

Transcranial Direct Current Stimulation over the Parietal Cortex Improves Approximate Numerical Averaging

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Abstract

■ The parietal cortex has been implicated in a variety of numerosity and numerical cognition tasks and was proposed to encompass dedicated neural populations that are tuned for analogue magnitudes as well as for symbolic numerals. Nonetheless, it remains unknown whether the parietal cortex plays a role in approximate numerical averaging (rapid, yet coarse computation of numbers' mean)—a process that is fundamental to preference formation and decision-making. To causally investigate the role of the parietal cortex in numerical averaging, we have conducted a transcranial direct current stimulation (tDCS) study, in which participants were presented with rapid sequences of numbers and asked to convey their intuitive estimation of each sequence's average. During the task, the par-

ticipants underwent anodal (excitatory) tDCS (or sham), applied either on a parietal or a frontal region. We found that, although participants exhibit above-chance accuracy in estimating the average of numerical sequences, they did so with higher precision under parietal stimulation. In a second experiment, we have replicated this finding and confirmed that the effect is number-specific rather than domain-general or attentional. We present a neurocomputational model postulating population-coding underlying rapid numerical averaging to account for our findings. According to this model, stimulation of the parietal cortex elevates neural activity in number-tuned dedicated detectors, leading to increase in the system's signal-to-noise level and thus resulting in more precise estimations. ■

INTRODUCTION

Recent neurophysiological and functional brain-imaging research has implicated the parietal cortex in the representation of numerosity stimuli and of numerals, showing that dedicated parietal neural populations are selectively but broadly tuned to these types of information (Harvey, Klein, Petridou, & Dumoulin, 2013; Eger et al., 2009; Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Nieder & Miller, 2003, 2004; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). In addition, a number of noninvasive brain stimulation studies have demonstrated that the parietal cortex plays a causal role in numerical processes, such as magnitude processing and mental arithmetic (Andres, Pelgrims, Michaux, Olivier, & Pesenti, 2011; Cohen Kadosh, Cohen Kadosh, Schuhmann, et al., 2007). Building on these studies, recent transcranial direct current stimulation (tDCS) experiments, in which neural activity of cortical regions or broader networks can be modulated (Rivera Urbina et al., 2015; Nitsche & Paulus, 2000), were able to enhance performance in symbolic numerical tasks, such as the acquisition of new number symbols (Cohen Kadosh, Soskic, Iuculano, Kanai, & Walsh,

2010) and mental arithmetic (Hauser, Rotzer, Grabner, Méryllat, & Jäncke, 2013).

Previous research has also distinguished between two mechanisms in numerical cognition: an analytic one, which is based on symbolic, exact representations, and an intuitive one, which is based on analog and fuzzy representations. For example, Dehaene, Spelke, Pinel, Stanescu, and Tsivkin (1999) have shown that exact numerical tasks exhibit large costs for language switching and for generalization to novel problems, whereas the intuitive ones are language and problem independent (Hyde & Spelke, 2011; Dehaene, Molko, Cohen, & Wilson, 2004; Feigenson, Dehaene, & Spelke, 2004; Pica, Lemer, Izard, & Dehaene, 2004; Stanescu-Cosson et al., 2000; but see Klein, Nuerk, Wood, Knops, & Willmes, 2009; Wood et al., 2008). According to this distinction, approximate numerical tasks are assumed to rely on perceptual-like mechanisms, such as those that operate in statistical estimations of the numerosity or size of visual elements (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Chong & Treisman, 2003; Ariely, 2001), whereas analytic calculations are seen as a product of a symbolic pathway used for the sequential application of arithmetic operations or heuristics (Dehaene, 2011; Rosenberg-Lee, Lovett, & Anderson, 2009; Gigerenzer & Selten, 2002).

Here we focus on a special type of numerical processing, the estimation of numerical averages (Malmi & Samson,

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1983; Levin, 1974; Anderson, 1968; Beach & Swenson, 1966; Spencer, 1961, 1963), which is fundamental for the formation of preferences (Anderson, 1962, 1971, 1981) as well as for making decisions between alternatives characterized by sequences of numerical values (e.g., stocks, probabilistic rewards, job candidates; Tsetsos, Chater, & Usher, 2012; Hertwig & Erev, 2009; Betsch, Plessner, Schwieren, & Gütig, 2001; Bechara, Damasio, Tranel, & Damasio, 1997). In a previous work (Brezis, Bronfman, & Usher, 2015), we have built on the exact/approximate numerical processing distinction and proposed that it plays a critical role in numerical averaging and in implicit preference formation. In particular, we suggested that approximate numerical averaging relies on a different mechanism than exact (analytic) averaging (e.g., calculation of the sum of the numbers and division by the number of elements), with the former relying on a population code, as in perceptual averaging (see also Modeling section below). However, although extensive research has focused on the role of the parietal cortex in symbolic-based arithmetic calculations, little is known with regards to the brain mechanism underlying rapid, non-symbolic-based averaging of numbers, which is an elementary facet of numerical cognition (Malmi & Samson, 1983; Levin, 1974; Anderson, 1968; Beach & Swenson, 1966; Spencer, 1961, 1963).

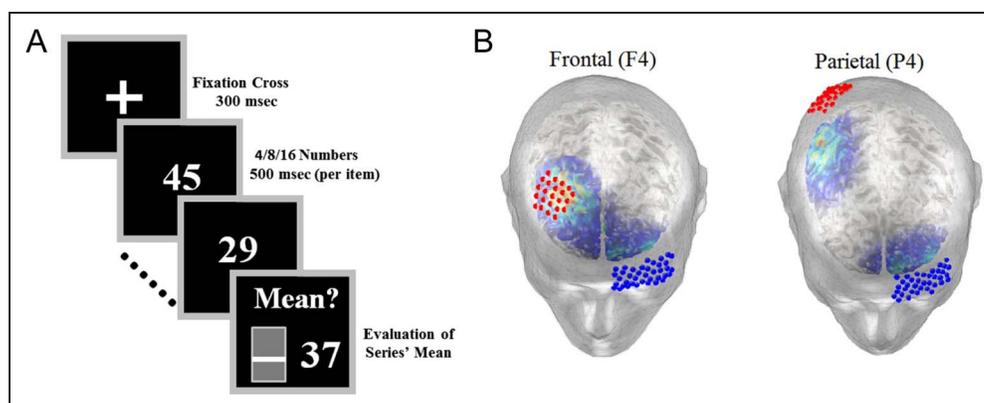
To investigate whether the parietal cortex is causally involved in approximate averaging, we have conducted two within-participant tDCS studies, in which observers were stimulated while being presented with rapid sequences (500 msec per number) of two-digit numbers after which they were requested to convey (using an analog scale) an estimation of the sequences' average (Figure 1A; see also Brezis et al., 2015). In both experiments, each participant attended two experimental sessions: one in which the anodal stimulation was delivered over the right parietal cortex¹ (Piazza et al., 2004; Dehaene, Piazza, Pinel, & Cohen, 2003; Dehaene et al., 1999) and another in which the anodal stimulation was

delivered over the right frontal cortex (order of sessions was counterbalanced; in both sessions, the cathode was placed over the contralateral supraorbital area; see Figure 1B).

We chose to stimulate the frontal cortex, because it has been repeatedly implicated in domain-general cognitive abilities, such as working memory and attention (Fregni et al., 2005; McCarthy et al., 1994), fluid intelligence (Duncan, Burgess, & Emslie, 1995), cognitive control (Gladwin, den Uyl, Fregni, & Wiers, 2012; MacDonald, Cohen, Stenger, & Carter, 2000), and task monitoring (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004), discussed and reviewed in Kane and Engle (2002), and hence served as a stringent control region. Any relative improvement in the precision of estimations observed under the parietal stimulation condition is thus likely to reflect a domain-specific effect rather than general cognitive facilitation. In Experiment 2, we have included an additional, nonnumeric, control task of sustained attention, comprising the detection of a target during rapid visual serial presentation (RSVP). Hence, Experiment 2 allowed us to further verify whether the stimulation effect is number-specific or general (i.e., attentional).

