Siegler, 1988) mainly with the process of fact retrieval.

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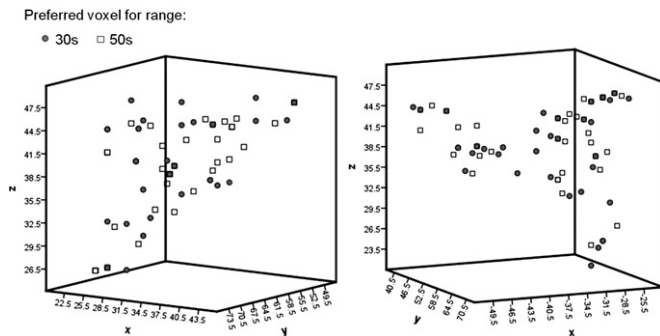


Fig. A.1. Distribution of the spatial location of preferred voxels for 30s (gray circles) and 50s (white squares) in each hemisphere. Each point corresponds to a preferred voxel of one participant. Axes correspond to Talairach coordinates (hence, z is the vertical axis).

Table A.1
Means (standard deviations) coordinates of the preferred voxels for each range in each hemisphere. The voxels were selected for having the largest adaptation effect within the parietal clusters identified in the group analysis (see Table 2, Fig. 1 in the main text, Section 3.1). Uncorrected $p = .00005$, minimum number of voxel: 8).

Hemisphere	Range	
	30s	50s
Left	-29(5), -61(7), 39(6)	-31(5), -61(7), 39(6)
Right	34(7), -57(9), 39(7)	35(7), -57(9), 41(5)

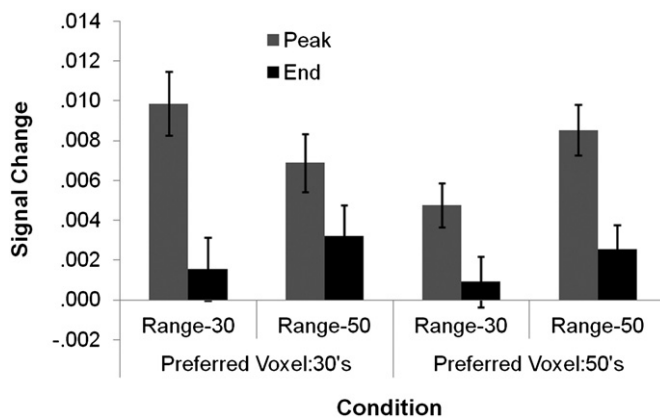


Fig. A.2. Signal change as a function of peak and end of adaptation period according to voxel preference (30s vs. 50s) and the presented range (30s vs. 50s), across hemispheres.

Table B.1
Statistics of ANOVAs conducted on deviant data extracted from the frontal and cerebellar ROIs that exhibited significant adaptation effects in the brain-wise analysis (Table 2). Distance effect is the quadratic function of Ratio. Preferredness effect is the interaction between Preferred Range and Presented Range. Differences in degrees of freedom are due to different number of participants missing a voxel that exhibited an adaptation effect above a threshold of $t = .5$ for one of the two ranges.

Region	Effect	F	df	MSE	p	η_p^2
Right middle frontal gyrus	Distance effect	16.24	1, 32	.23	.000	.34
	Preferredness effect	1.15	1, 32	.24	.29	.04
	Distance \times preferredness	.08	1, 32	.06	.77	.04
Right precentral gyrus	Distance effect	4.72	1, 31	.28	.04	.13
	Preferredness effect	1.76	1, 31	.17	.19	.05
	Distance \times preferredness	1.52	1, 31	.06	.23	.07
Left inferior frontal gyrus	Distance effect	3.63	1, 28	.16	.07	.12
	Preferredness effect	1.08	1, 28	.06	.31	.04
	Distance \times preferredness	1.85	1, 28	.02	.19	.06
Right medial cerebellum	Distance effect	9.53	1, 26	.11	.005	.27
	Preferredness effect	1.76	1, 26	.06	.2	.06
	Distance \times preferredness	3.74	1, 26	.01	.06	.13
Left medial cerebellum	Distance effect	8.59	1, 30	.13	.006	.22
	Preferredness effect	1.77	1, 30	.17	.19	.06
	Distance \times preferredness	.05	1, 30	.04	.82	.002

Appendix A. Investigation of range differences

A.1. Spatial difference between voxels that were adapted for each range

A secondary purpose for using two ranges (30s and 50s) in the stimulus set was to examine a possible difference in the population of neurons that process each range. As can be seen in Fig. A.1, the distributions of preferred voxels for the two ranges largely overlapped. Mean and standard deviation of coordinates for each of the four selected voxels from each individual (left and right hemispheres for each range) are detailed in Table A.1. In order to examine the possibility of a systematic shift of coordinates, two MANOVAs were conducted, one for each hemisphere. The independent variable in each analysis was Range (30s vs. 50s) and the dependent variables were the three coordinate values (x, y, and z). No significant difference was found between ranges ($F < 1$ for both hemispheres), which might be a result of the coarse voxel size used (3.2 mm \times 3 mm \times 3 mm).

A.2. Adaptation differences between voxels that were adapted for each range

In the ANOVA reported in the main text, with Hemisphere, Preferred Range, Presented Range, and Phase as factors, the three-way interaction between Preferred Range, Presented Range, and Phase showed that the Phase effect was slightly larger for the range of 30s in its preferred voxel ($\eta_p^2 = .62$) (leftmost column, Fig. A.2), than it was for the range of 50s in its preferred voxel ($\eta_p^2 = .48$) (rightmost column, Fig. A.2), but this difference was not statistically significant: $F(1, 32) = 2.63$, $MSE = .000$, $p = .12$, $\eta_p^2 = .08$.

Appendix B. Analysis of deviant data extracted from frontal and cerebellar ROIs

Individual voxels were selected for analysis using the adaptation period data from each participant. The analysis included three within-subject variables: Preferred Range (2) \times Presented Range (2) \times Ratio (7). The results for each ROI are detailed in Table B.1.

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