

Theta synchrony supports Weber–Fechner and Stevens’ Laws for error processing, uniting high and low mental processes

GABRIEL TZUR,^a ANDREA BERGER,^a ROY LURIA,^b AND MICHAEL I. POSNER^b

^aDepartment of Psychology and Zlotowski Centre for Neuroscience, Ben-Gurion University of the Negev, Beer Sheva, Israel

^bDepartment of Psychology, University of Oregon, Eugene, Oregon, USA

Abstract

Human brain theta rhythm has been related to the operation of a generic mechanism involved in error detection processes of different types (e.g., detecting incorrect motor responses or incorrect arithmetic equations). This theta activity seems to be sensitive to error salience or magnitude, that is, stronger theta activity is found with larger or more deviant errors (e.g., $1+2=8$) than with smaller or less deviant ones (e.g., $1+2=4$). A time-frequency decomposition analysis indicated that theta activity is modulated by the magnitude of erroneous information in a nonlinear fashion, which can be characterized using Weber–Fechner’s law of logarithmic function and Stevens’ law of power function. The present study suggests that the generic mechanisms for error detection and evaluation may share similar fundamental neural schemes with primary cognitive and sensory or perceptual processes, which are directly involved in processing the specific type of input.

Descriptors: Weber–Fechner Law, Stevens’ Law, EEG oscillations, theta, ACC, rule violation

The ability to differentiate between correct and erroneous information, that is, the ability to detect and evaluate errors, is a basic and essential ability that accompanies us from early childhood through adulthood and old age. The idea that even infants react to violations of their expectations in the physical world (Bailargeon, 1987; Wynn, 1996) suggests that this ability is one of the cornerstones involved in our understanding and adjustment to our surroundings.

Electrophysiological and brain-imaging studies have suggested that monitoring of self-performance, such as detecting an error or evaluating outcomes and feedbacks, is related to theta (4–8 Hz) activity involving the anterior cingulate cortex (ACC; Carter et al., 1998; Dehaene, Posner, & Tucker, 1994; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Klein et al., 2007; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Yeung, Botvinick, & Cohen, 2004). Moreover, recent studies (Tzur & Berger, 2007, 2009) showed that this ACC theta activity is not exclusively related to monitoring of self-performance (i.e., the error related negativity and the feedback related negativity brain electrical

components), but is also found in rule-violation monitoring tasks, such as distinguishing between correct and incorrect simple arithmetic equations (e.g., $1+2=?$, correct solution 3 or incorrect solution 8).

Tzur and Berger (2007, 2009) suggested that this theta activity signifies the operation of a generic mechanism involved in error detection and evaluation processes of different types (e.g., detecting incorrect motor responses or incorrect arithmetic equations). They proposed that the evaluation processes should be seen as violation of expectation processes, that is, processes that compare and analyze the similarities and differences between an expected stimulus or action and a presented or performed stimulus or action. This suggestion predicts that the larger the conflict or mismatch between the expected and the presented or performed stimulus or action is, the greater the neural energy (power) and phase synchrony in the theta band will be. In fact, this idea is fully consistent with the findings of Tzur and Berger (2007), which indicated that the theta effects depended on the salience of the error. That is, incorrect solutions with bigger deviations from the correct solutions (e.g., $1+2=8$ is a “big” error) were related to greater increases in phase-lock theta activity than smaller deviations were (e.g., $1+2=4$ is a “small” error). This indicates that the monitoring process is not a dichotomous process when related to errors (i.e., error or no-error situation), but rather a process that also evaluates the magnitude or context of the erroneous information.

However, an important question regarding this idea is, “How does this generic mechanism evaluate the magnitude of different

We would like to thank Yoav Kessler for his important statistical recommendation and Desiree Meloul for her professional and generous help. This study was supported by the United States–Israel Bi-national Science Foundation, grant 2005133, to Andrea Berger and Michael I. Posner.

Address reprint requests to: Andrea Berger, Ph.D., Department of Psychology, Ben-Gurion University of the Negev, P.O.B. 653, Beer Sheva, 84105, Israel. E-mail: andrea@bgu.ac.il

types of errors?" One possible explanation would be that the generic mechanism shares similar fundamental neural schemes with perceptual and primary cognitive processes involved directly in processing the specific type of input. In the case of an arithmetic violation, this mechanism should resemble primary processes involving numerical processing. To test this assumption, we should first consider the way different mental processes interact and communicate. In the field of cognition, a debate still remains between two opposite views, the *analog coding hypothesis* and the *computational theories* of mind. The analog coding hypothesis emphasizes a continuum between mental processes (Barsalou, 1999; Shepard & Metzler, 1971). That is, higher-level cognitive representations are fundamentally similar to lower-level sensory or perceptual representations and thus should follow the same laws and exhibit similar attributes (Barsalou, 1999). In contrast, the computational theories of mind suggest that cognitive and sensory or perceptual representations constitute separate systems that work according to different principles (Fodor, 1975; Pylyshyn, 1984).