To anticipate our results, we find that anodal stimulation of the right parietal cortex (as compared with frontal or sham stimulations) improves the precision with which humans estimate averages of rapidly presented numerical sequences. Moreover, we find that this effect is not due to general, attentional, improvement, but rather that it is number-specific. To account for the observed tDCS-induced improvement in approximate numerical averaging, we present a model that is based on population coding of broadly tuned numerosity detectors. According to the model, by exciting cells' membrane, direct current stimulation leads to an increase in neurons' response function, which in turn elevates the population signal-to-noise level of numerosity detectors, resulting in improved precision of average estimations.

Figure 1. Experimental method and tDCS montage. (A) Schematic illustration of an experimental trial: Each trial began with a 300-msec fixation cross, after which a sequence of two-digit numbers was presented (500 msec per numeral; 4, 8, or 16 numbers). Following the sequence, participants were asked to convey the numbers' average by sliding a "number ruler," indicated by the white bar and its corresponding number between 0 and 100 (here, for illustration, 37). (B) Illustration of the tDCS montage in the experiment: Participants attended two experimental sessions, in which the anode (red patch) was placed either over the right parietal (electrode P4) or the right frontal (electrode F4), whereas on both sessions the cathode (blue patch) was placed over the contralateral supraorbital area (order of sessions counterbalanced; illustration done using Comets toolbox; Jung, Kim, & Im, 2013).



METHODS

Participants

A group of 20 healthy human participants (13 women) were tested in Experiment 1 (age range = 20–35 years, mean = 25 years), and a different group of 12 participants (6 women) were tested in Experiment 2 (age range = 21–30 years, mean = 26 years). A subgroup of 12 participants who participated in Experiment 1 or Experiment 2 were tested in a control sham condition (Experiment 3). All participants were students naive to the purpose of the experiment, were right-handed, and had normal or corrected-to-normal vision. Participants were recruited through the Bar Ilan University Psychology Department's participant pool; informed consent was obtained from all participants. Participants were awarded either course credit or a financial compensation (100 NIS; equivalent to about \$25) for their participation. All procedures and experimental protocols were approved by the local ethics committee. The experiment was carried out in accordance with the approved guidelines and in strict adherence to the Declaration of Helsinki.

Experiment 1

Stimulus Materials

The basic setup of a trial is depicted in Figure 1A. Each trial began with a central fixation cross (300 msec) after which a sequence of two-digit numbers was presented (white Arabic numerals on black background; each number was displayed for 500 msec). The numbers ranged between 10 and 90 and were sampled from four predefined triangular distributions (see also Brezis et al., 2015). The sequence set size (i.e., the quantity of presented numbers) was 4, 8, or 16 and was randomized between trials. Participants were asked to convey as accurately as possible the sequence's average by vertically sliding a mouse-controlled bar set on a number ruler between 0 and 100 and pressing the left mouse button when reaching the desired number (Figure 1A; the number corresponding to the bar's location was concurrently displayed). No RT limitation was applied. All stimuli were generated using Matlab Psychtoolbox (Brainard, 1997) and were presented on a gamma-corrected ViewSonic (Walnut, CA) 17-in. monitor viewed at a distance of 41 cm. The screen resolution was set to 1024 × 768 pixels, and the monitor had a refresh rate of 60 Hz.

tDCS Protocol

Direct current of 1 mA was transferred by a saline-soaked pair of surface sponge electrodes (anode 3 × 3 cm; cathode 3 × 5 cm) and delivered by a constant current stimulator (Neuroconn, Ilmenau, Germany). To stimulate the parietal cortex, the anode electrode was placed over the P4 according to the 10–20 international system for EEG electrode placement. To stimulate the frontal cortex, the

anode electrode was placed over F4 according to the 10–20 international system for EEG electrode placement. In both sessions, the cathode was placed over the contralateral supraorbital area.

Procedure

The participants attended two experimental sessions (with 1-week interval between the two sessions). On each session, participants were engaged in the same numerical averaging task, yet a different brain region was stimulated: Half of the participants ($n = 10$) underwent parietal stimulation in the first session and frontal stimulation in the second session, whereas the remaining participants ($n = 10$) underwent the opposite stimulation regime (see Figure 1B). On each session, participants were stimulated for 5 min before the beginning of the experimental trials. During this period, they completed 15 practice trials. Next, participants underwent 204 experimental trials divided into six blocks. Each block terminated with performance feedback (block average correlation) and a short, self-paced break. Each session lasted approximately 45 min. Stimulation was delivered at the beginning of the session for 25 min with additional 30 sec of graded ramping at the beginning and at the end of the stimulation. The numbers presented in frontal/parietal sessions were sampled from the same distributions (described above). The experiment was single blind.

Experiment 2

The aim of the experiment was to replicate the results of the first experiment while also probing for an alternative account, which attributes the results to an attentional effect. Experiment 2 involved two tasks. The first one was identical to Experiment 1 (numerical averaging), with the only exceptions that we included fewer trials in the numerical averaging task (66 trials instead of 204; 22 per each set size condition), to allow sufficient online stimulation time for the additional control task. The second (attentional) task was a target detection with an RSVP sequence of letter pairs, which was added to rule out an attentional account of the previous results (the order of tasks and stimulated regions was counterbalanced between participants and sessions). In the RSVP task (overall 180 trials, divided into six blocks), participants were presented with rapid sequence of two-letter stimuli (100 msec per a two-letter item; items were white on a black background; sequences were of 4, 8, or 16 letter pairs, randomized across trials). At the termination of the letter sequence, the participants were asked to indicate, using a keyboard, whether a target letter pair was present within the sequence or whether it was absent ("z" and "m" keys, respectively; target was present on random 50% of trials; the participants received auditory error feedback). A two-letter stimulus (e.g., "RF") appeared at the beginning of each experimental block, indicating the

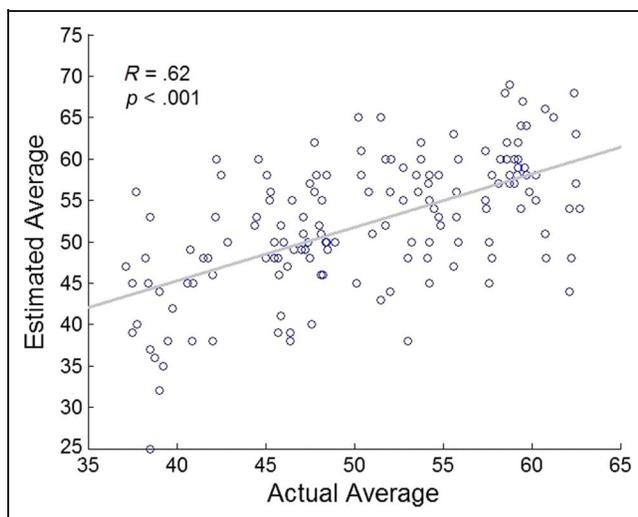


Figure 2. Performance of a typical participant. The scatter plot depicts the participant's evaluations (*y* axis) for each of the presented number sequence averages (*x* axis). Dashed line is the regression line ($r = .62$; mean R for the 20 participants = $.61$).

target for this block (random targets across blocks and participants).

Experiment 3

We have conducted sham stimulation over the parietal region during the numerical averaging task (identical montage and setup as in Experiments 1 and 2, but with only 30 sec of stimulation), for 12 of the participants that participated in Experiment 1 or Experiment 2.