Numerical judgments studies (Dehaene, 2003; Moyer & Landauer, 1967; Nieder & Miller, 2003) seem to support the analog coding theory, as cognitive and perceptual or sensory processes share similar fundamental effects, such as the numerical *distance effect*. This effect was originally reported by Moyer and Landauer (1967), who measured the reaction times (RT) in a task in which adult human participants were asked to indicate which of two numerals represented the larger number. The bigger the distance between the two numbers (distance effect), the faster the participants were at choosing the numeral representing the correct response (Moyer & Landauer, 1967). The distance effect is independent of the physical characteristics of the stimuli and depends only on conceptual similarity in number meaning. It affects the participants' performance even if the numerical distance is irrelevant in the given task (Henik & Tzelgov, 1982). Moyer and Landauer explained the distance effect by assuming that numbers were mentally represented according to their magnitudes (i.e., a mental "number line"), which obeyed Weber's Law.

In 1834, Ernst Weber published what we now know as Weber's Law, which has provided a mathematical description for different sensory responses for more than 170 years (Dehaene, 2003; Lanzara, 1994; Nieder & Miller, 2003). A large number of sensory systems and their respective stimuli, including sound, light, smell, and taste stimuli, were found to follow this law. Weber's Law asserts that over a large dynamic range and for many parameters, the threshold of discrimination between two stimuli increases linearly with stimulus intensity (Dehaene, 2003; Lanzara, 1994; Nieder & Miller, 2003). In general, it was discovered that if S is the magnitude of a stimulus and JND is the just noticeable difference for discrimination, then their ratio is constant, that is, $r = JND/S$ (Lanzara, 1994). The JND in sensation occurs only when the increases (or changes) in stimuli are a constant percentage of the stimulus itself. For example, a person can discriminate reliably between two sets of weights if the difference between them is at least 5% (e.g., 20 g vs. 21 g; 40 g vs. 42 g; 60 g vs. 63 g; Lanzara, 1994). Later, in 1860, Gustav Fechner showed how Weber's Law could be accounted for by postulating that the external stimulus is scaled into a logarithmic internal representation of sensation, that is, $JND = A \times \log(S) + B$, where A and B are fitted constants (Dehaene, 2003; Lanzara, 1994; Nieder & Miller, 2003). This nonlinear scaling of stimulus magnitude has also been modeled by Stevens' Power

Law ($A \times (S)^B$), which postulates that sensation is a power function of the stimulus magnitude (Stevens, 1961).

Therefore, given that in some cases (e.g., numerical judgments) high cognitive processes follow fundamental laws similar to those that low sensory or perceptual processes do, it could be argued that the suggested generic mechanism of evaluation might also follow these fundamental laws.

To test this hypothesis, we used a new methodology of time-frequency decomposition analyses, from which one can obtain estimates of instantaneous power (Samar, Bopardikar, Rao, & Swartz, 1999) and intertrial phase synchrony (Lachaux, Rodriguez, Martinerie, & Varela, 1999), that is, extracting the relative energy and phase synchrony at different frequencies and different time points. This offered a novel opportunity for understanding brain activity related to cognitive processes beyond the classic averaged event related potentials (ERPs; Fell et al., 2004; Makeig et al., 2002). This wavelet representation provides a precise measurement of when and how the frequency content of an electroencephalogram (EEG) waveform changes over time. In this sense, this method offers a new view for understanding the relevant brain frequencies that are related to a specific event (i.e., an evaluation of an error). Moreover, by directly computing phase synchrony, we should detect alteration in human brain activity that is related to the error evaluation process. Therefore, in the present study, we have applied this novel technique for analyzing human brain electrophysiological intertrial phase synchrony during high cognitive processes of arithmetic violations and have looked for evidence that relates the ACC theta activity to logarithmic/power encoding.

Furthermore, because recent studies have suggested that theta activity modulates gamma activity (Canolty et al., 2006), we expected to find a greater increase in phase synchrony for the incorrect condition compared to the correct one in fast frequency bands also (i.e., beta and gamma bands, i.e., above 20 Hz), as we reported in our previous study (Tzur & Berger, 2009).

Participants were asked to distinguish between correct and incorrect solutions in which the incorrect condition was manipulated along four constant levels of deviation from the correct solution (e.g., for the equation $6 - 5 = ?$, the correct solution was 1, and the incorrect solutions were either 2 [L1], 4 [L3], 6 [L5], or 8 [L7]).

We expected to find that greater deviations of the incorrect solutions would be related to greater phase synchrony values in the theta frequency band (4–8 Hz). Moreover, our goal was to study whether the increase in theta synchronization for greater deviations of incorrect conditions could be correlated well with nonlinear functions that express Weber–Fechner's ($A \times \log(S) + B$) and the Stevens' ($A \times (S)^B$) Laws.

Method

Participants

Twenty-two participants (18 women and 4 men) with a mean age of 23.2 years ($SD = 1.5$) took part in the experiment. All participants were right-handed undergraduate students at Ben-Gurion University of the Negev. They were all healthy with no history of neurological illnesses and had normal or corrected-to-normal vision. Participants gave informed consent and participated in the study as partial fulfillment of course requirements.

Procedure

Participants were presented with 480 trials (plus 8 practice trials) of simple arithmetical equations (addition or subtraction), which were followed randomly by either correct solutions (240 trials) or incorrect solutions (240 trials). The presented arithmetical equations involved addition or subtraction of single-digit operands only, in order to keep the calculations as simple as possible and dismiss effects related to two-digit number processing, such as the unit-decade-compatibility effect (Nuerk, Weger, & Willmes, 2002). Within the incorrect solution condition, there were four constant possible levels of deviation, appearing with equal probability. For example, for the equation $6-5=?$, the incorrect solution could be either 2 (L1), 4 (L3), 6 (L5), or 8 (L7). The 480 trials were presented in a random order in 10 blocks (24 correct and 24 incorrect trials in each block).

Participants were seated 60 cm in front of a computer monitor and asked to be as relaxed as possible in order to reduce muscle tension. They were told at the beginning of the experiment that they were participating in cognitive research in the field of numerical processing and that they would be presented with simple arithmetical equations followed by either correct or incorrect solutions. They were asked to distinguish between correct and incorrect solutions by pressing a button (i.e., left key for correct and right key for incorrect; the side of the buttons was counter-balanced between participants). The button press response helped to engage the participants in the task. This manipulation also ensured that only trials in which participants succeeded in distinguishing a correct solution from an incorrect one were included in the analyses. Participants were asked to respond only when they were sure of their decisions and not as quickly as possible.

Each trial began with a fixation point (500 ms), followed by an equation (1500 ms), then a black screen (600 ms—for baseline calculation) followed by a solution (1500 ms), and ended with a screen asking for the participant's response (correct or incorrect solution). Random intertrial intervals (ITIs; 200, 400, or 600 ms) were inserted in order to reduce a monotonous task rhythm.

Electroencephalogram Recording

The EEG was recorded from 128 scalp sites using the EGI's Geodesic Sensor net and system (Tucker, 1993). Electrode impedances were kept below 40 k Ω , an acceptable level for this system (Ferree, Luu, Russell, & Tucker, 2001). All channels were referenced to the Cz channel, and data were collected using a 0.1–100-Hz bandpass filter. Signals were collected at 250 samples per second and digitized with a 16-bit A/D converter.

Time-Frequency Analysis

Time-frequency analysis of the data was conducted using wavelet-based analysis (Lachaux et al., 1999; Samar et al., 1999). Before the wavelet analysis, each participant's raw unfiltered (0.1–100 Hz) EEG data were segmented into trials, time-locked to the presentation of the solution. The segmented data was inspected for artifacts, such as bad channels resulting from channel saturation and muscle movement. Eye movements and blinks were monitored with three electrodes surrounding each eye (placed above, below, and to the left or right of the eye) providing bipolar recordings of the horizontal and vertical electrooculogram (EOG). Segments were discarded from analysis if they contained an eyeblink or eye movement artifact (EOG > 70 mV) or more than 10 electrode channels exceeded a voltage threshold of 200 μ V (absolute) or a transition threshold of 100 μ V (sample

to sample; Luu et al., 2003). Segments with fewer than 10 bad channels were included after replacing the bad-channel data with spherical interpolation of the neighboring channel values.

The data of each trial were then re-referenced to the average of all of the sensors at each time point. For calculating the phase synchrony values between trials (based on the circular variance [CV]; Lachaux et al., 1999), trials were segmented into one correct and four incorrect (i.e., L1, L3, L5, L7) conditions (stimulus-locked to the solution presentation), whereas the trials within each condition were kept unaveraged. Following this, a family of Morlet wavelets was constructed at intervals of 0.5 Hz frequency, ranging from 1 Hz to 95 Hz. Our wavelet family was computed using a f_0/σ_f ratio of 7 (Muthukumaraswamy & Johnson, 2004; Samar et al., 1999). The phase synchrony values (range from 0 [*no synchrony*] to 1 [*full synchrony*]) were obtained relative to a 200-ms baseline presolution interval. The time-frequency analysis was conducted for the frequency bands ranging from 1–45 Hz to 65–95 Hz, excluding the 45–65 Hz band because this was in the range of our electrical power network frequency and might have been vulnerable to electromagnetic interference.