RESULTS

Experiment 1

Behavioral Results

We used two measures to quantify each participant's precision of evaluations: (i) Pearson correlation across trials between the sequence's average and estimations and (ii) root mean square deviation (RMSD) given by

$$\sqrt{\left(\frac{\sum_{i=1}^n (x_i - \mu_i)^2}{n}\right)},$$

where x_i corresponds to the estimated

average of sequence i and μ_i corresponds to that sequence's actual average. Note that lower values of RMSD correspond to higher accuracy.

Overall and despite the rapid presentation and the large quantity of numbers, participants exhibit above-chance sensitivity to the average of the presented numbers: Participants' Pearson correlation across trials between the sequence's average and estimations is moderately high and significantly larger than 0 ($r = .61$, $SD = .11$; $p < .0001$; for all participants; see Figure 2 for a typical participant and Appendix B, for all participants). In addition,

each participant's square deviations between the estimation and the actual average are significantly lower than the square deviations obtained by randomly shuffling the participant's responses across trials and comparing the average square deviations between the actual mean and the shuffled estimations across 500 independent shuffles (Actual = 66.56; $SD = 25.64$; Shuffled = 147.34; 95% CI = ± 1.65 ; $p < .001$, for all participants). Importantly, this sensitivity is observed also specifically for the longest sequence length (16 items) in term of both correlation ($r = .65$, $SD = .11$; $p < .05$; for all participants) and square deviations (Actual = 64.75; Shuffled = 145; $p < .05$, for all participants). We do not find a significant main effect of sequence length on estimation accuracy indicated by RMSD ($F(2, 38) = 1.3$; $p = .28$).

Our main contrast of interest is the difference in accuracy under the two brain region stimulation conditions. We find that both measures of participants' accuracy have increased following parietal stimulation. Specifically, RMSD is lower (i.e., evaluations are more accurate) (parietal = 7.66; frontal = 8.34; $t(19) = 2.54$; $p = .02$; $\eta^2 = 0.038$; Figure 3A), and the correlation is higher under parietal stimulation as compared with frontal stimulation (parietal = 0.63; frontal = 0.58; $t(19) = -2.56$; $p = .019$; $\eta^2 = 0.045$; see Figure 3B). Moreover, we find a numerical improvement at the individual level in $\sim 70\%$ of participants (14/20 in RMSD; 15/20 in correlation; see Figure A.1). We found no significant interaction of Brain region with Set size (repeated-measures ANOVA; $F(2, 38) = 2.32$; $p = .11$) and no significant effect of Stimulation region on RTs (parietal = 7.3; $SD = 2.74$; frontal = 6.52; $SD = 3.94$; $t(19) = 1.44$; $p = .17$). A further analysis of brain region effect, with RT as covariate, shows that the effect is independent of RT ($t(19) = 2.54$; $p = .02$; $\eta^2 = 0.045$). These results thus suggest that tDCS over the parietal cortex results in more accurate numerical averaging as compared with control.

Finally, we examined the extent to which the effect of the tDCS continues once the stimulation is terminated (also referred to as offline or aftereffect). Because the tDCS was delivered only during the first 25 min of each experimental session (see Methods), we were able to test the difference between online and offline stimulation ($\sim 80\%$ and $\sim 20\%$ of trials, respectively) by measuring the precision of the estimations during and following tDCS delivery in each session.² As shown in Figure 4, we find a significant Online/offline region interaction (repeated-measures ANOVA: $F(1, 19) = 4.49$; $p = .047$; $\eta^2 = 0.012$). Post hoc comparisons reveal that under frontal stimulation there is no difference in accuracy during and following the stimulation (first = 8.31; second = 8.43; $t(19) = -0.37$; $p = .72$), whereas under parietal stimulation, estimations made during tDCS delivery are more accurate than offline estimations (first = 7.42; second = 8.43; $t(19) = -2.11$; $p = .049$; $\eta^2 = 0.056$). This suggests that the precision of estimations of numerical averages increases only during the online delivery of tDCS over the parietal cortex (i.e., we find no aftereffect, which may depend upon task and

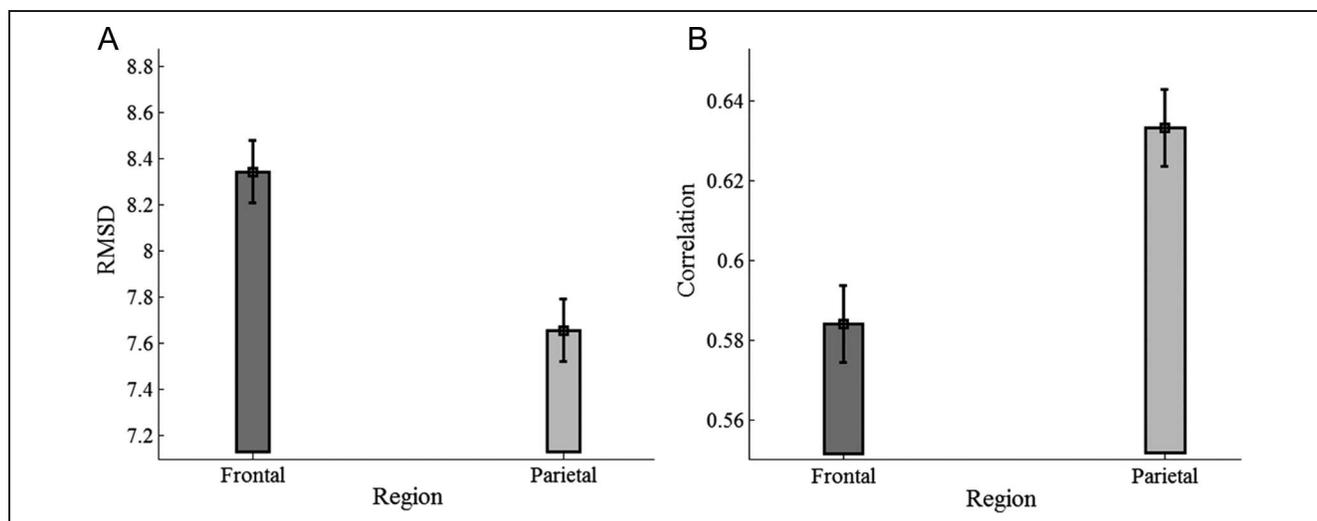


Figure 3. Accuracy in rapid numerical averaging under frontal and parietal tDCS (Experiment 1; $n = 20$). (A) The participants' RMSD is lower (evaluations are more precise) under parietal stimulation. (B) The participants' correlation (Pearson's r) is higher under parietal stimulation. Error bars denote within-participant 95% confidence interval (Loftus & Masson, 1994). Data are based on all sequence duration conditions.

stimulation intensity and duration; see also Stagg et al., 2011; Nitsche & Paulus, 2000). Moreover, performance remained unchanged during tDCS over the frontal cortex, thus supporting the conjecture that the effect is caused by a parietal enhancement rather than by a frontal decrement.

Discussion of Experiment 1

We have observed that during online anodal stimulation of the right parietal cortex, rapid approximate numerical averaging was more accurate than under offline stimulation or under both online and offline frontal stimulation. Although this effect suggests that the parietal cortex plays a causal role in the averaging task, as the parietal cortex has also been suggested to be involved in attentional processes (reviewed in Behrmann, Geng, & Shomstein, 2004), it is also possible that our results are due to general attentional enhancement rather than being number-specific. This is because, although our task did not require spatial attention (all numbers were presented at the same location), it did require sustained temporal attention. If the effect of the parietal cortex stimulation reflects solely sustained attention, exceeding that of frontal stimulation, one would predict that it would enhance performance in a sustained attention task, compared with frontal stimulation. Contrariwise, if the parietal effect is number-specific (in addition to a potentially attentional one), we should predict that, in a sustained attention task without numerical processing, there will be no difference in performance between the frontal and parietal stimulation conditions or that there will be a reverse effect, namely that performance will be better under frontal stimulation.