Consistent with our previous studies (Berger, Tzur, & Posner, 2006; Tzur & Berger, 2007), the statistical analyses were carried out on the mean synchrony of a group of nine channels, located between (and including) Cz and Fz of the 10–20 system of electrode placement (see Figure 1).

The wavelet phase synchrony analysis was conducted in the following way. For each condition (i.e., correct, L1, L3, L5, L7), the maximum phase synchrony value of each frequency band (i.e., delta: 1–4 Hz, theta: 4–8 Hz, alpha: 8–12 Hz, beta: 12–30 Hz, lower gamma: 30–45 Hz, medial gamma: 65–80 Hz, and upper gamma: 80–95 Hz; the gamma band was divided into three equal bands for a better resolution of the data) was extracted from a 0–600-ms time window for each participant. The extracted values were then analyzed using repeated measures analyses of variance (ANOVAs; Kiebel, Tallon-Baudry, & Friston, 2005) with the solution conditions and the frequency bands as within-participant variables (significance level was set to .05). When appropriate, all critical values were adjusted using the correction of Greenhouse and Geisser (1959).

Within each of the solution \times frequency interaction effects, a planned comparison (i.e., A vs. B) was conducted comparing correct (A) versus incorrect (B) conditions for each frequency band separately. This was done in order to evaluate which of the frequency bands expressed phase synchrony differences between the correct and incorrect conditions. Whenever a significant difference was found, three additional planned orthogonal comparisons—L1 versus (L3, L5, and L7), L3 versus (L5 and L7), and L5 versus (L7)—were conducted sequentially only if the previous comparison reached statistical significance. This was done in order to find out whether greater deviations of the incorrect solution (i.e., L3, L5, and L7) from the correct one were related to greater phase synchrony increases than smaller deviations (i.e., L1) were.

Results

The wavelet analysis results showed a relative increase in phase synchrony, especially in the theta frequency band (4–8 Hz), for the incorrect conditions compared to the correct condition (Figure 2). Moreover, a greater increase was seen for higher deviation levels of the incorrect conditions (e.g., L7) compared to the lower

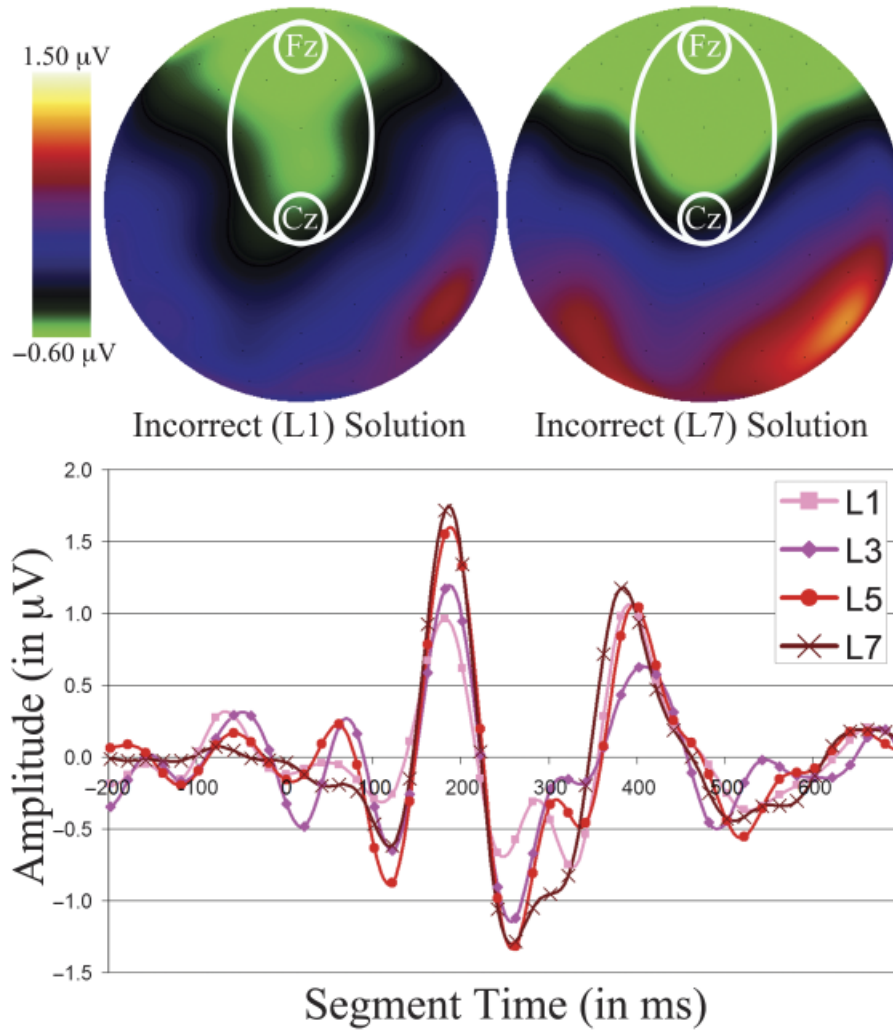


Figure 1. Grand averaged voltage distribution in two-dimensional scalp topographic maps (top row) and the ERP mean from channel Fz of the 10–20 system (bottom row) of the 22 participants (filtered with 4–12 Hz bandpass). Greater negative voltage distributions (top row, circled in white) and ERP (bottom row) are seen (about 251 ms after the solution presentation) over the medial frontal cortex for greater deviations of the incorrect solution than for smaller ones.

ones (e.g., L1). This phase synchrony increase began approximately 100 ms after the presentation of the solution and ended about 400 ms later (Figure 2).

All effects reached statistical significance, that is, both frequency bands and solution main effects, $F(6,126) = 5.05$, $p < .005$, and $F(4,84) = 80.71$, $p < .001$, respectively, and the so-

lution \times frequency bands interaction effect, $F(24,504) = 6.35$, $p < .001$.

As summarized in Table 1, the phase synchrony planned comparisons analyses revealed a significant increase in phase synchrony for the incorrect condition compared to the correct one in all frequency bands. These results are consistent with our

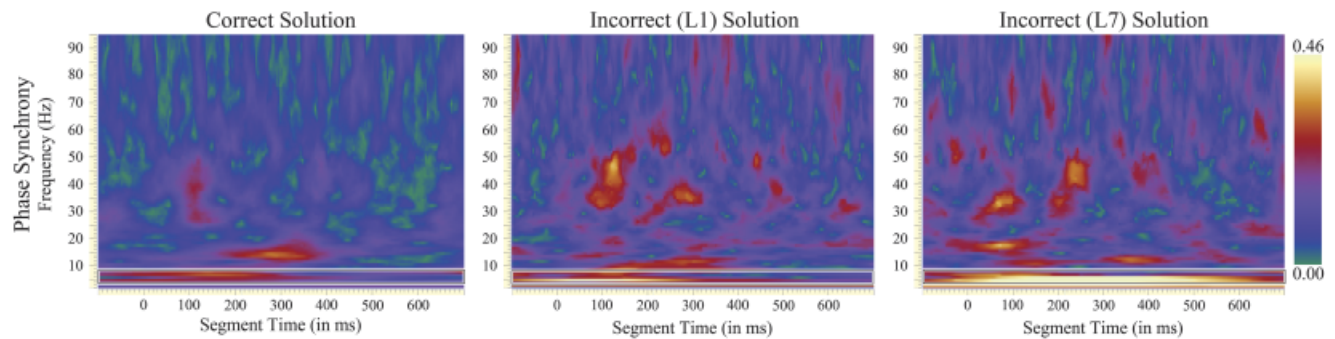


Figure 2. An example of phase synchrony time–frequency plots (from the Fz channel) of one individual participant, calculated for correct and incorrect conditions (L1, L7). Dark areas indicate low phase synchrony values, whereas light areas denote high phase synchrony. A relative increase in phase synchrony is seen mostly in the theta band (4–8 Hz, marked with a white rectangle) for the incorrect conditions compared to the correct one.

Table 1. Modeled Power Functions and Simple Comparison Analyses of the Medial-Frontal Phase Synchrony Effects across the Frequency Bands

Frequency	Comparison (A vs. B)	Phase synchrony		Incorrect conditions	
		F value	p value	Power function	R ²
Delta, 1–4 Hz	Crr vs. Incrr (L1, L3, L5, L7)	7.507	.013*	.262 × (S) ^{.031}	.583
	L1 vs. (L3, L5, L7)	1.612	.219		
	L3 vs. (L5, L7)				
Theta, 4–8 Hz	Crr vs. Incrr (L1, L3, L5, L7)	54.540	.001*	.275 × (S) ^{.054}	.955
	L1 vs. (L3, L5, L7)	4.674	.043*		
	L3 vs. (L5, L7)	0.329	.572		
Alpha, 8–12 Hz	Crr vs. Incrr (L1, L3, L5, L7)	17.126	.001*	.306 × (S) ^{-.016}	.479
	L1 vs. (L3, L5, L7)	0.255	.618		
	L3 vs. (L5, L7)				
Beta, 12–30 Hz	Crr vs. Incrr (L1, L3, L5, L7)	128.282	.001*	.261 × (S) ^{-.032}	.396
	L1 vs. (L3, L5, L7)	0.249	.623		
	L3 vs. (L5, L7)				
Lower gamma, 30–45 Hz	Crr vs. Incrr (L1, L3, L5, L7)	203.347	.001*	.268 × (S) ^{-.001}	.002
	L1 vs. (L3, L5, L7)	0.025	.874		
	L3 vs. (L5, L7)				
Medial gamma, 65–80 Hz	Crr vs. Incrr (L1, L3, L5, L7)	273.919	.001*	.306 × (S) ^{-.003}	.002
	L1 vs. (L3, L5, L7)	0.146	.706		
	L3 vs. (L5, L7)				
Upper gamma, 80–95 Hz	Crr vs. Incrr (L1, L3, L5, L7)	313.498	.001*	.307 × (S) ^{-.044}	.856
	L1 vs. (L3, L5, L7)	3.751	.066		
	L3 vs. (L5, L7)				