To investigate whether the improved numerical averaging is due to number-specific effect or to an attentional facilitation solely, we have conducted a second experiment (Experiment 2), in which participants were en-

gaged in two tasks only during online stimulation (the order of the tasks was counterbalanced between participants). One task was identical to the averaging task in Experiment 1, and the other task involved an RSVP detection task without numerical stimuli, which included a component of sustained attention to a series of rapidly presented (nonnumerical) items.

Experiment 2

Numerical Averaging

As in Experiment 1, we find that parietal stimulation enhances the participants' accuracy. As shown in Figure 5,

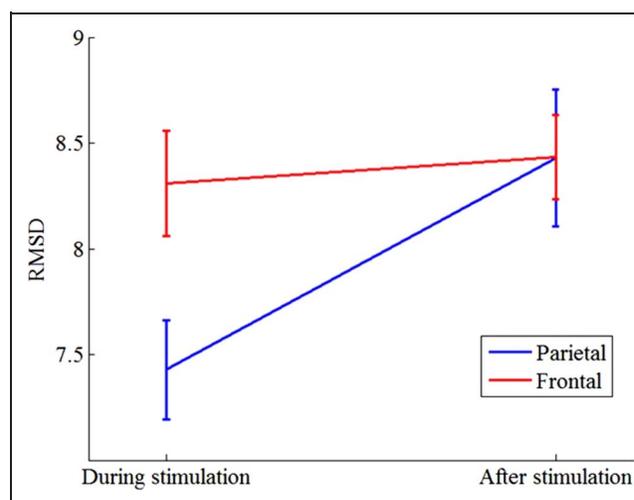


Figure 4. Temporal effects of the tDCS (Experiment 1). Only during the delivery of tDCS over the parietal cortex was numerical averaging enhanced (blue line). The participants' performance during online and offline frontal stimulation remained unchanged. Error bars denote within-participant 95% confidence interval (Loftus & Masson, 1994).

RMSD is lower (parietal = 8.62; frontal = 10.42; $t(11) = 2.24$; $p = .047$; $\eta^2 = 0.091$) and the correlation is higher under parietal stimulation as compared with frontal stimulation (parietal = 0.58; frontal = 0.48; $t(11) = -2.85$; $p = .016$; $\eta^2 = 0.106$). Moreover, we find a numerical improvement at the individual level in $\sim 80\%$ of the participants (10/12 in RMSD; 9/12 in correlation). RTs did not differ between stimulation conditions ($t(11) = 1.22$; $p = .25$), yet were numerically faster under parietal stimulation (parietal = 4.32 sec; frontal = 4.7 sec), indicating that the improvement in accuracy did not stem from RT–accuracy tradeoff. Furthermore, we find no interaction of Brain region with Set size (repeated-measures ANOVA; $F(2, 22) = 1.16$; $p = .33$). Thus, we have replicated the results of Experiment 1, showing that parietal stimulation enhances the accuracy of rapid numerical averaging.

Sustained-attention RSVP

Our second variable of interest in this task was the target detection accuracy of the participants under either frontal or parietal stimulation. As hypothesized, we find that overall detection accuracy did not differ between the stimulation regions (frontal = 67%; parietal = 66.6%; $t(11) = 0.4$; $p = .7$). Furthermore, detection accuracy did not differ between the regions for all three set sizes (frontal_4 = 72%; parietal_4 = 70%; frontal_8 = 68%; parietal_8 = 68%; frontal_16 = 62%; parietal_16 = 61%). To ensure that the difficulty level in the RSVP task was comparable to that of the numerical averaging task, we have computed an estimation of binary accuracy in the numerical task (in which responses are continuous). We did so by transforming the actual averages and the evaluations to a binary index with respect to the global average—of 50—in the experiment. Thus, when the sequence’s actual mean was lower than 50 it was coded as 0 whereas when it was higher than 50 it was coded as 1, and the same coding

was applied to the evaluations. Indeed, detection accuracy in the RSVP task ($\sim 70\%$) was numerically identical to accuracy in the numerical averaging task ($\sim 70\%$), thus indicating that task difficulty was similar between the two tasks.

Discussion of Experiment 2

The results of Experiment 2 replicate the enhanced numerical averaging performance under parietal compared with frontal stimulation. Moreover, they show that no parallel enhancement in a sustained attention task takes place for parietal compared with frontal stimulation, indicating that the enhancement of numerical averaging under parietal stimulation does not stem solely from attentional or executive enhancement, but rather from a number-specific effect. We discuss these results in more detail in the General Discussion. One issue that requires consideration is the fact that, in both experiments, the control region was a frontal area. Although we selected this region to obtain a more strict control (as the frontal cortex is implicated in attentional and executive functions), it is important to assess whether the results are due to parietal improvements or to frontal-induced deterioration. Although the online–offline interaction we observed in Experiment 1 is not consistent with the latter, we have nonetheless conducted an additional experimental sham stimulation session to further validate our results. To do so in a within-participant manner, we have contacted 12 of the participants who participated in Experiment 1 or Experiment 2 and invited them for an additional (sham) session. On the basis of our online–offline results in Experiment 1 (Figure 4), we predict that the accuracy of the numerical estimations will not differ between sham and frontal conditions, whereas estimations made under parietal stimulation will be more accurate.

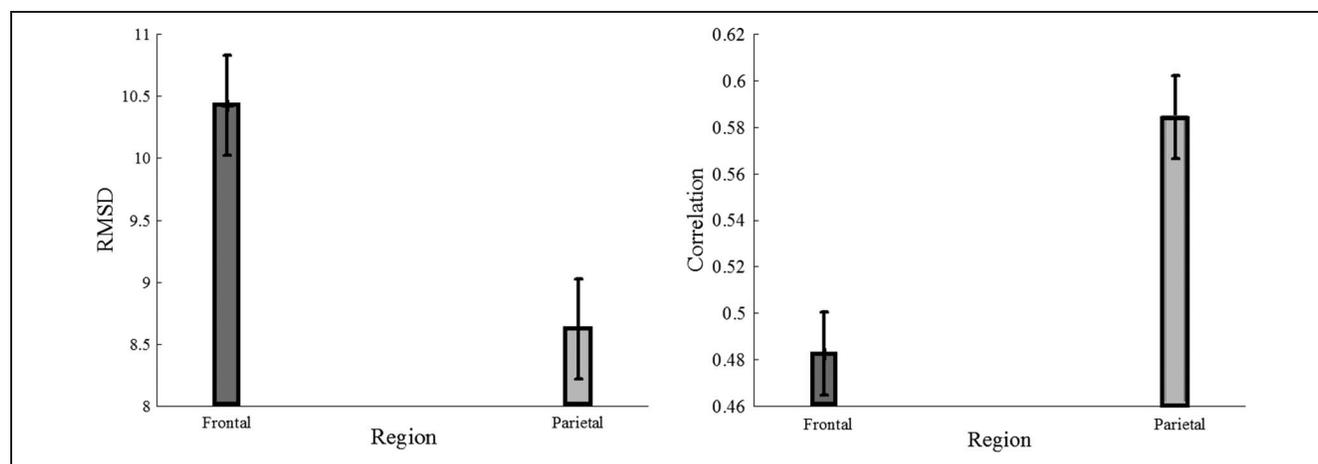


Figure 5. Accuracy in rapid numerical averaging under frontal and parietal tDCS (Experiment 2; $n = 12$). (Left) The participants’ RMSD is lower (evaluations are more precise) under parietal stimulation. (Right) The participants’ correlation (Pearson’s r) is higher under parietal stimulation. Error bars denote within-participant 95% confidence interval (Loftus & Masson, 1994). Data are based on all sequence duration conditions.