Note: Crr: Correct, Incrr: Incorrect.
 *Statistically significant effects ($p < .05$), $A < B$.

previous findings on fast and slow brain rhythms in rule or expectation violation tasks (Tzur & Berger, 2009). Moreover, only in the theta frequency band (4–8 Hz) did the first two sequential comparisons (i.e., correct vs. incorrect and L1 vs. [L3, L5, L7]) reach statistical significance. This implies that only the theta effects are sensitive to the degree of deviation of the incorrect solution from the correct one, showing greater phase synchrony for greater deviations (Figure 2 and Table 1).

To test the Weber–Fechner and Stevens’ Laws on the theta band effects, a logarithmic function ($A \times \ln(S) + B$) and a power function ($A \times (S)^B$) were fitted to the phase synchrony data. These functions were fitted to each participant’s phase synchrony data separately (Estes & Maddox, 2005; Lorch & Myers, 1990). Then, each participant’s incorrect conditions (i.e., L1, L3, L5, L7) phase synchrony indexes were modeled and then averaged across participants. A correlation between the predicted indexes and the observed ones yielded a very high goodness of fit for both

logarithmic ($R^2 = .979$) and power ($R^2 = .955$) functions (Figure 3). Furthermore, when the categorical variables of the predicted and the observed phase synchrony indexes were analyzed using an ANOVA, with the incorrect conditions as within-participant variables, the categorical main effect and the Categorical × Incorrect Conditions interaction effect were far from reaching statistical significance for both logarithmic, $F(1,42) < 1$ and $F(3,126) < 1$, respectively, and power, $F(1,42) < 1$ and $F(3,126) < 1$, respectively, modeled data. This indicates that the logarithmic and power modeled data were similar to the observed data. Moreover, the goodness of fit was markedly smaller, $R^2 = .84$, when the data were modeled using a linear function ($.005 \times (S) + .275$; see Figure 3).

Source Localization

A source localization analysis was conducted in order verify the connection between the theta effect and the ACC (Luu et al., 2003; Tzur & Berger, 2007). For the source localization analysis, we used the sLORETA method (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002; Pascual-Marqui, 2002; Valer, Daisuke, & Ippeita, 2007) that computes images of electric neural activity from ERPs. This new method has a better resolution capability than the old LORETA method and should express a better localization of brain generators than the ones reported by Tzur and Berger (2007) using the LORETA method. The ERP data of each participant (i.e., segmented, averaged, etc.) were filtered to 4–12 Hz, focusing on theta and alpha rhythms (Tzur & Berger, 2007) and then were analyzed using the sLORETA source localization method (Fuchs et al., 2002; Pascual-Marqui, 2002; Valer et al., 2007). Two-tailed t tests for dependent samples were used to compare the neurophysiological parameters between the correct condition and the incorrect condition (L5 and L7). This was done in order to determine the brain generators related to the increase of phase synchrony in the theta band between the correct and incorrect conditions (Figure 2 and Table 1).

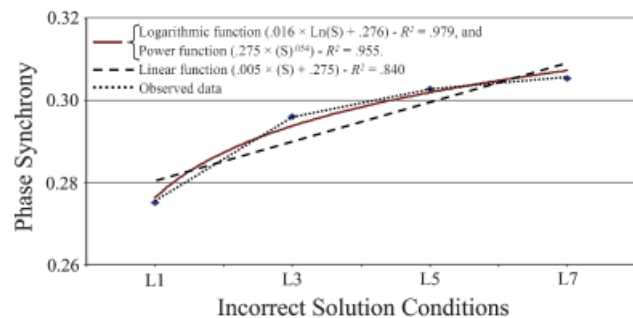


Figure 3. Grand average (22 participants) quantification phase synchrony indexes of the incorrect condition theta into curves. The curves indicate that the observed phase synchrony data (marked with blue dotted line) fits better the logarithmic and power functions ($R^2 = .979$ and $R^2 = .955$, respectively, marked with brown solid line) than a linear function ($R^2 = .840$, marked with green dotted line).

The statistical comparison of the cortical sources between the conditions revealed a significantly ($p < .05$) stronger activation after incorrect solutions only in the left ACC (Brodmann area 32, MNI: $X = -12, Y = 45, Z = 10$; Figure 4). This analysis presents a focalized involvement of the left ACC that rectifies Tzur and Berger's (2007) LORETA analysis, which suggested more brain generators than the ACC.

Discussion

In the present study we examined whether human brain neural activity related to a high cognitive task, such as distinguishing between correct and incorrect simple arithmetic equations, can be characterized using Weber–Fechner's law of logarithmic function ($A \times \log(S) + B$) and Stevens' law of power function ($A \times (S)^B$; Dehaene, 2003; Lanzara, 1994; Nieder & Miller, 2003).

A time–frequency decomposition analysis showed that the theta frequency band (4–8 Hz) was sensitive to the salience of the incorrect solutions. That is, higher phase synchrony was found in this band for greater deviations of the incorrect solution than for smaller deviations (Figure 2). Moreover, the results suggest that the nonlinear Weber–Fechner and Stevens' Laws explain this theta band neural activity with a high goodness of fit. In other words, without entering into the debate regarding which of the laws (i.e., the Weber–Fechner or Stevens' Laws) best characterizes psychological sensory perception, the present study results support the notion that synchrony in brain activity might encode high-level representations in a nonlinear fashion, either with a logarithmic or a power function.

These findings are consistent with our previous results (Tzur & Berger, 2007, 2009) and the idea of a generic mechanism for error detection and evaluation processes, which should be seen as violation of expectation processes. That is, processes that compare and analyze the similarities and differences between an expected stimulus or action and a presented or performed stimulus or action. This suggestion predicts that the larger the conflict or mismatch between the expected and the presented or performed stimulus or action is, the greater the phase synchrony in the theta band will be. Nevertheless, why did the differences between more salient violations and less salient ones emerge in a *nonlinear pattern*? One possible explanation is related to the type or nature of the mismatch. In the case of incorrect arithmetical equations, the

mismatch is a number, and numbers are mentally represented according to their magnitudes. According to this view, the magnitude of the perceived error in our paradigm, that is, the conflict or mismatch between the expected and the presented stimuli, depends on the mentally represented distance between the incorrect and correct solutions. Because numbers are cognitively represented in a logarithmic number line, the magnitude of the perceived error would be represented accordingly. This idea suggests that high evaluation processes, in this case an arithmetical evaluation, might rely on and share similar fundamental neural schemes with primary numerical cognitive processes, in this case, the mental representation of the number line.

The representation of numbers in tasks involving magnitude evaluations in general and the distance effect in particular seems to involve parietal areas (Szucs & Csepe, 2005) or, more specifically, the intraparietal sulci (Dehaene, Dehaene-Lambertz, & Cohen, 1998). Moreover, the right parietal lobe shows a preference for quantity if represented by digits but not if represented by number words (Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007).

Indeed, in our study, we can find clear expected evidence of a distance effect in the right parietal area (see Figure 5 and Table 2). Two important features should be noticed in Figure 1 and Figure 5. First, the amplitudes show gradual nonlinear differences between the different deviation conditions, consistent with the theta effects we found over the medial-frontal cortex (Figure 1). Second, this parietal effect clearly precedes the middle-frontal one in time, but also continues parallel to it.

These findings are important, because studying behavior alone (e.g., reaction time; Moyer & Landauer, 1967) cannot tell us whether numerical judgments and other magnitude estimations truly depend on neural representations that follow the Weber–Fechner and Stevens' Laws (Johnson, Hsiao, & Yoshioka, 2002; MacKay, 1963). Showing that human brain activity expresses the magnitude of the perceived error in a nonlinear function similar to the Weber–Fechner and Stevens' Laws indicates that these laws indeed express human high cognitive processes and not only behavioral outcomes. Our results in this sense are also consistent with the study by Nieder and Miller (2003) on Rhesus monkeys, which showed that the neural representation of nonverbal visual numerosities might be better described by logarithmic and power scales than linear ones. However, to our