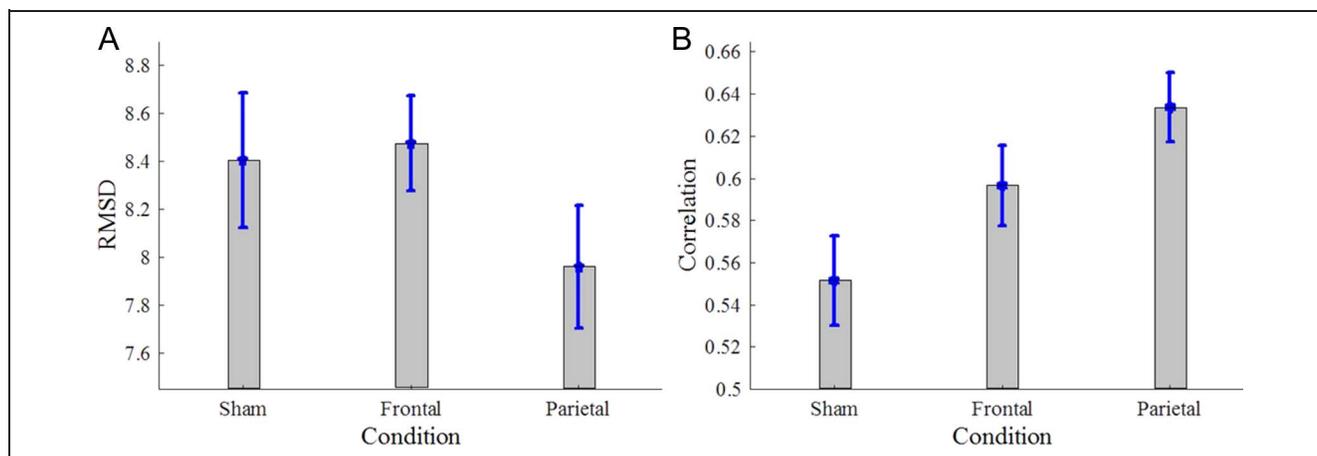


Figure 6. Accuracy in sham, frontal, and parietal stimulation (within-participant results; $n = 12$). Error bars denote within-participant 95% confidence interval (Loftus & Masson, 1994).

Experiment 3: Sham Control

As we predicted and as shown in Figure 6, we find that under sham stimulation correlation was lower than under parietal stimulation (sham = 0.55; parietal = 0.63; $t(11) = 2.52$; $p = .02$; $\eta^2 = 0.11$, two-tailed t test). Similarly, RMSD was higher (less accurate) under sham than under parietal stimulation, although this effect was not significant (sham = 8.4; parietal = 7.96; $t(11) = 0.88$; $p = .39$). No significant difference between sham and frontal performance is found for both measures ($p > .25$, for RMSD and correlation). These results suggest that parietal stimulation indeed enhances numerical averaging as compared with baseline.

Discussion of Experiment 3

The results of the sham session indicate that the effects we obtained in Experiments 1 and 2 are due to a parietal improvement, rather than to a frontal deterioration. Note that the reduction in the performance that participants obtained in the sham session takes place despite potential practice effects (the sham session was always the third, whereas the parietal session was either first or second; sessions were conducted separately so there was no fatigue effect).

Our final aim is to provide a neural mechanism for numerical averaging based on parietal detectors broadly tuned for numerosity and to show that it can account for the tDCS effect.

Neurocomputational Model and Fitting Results

Although the mechanism underlying rapid numerical averaging remains largely unknown, it has been recently hypothesized that approximate averaging relies on lower-level processes of summary statistics extraction (Brezis et al., 2015; Dotan, Friedmann, & Dehaene, 2014; Van Opstal, de Lange, & Dehaene, 2011; Verguts & Fias, 2004; Dehaene, 2001), whereby upon exposure to a multitude of continuous features (e.g., spatial-orientation, circle-diameter)

observers exhibit high sensitivity to the average of the ensemble (Alvarez & Oliva, 2008; Chong & Treisman, 2003; Ariely, 2001). Thus, according to this hypothesis, sensitivity to summary statistics arises as a result of a process where the activation of dedicated feature-tuned neural populations is pooled together and the centroid of this activation profile, representing the features' average, is extracted (Pouget, Dayan, & Zemel, 2003; Georgopoulos, Schwartz, & Kettner, 1986). Building on previous neurocomputational studies (Brezis et al., 2015), we suggest that such a population-coding model can account for the observed increase in precision of the numerical averages estimations under parietal stimulation. Below, we describe the model and show its account of the behavioral data.

Population-coding Model

The model assumes that each number (10–90) activates a distinct Gaussian distribution over a layer of broadly tuned numerosity detectors (Figure 7A). Upon the presentation of a number, each unit/neuron responds probabilistically by triggering a number of spikes that is sampled from a Poisson distribution with a mean, λ , determined by the corresponding numerical tuning curve (Figure 7B). Each successive number presented triggers an additional, accumulated probabilistic neural activation. The output of this population code is obtained via a weighted average (center of gravity) as described in Equation 1. In addition, the model assumes a nondecision, late noise—a stochastically independent internal noise sampled from a normal distribution (with mean 0 and variance σ^2), which reflects the general noise associated with the decoding process and motor noise (Solomon, Morgan, & Chubb, 2011). We label this late noise and distinguish it from the encoding noise.

$$\text{Perceived Mean} = \left(\sum F_i \times T_i \right) / \sum F_i \quad (1)$$

where, for each neuron i , F = firing rate and T = preferred number.

We assume that anodal tDCS depolarizes the stimulated cells' membrane potential, thus effectively lowering their firing threshold (Nitsche & Paulus, 2000; reviewed in Bestmann, de Berker, & Bonaiuto, 2015). This change in excitability in turn increases the input–output response function of the units in the network, which is reflected by enhanced response to the same input (Figure 8A; dashed curves as compared with solid curves; see Appendix for a demonstration that lowering the threshold results effectively in a multiplicative change of the tuning curve). The increase of the tuning curves predicts that the network's sensitivity/discrimination is enhanced (Ma, Beck, Latham, & Pouget, 2006). We illustrate the assumed effect of stimulation in Figure 8. In Figure 8B, we show a typical response profile of the network's units triggered by the presentation of a single number (100). The blue profile corresponds to the baseline network, and the red profile to the stimulated network (i.e., a network whose overall activation level is increased by a factor of 3). The profiles are noisy because each unit responds probabilistically according to a Poisson statistics with a mean firing rate λ —proportional to the tuning curve depicted in Figure 8A. However, the level of signal-to-noise differs between the two networks: The higher-in-activity network (red) is less noisy; in Figure 8C, we show the histogram of the network's most active unit (representing the network outcome) upon 10,000 independent presentations of a certain number (e.g., 100). We show this histogram both for baseline (blue bars) and the stimulated network (red bars). As shown, the model's responses were closer to the actual input (i.e., 100) under the stimulated condition, as compared with baseline. Thus, although the absolute level of the noise has increased with activation, the signal-to-noise has decreased. This is a result of Poisson statistics, whereby the signal increases with n (the amount of samples), yet noise (std of the cells' firing rate) only with the square root of n .

Data Fitting

To test our hypothesis, we fitted the two parameters of the model (λ , the mean firing rate which is inversely re-

lated to encoding noise, and σ , the late noise) to the participants' evaluations and obtained estimations of the best-fitting parameters. We fitted data from Experiment 1 and only the 8- and 16-number conditions because of the possibility that in the 4-number condition participants employ an analytic strategy in calculating the average (Brezis et al., 2015). Because the analytic process is more complex (e.g., involving reliance on working-memory), we have excluded it from the model. In addition, because the difference between the frontal and parietal conditions is obtained only during online tDCS delivery (see Figure 4), we fitted only these online trials. We generated 1000 simulations of each actual trial for a given set of parameters. Thus, we obtained the density distribution of the model's estimations. Using the density distribution, we assigned likelihood for the observed evaluation for each trial. The likelihood for the entire data was calculated by multiplying the likelihood for the separate trials. Finally, parameters were estimated by maximizing the likelihood term using a grid search over λ and σ .

We find that the mean firing rate (λ) increased under parietal stimulation as compared with frontal stimulation ($\lambda_{\text{frontal}} = 45$; $\lambda_{\text{parietal}} = 95$), whereas the general decoding noise did not change ($\sigma_{\text{frontal}} = 7$; $\sigma_{\text{parietal}} = 7$; $\text{Max_Likelihood_frontal} = -3,494$; $\text{Max_Likelihood_parietal} = -3,441$). This suggests that, as expected, tDCS over the right parietal had decreased the encoding noise (i.e., had increased signal-to-noise level of the individual item) but did not reduce late (general or motor) noise.

We used these parameters to assess the model's predictions for the RMSDs in the 8- and 16-number conditions (generalizability criterion; Ahn, Busemeyer, Wagenmakers, & Stout, 2008; Busemeyer & Wang, 2000). Figure 9 shows these predictions. Note that the model predicts that accuracy will improve with set size and that this improvement should be proportional to the level of the intrinsic noise at the individual number (i.e., lower values of λ predict steeper improvement). Conversely, general noise should not influence changes in accuracy with set size. This is because only noise at the single-item level averages out with each additional sample (see also Brezis et al.,

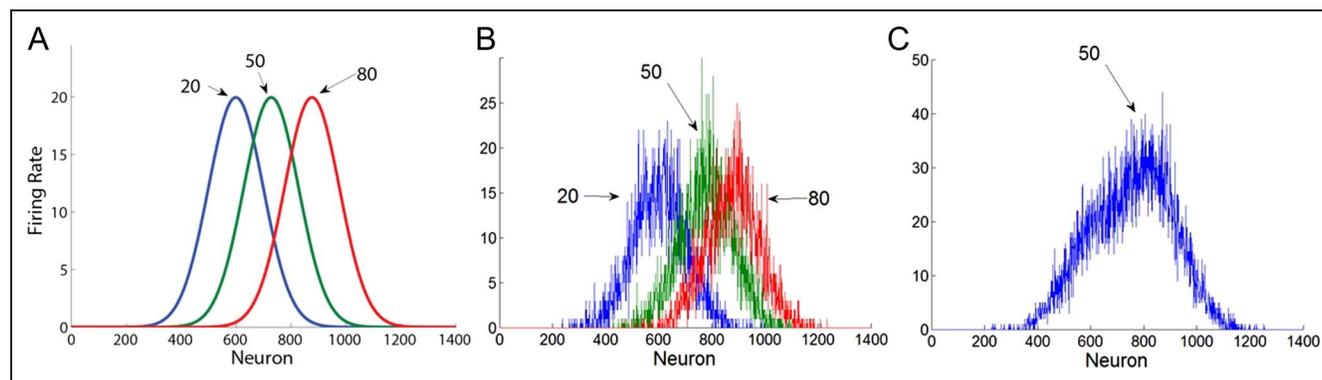


Figure 7. The neuronal population-coding model. (A) Numerosity tuned neural detectors. (B) Presented numbers activate noisy neural detectors (superimposed). (C) The activation profile of the weighting units summing each neuron's firing rate; the center-of-mass unit represents the perceived numerical average. Reproduced from Brezis et al. (2015).

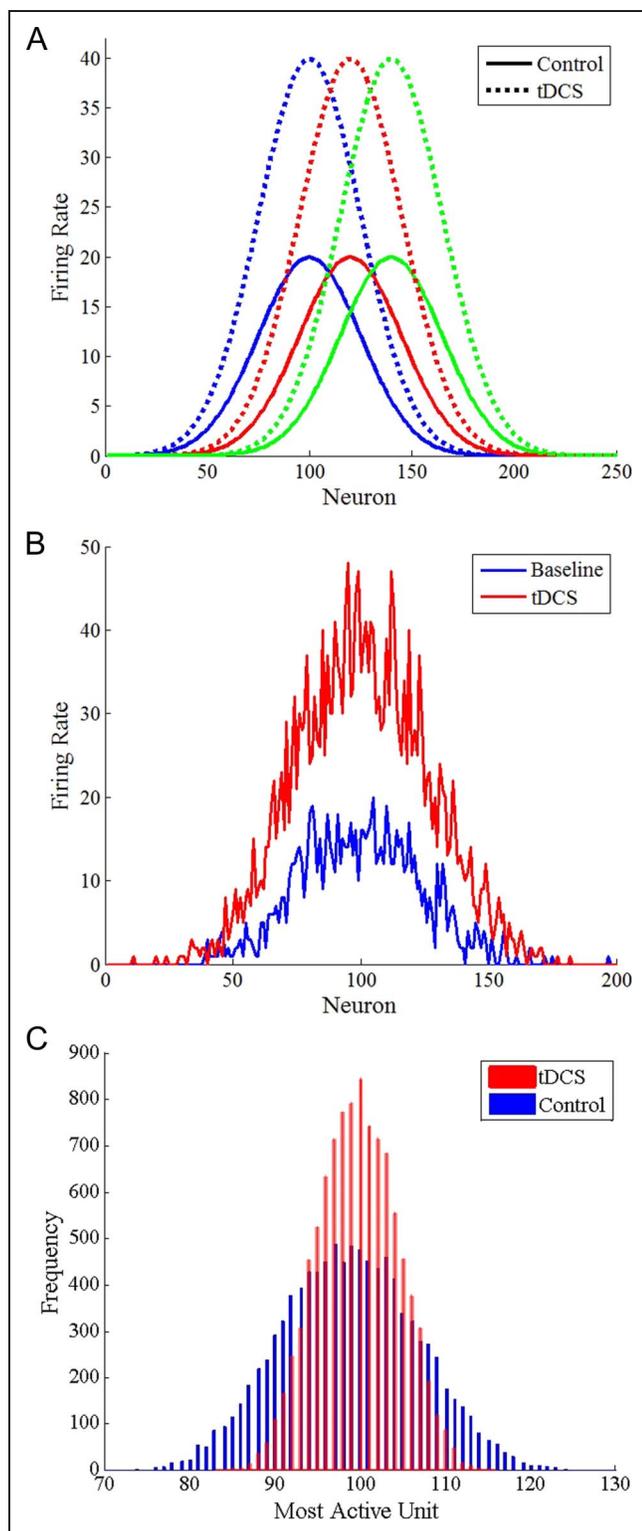


Figure 8. Proposed mechanism underlying the tDCS-induced enhancement of rapid numerical averaging. (A) According to the population vector model, numerical averaging results from pooling together population activity, determined by the neuronal tuning curves (solid Gaussian curves). We suggest that anodal tDCS over the parietal cortex excites these cell assemblies, hence increasing their activation levels (dashed curves). (B) Representative examples of a typical response profile of the baseline (blue) and stimulated (red) networks. (C) The overall increase in activity renders the network's responses

2015). Importantly, this qualitative prediction is observed in the data, suggesting that the difference between frontal and parietal stimulation stems from changes in single-item noise (λ), rather than in general noise that is independent of the underlying samples (σ).

GENERAL DISCUSSION

In three within-participant experiments, we have demonstrated that tDCS over the right parietal cortex improves the precision of participants' intuitive numerical averaging. We found that, under parietal stimulation, average estimations of rapid sequences of two-digit numbers both correlated more with the actual means and were less deviant as compared with frontal stimulation (Figure 3A, B). Moreover, we found that this effect was specific to online stimulation—upon the termination of the tDCS delivery, performance in the parietal and frontal conditions did not differ (Figure 4). Finally, we find that, under sham stimulation, performance is worse than under parietal stimulation. Thus, our results causally implicate the parietal cortex in approximate/intuitive numerical cognition (Dehaene, 2011) and specifically in intuitive averaging (Brezis et al., 2015), which is fundamental to decisions made between alternatives characterized by sequences of numerical values (Tsetsos et al., 2012; Hertwig & Erev, 2009; Betsch et al., 2001; Bechara et al., 1997). Our results are also consistent with previous findings showing a distinct functional role for the parietal cortex in numerical processing (Harvey et al., 2013; Cohen Kadosh, Cohen Kadosh, Kaas, et al., 2007; Cohen Kadosh, Cohen Kadosh, Schuhmann, et al., 2007; Piazza et al., 2004, 2007; Nieder & Miller, 2003). Although we chose to stimulate the right parietal region, we predict that similar results will be obtained under left parietal stimulation; however, this contrast remains an important topic for future research.

Although the parietal cortex has been implicated in numerical processing, it has been also associated with various attentional and executive control functions, which include components of spatial shifts of attention (e.g., Bolognini, Fregni, Casati, Olgiati, & Vallar, 2010; Bolognini, Olgiati, Rossetti, & Maravita, 2010), selection processes (e.g., Weiss & Lavidor, 2012), and working memory capacity (Heimrath, Sandmann, Becke, Müller, & Zaehle, 2012; Tseng et al., 2012). Although it is not likely that participants had relied on working memory in the task, in particular at longer sequence durations, at which working memory capacity would severely degrade performance (see Brezis

more sensitive. We illustrate this by presenting the network with a certain number (100) for 10,000 times and plotting the histogram of the most active unit on each presentation. As can be seen, the networks response profile is sharper when its overall activity is increased (red bars) as compared with baseline (blue bars). Thus, tDCS increases the network's overall activity results in more precise average estimations.

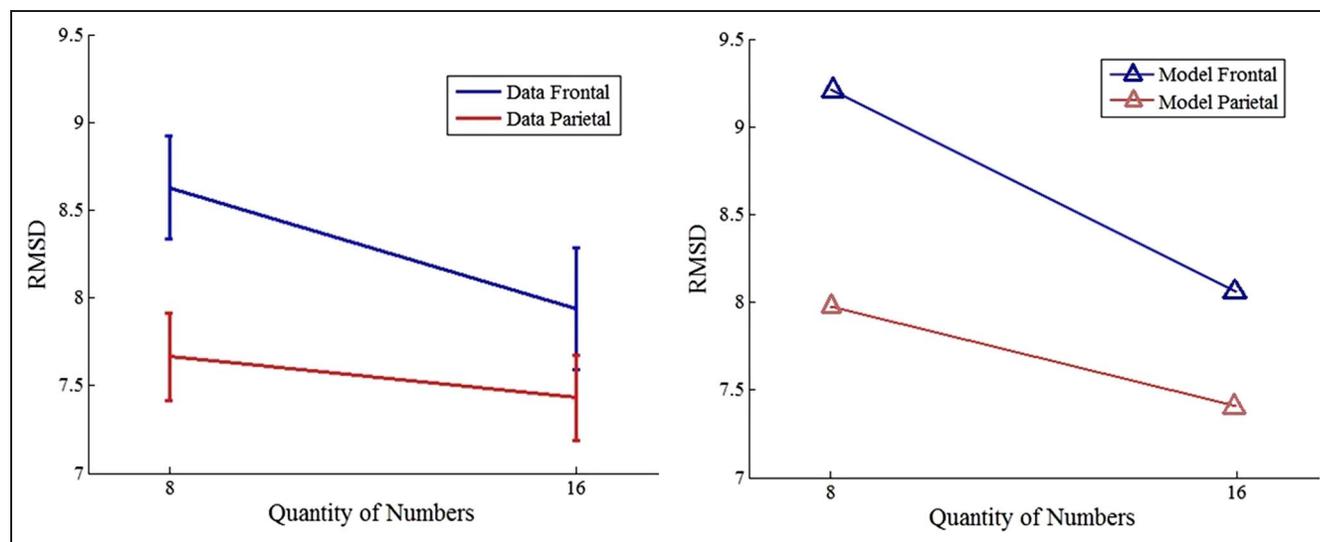


Figure 9. Observed (left) and predicted (right) RMSD in the 8- and 16-number conditions during parietal (red) and frontal (blue) tDCS. Model predictions were generated using the best-fitting parameters.

et al., 2015, for a detailed study of this question), it could nonetheless be argued that the enhanced accuracy we observed under parietal stimulation is due solely to enhanced attentional capacities rather than to enhanced numerical precision. Several considerations, however, indicate that this interpretation is unlikely to account for the present results. First, we included a control condition of anodal stimulation of the frontal region, which is implicated in a variety of general-domain functions, such as executive functions, attention and working memory capacities. Therefore, it is expected that possible augmentation of attentional capacities (if any) will not vary substantially between parietal and frontal stimulation. Furthermore, the numerical averaging task that was used in this study did not involve spatial shifts of attention nor did it include distractors of which the participants should have ignored. Rather, the significant general-domain component of this task was a sustained attention component, underlying the ability to maintain processing resources for a relatively prolonged period.

Although sustained attention has been found to improve under frontal stimulation (Nelson, McKinley, Golob, Warm, & Parasuraman, 2014), it was important to specifically test whether parietal stimulation enhances sustained attention more than frontal stimulation. Using a within-subject design in Experiment 2, we showed that the results of Experiment 1 (numerical averaging) were replicated and that, critically, we observed no parallel effect in the RSVP detection task. In particular, we found that RSVP accuracy did not differ between the frontal and parietal conditions (67% and 66.6%, respectively), suggesting that both regions are subject to equal attentional enhancement (if at all) upon stimulation. Thus, this indicates that the enhancement in numerical averaging that was obtained in both Experiments 1 and 2, between the

frontal and parietal conditions, is not likely to stem solely from attentional factors, which, if at all, are of equal magnitude, but rather is number-specific. Our interpretation of the lack of difference between frontal and parietal stimulation is that both regions are equally relevant for the RSVP task. Thus, the observation that in the sustained attention task there was no difference in favor of the parietal condition demonstrates that the enhanced numerical accuracy we report for parietal compared with frontal stimulation is not solely the result of an attentional effect. To quantify precise numerical and attentional contributions, future studies should nonetheless test whether performance in the RSVP task is better under parietal or frontal stimulation than under sham stimulation. One limitation of this study is that the experiments were single blind. Future studies should therefore also determine whether our results replicate under double-blind design.

To explain how tDCS improves numerical averaging, we developed a neurocomputational model that accounts for the stimulation-induced improvement, according to which numerical averaging relies on perceptual-like population coding (Pouget et al., 2003; Georgopoulos et al., 1986). Assuming that tDCS increases the mean response function of number-tuned cells in the parietal cortex (see Appendix), we showed, using simulation studies and model fitting, that changes in firing rate predict an increase in the signal-to-noise level in the individual number representations and not a general reduction in the system's late noise levels. This conclusion is in line with a recent study, showing that tDCS in a numerosity judgment task enhances performance due to the narrowing of the underlying tuning curve (Javadi, Brunec, Walsh, Penny, & Spiers, 2014). Our computational study thus allowed us to bridge between well-established tDCS-induced changes in neuronal excitability and functional

improvement in overt accuracy. Future studies should test whether this bridging principle applies to other domains and to examine in more detail the nature of the number representation system and to extend the model to address them.

Our results predict that the parietal cortex will take part in decisions made between competing alternatives characterized by a multitude of numerical values (e.g., Hertwig & Erev, 2009; Betsch et al., 2001; Bechara et al., 1997; Anderson, 1981) and that delivery of tDCS over the parietal cortex will thus improve performance in these decisions, consistent with the role attributed to the lateral intraparietal area in representing subjective values (which may in turn rely on approximate numerical averaging of a series of values) in neuroeconomic studies (Louie & Glimcher, 2010; Dorris & Glimcher, 2004).

The results have also implications for patients with specific deficits in numerical cognition. A growing body of literature suggests that some forms of developmental dyscalculia involve developmental deficits in representations of numerical magnitudes (Piazza et al., 2010; Landerl, Bevan, & Butterworth, 2004). Although a recent study has shown that tDCS can improve numerical processing in dyscalculia (Iuculano & Kadosh, 2014), future studies should test whether tDCS can also improve intuitive numerical averaging in this population.

Conclusion

We delivered tDCS over either the parietal or the frontal cortex while participants were engaged in rapid averaging of sequences of two-digit numbers. We found that parietal stimulation enhanced the accuracy of the estimations as compared to frontal or sham stimulation and that this effect was specific to online stimulation only. Moreover, we have shown that the stimulation-induced improvement is not due to attentional enhancement but rather is number-specific. These results provide evidence

for the causal involvement of the parietal cortex in approximate numerical averaging, which is fundamental to decision-making and preference formation. We account for this result using a neurocomputational model postulating neuronal population-coding underlying intuitive averaging. Fitting the model to the participants' estimations, we find that tDCS enhances the signal-to-noise ratio in the neural network engaged in numerical averaging.

APPENDIX A

The Effect of Lowered Threshold on Neurons' Tuning Curve

We have tested the effect of threshold decrease (due to anodal direct current stimulation, which elevates membrane excitability) on neurons' firing rate and tuning curve. To simulate neurons' firing rate, we have used the following firing rate function (adapted from Usher & Niebur, 1996):

$$F(I) = \frac{1}{T_r - \tau \log \left[1 - \frac{\theta}{I} \right]},$$

where I is the input/current, T_r is the neuron's refractory time period (here 1 msec), θ is the threshold (here 1 before change; 0.5 after change), and τ is the membrane time constant (here 20 msec).

As can be seen in Figure A.1 (left), we find that when the threshold decreases (from 1 to 0.5), the firing rate function changes mostly in a multiplicative manner (red line, as compared with cyan, which shows an additive-only effect) and only slightly in an additive fashion (Figure A.2). Furthermore, the resulting tuning curve (Figure A.1 (right)) is mostly multiplicative as well (red line, as compared with cyan, which shows an additive-only effect) and is very similar to the multiplicative tuning curve, which we assumed in the text (cf. Figure 8B).

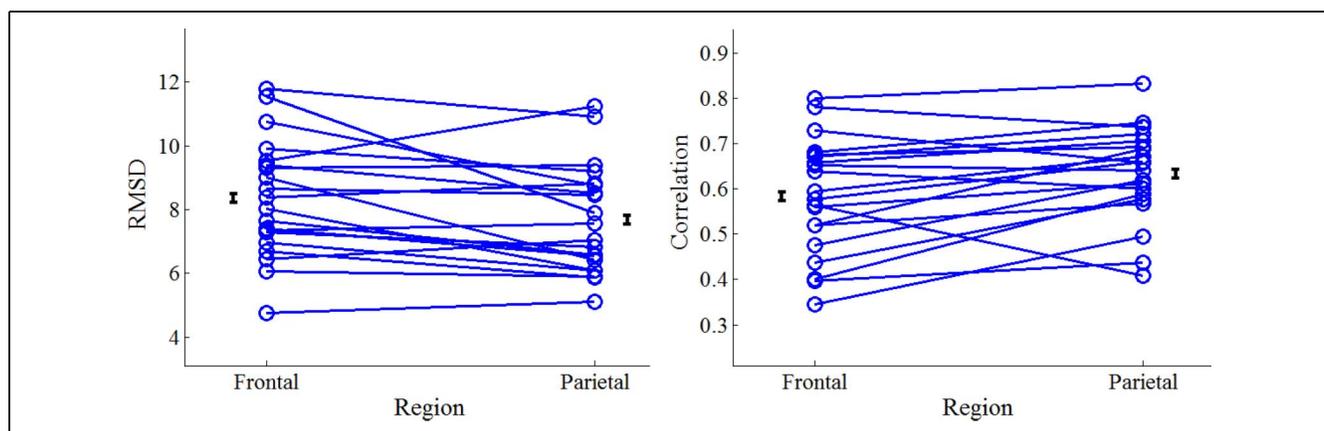


Figure A.1. Effect of frontal and parietal stimulation on performance at the individual level (each line corresponds to a single participant) in RMSD (left) and correlation (right) in Experiment 1 (error bars denote group means with 1 SE).

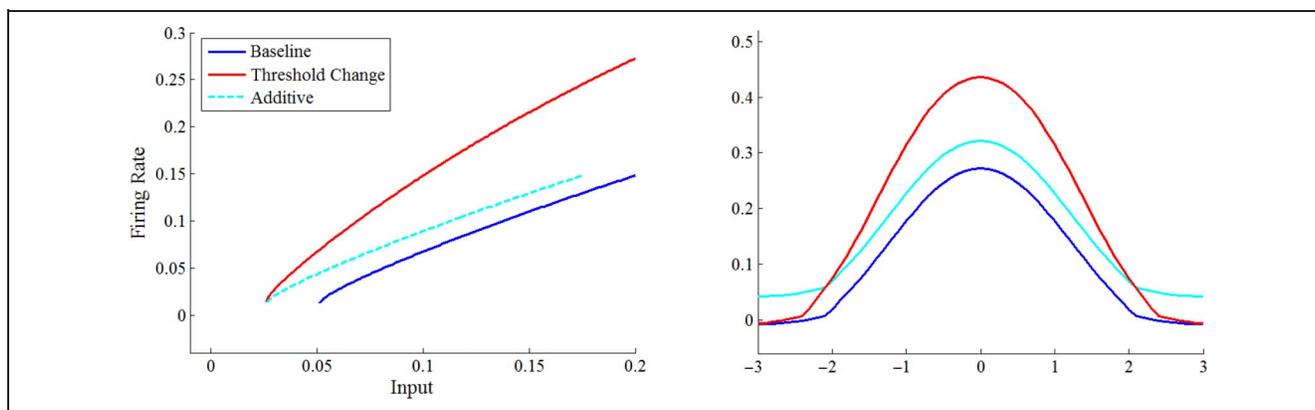


Figure A.2. Effect of lowered threshold (increased membrane excitability) on neurons' tuning curve. (Left) Firing rate to input functions for baseline (blue), lowered threshold (red), and additive (cyan; equals blue + constant). (Right) The corresponding tuning curves for each function. As can be seen, the lowered threshold tuning curve is mostly multiplicative.

APPENDIX B. Correlations between Actual Mean (x Axis) and Evaluations (y Axis) for All Participants

Participant	Pearson's r	p
1	.7587	<.001
2	.4858	<.001
3	.6967	<.001
4	.7141	<.001
5	.4956	<.001
6	.5856	<.001
7	.5447	<.001
8	.4176	<.001
9	.4202	<.001
10	.6197	<.001
11	.6329	<.001
12	.6821	<.001
13	.6471	<.001
14	.5475	<.001
15	.6932	<.001
16	.6182	<.001
17	.6837	<.001
18	.5075	<.001
19	.6049	<.001
20	.8164	<.001

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Notes

- Both the right and left parietal cortex have been implicated in numerical processing; thus, our decision to focus here on the right parietal is somewhat arbitrary. Future research should examine if our conclusions hold for the left-parietal cortex as well.
- For this analysis, we estimated precision using RMSD, as correlational analysis may be distorted by selecting subsets of trials.

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