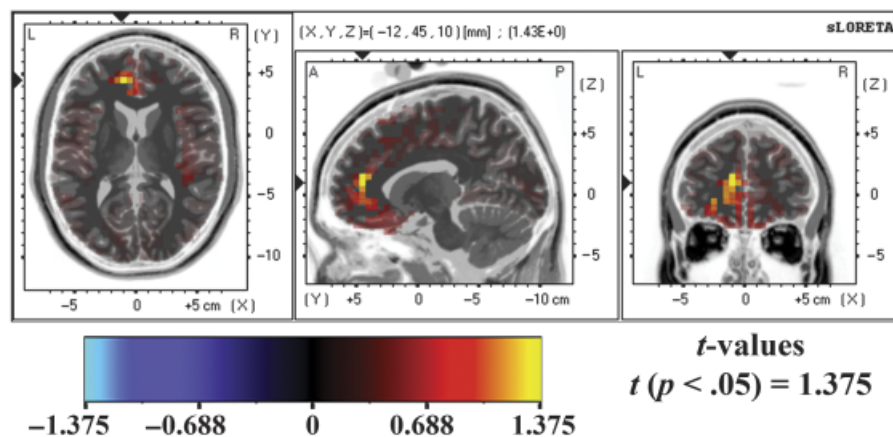


Figure 4. Graphical representation of the sLORETA t statistics comparing the ERPs for incorrect (L5 and L7) and correct conditions. The light yellow color indicates local maxima of increased electrical activity for incorrect compared to correct conditions (t threshold for $p < .05$ is 1.375). Black arrows mark the left ACC ($t = 1.43$; MNI cords: $X = -12, Y = 45, Z = 10$) as the source center of significantly increased activity in the incorrect condition.

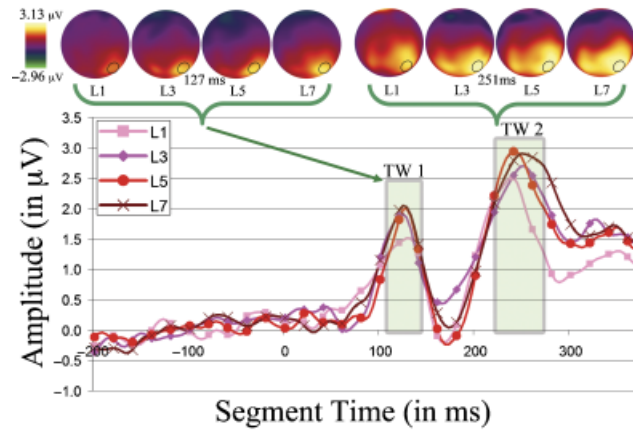


Figure 5. Grand averaged voltage distribution in two-dimensional scalp topographic maps (top row) and the ERP mean of a group of three channels (bottom row), representing the P4 (right parietal) channel of the 10–20 system of the 22 participants (filtered with 40 Hz lowpass). Greater positive voltage distributions (top row, circled in white) and ERP (bottom row) are seen in two time-windows (TW 1 and TW 2, about 127 and 251 ms after the solution presentation, respectively) over the right parietal cortex for greater deviations of the incorrect solution than for smaller ones. The ERP amplitudes (bottom row) show gradual nonlinear differences between the different deviation conditions (see Table 2), consistent with the logarithmic/power distance effect and the theta effects we presented over the medial-frontal cortex (Figure 1, bottom row). Notice that this parietal effect clearly precedes the middle-frontal one in time, but also continues parallel to it.

knowledge, the results of the present study are the first to show that human brain activity of high cognitive processes are coded nonlinearly. This suggests that high cognitive processes, such as distinguishing between correct and incorrect arithmetic equations, follow nonlinear laws (i.e., the Weber–Fechner and Stevens’ Laws), similar to perceptual and sensory processes. This finding is in line with the analog coding hypothesis (Barsalou, 1999; Shepard & Metzler, 1971), which emphasizes a continuum between mental processes. That is, higher-level cognitive representations are fundamentally similar to lower-level sensory or perceptual representations and thus should follow the same laws and exhibit similar attributes (Barsalou, 1999).

Our source localization analysis suggested the left ACC as a possible generator for the incorrect conditions effects (e.g., L5 and L7). In a previous study, we suggested that these theta effects were related to more brain generators than the ACC (e.g., the precentral and postcentral gyrus, the superior, medial, and inferior frontal gyrus; Tzur & Berger, 2007). However, in this study we used the new sLORETA source localization analysis (Pascual-Marqui, 2002), which has a better resolution capability than the old

LORETA and should express a better localization of brain generators than the ones reported in our previous study (Tzur & Berger, 2007). Moreover, when we used this new sLORETA method on the data from our previous study (Tzur & Berger, 2007), the source localization analysis detected only the ACC as a related generator to these theta effects (as in this study). These findings and the idea of connecting conflict and error detection processes with theta activity related to the ACC are consistent with previous reports in the literature (Carter et al., 1998; Dehaene et al., 1994; Gehring et al., 1993; Klein et al., 2007; Luu et al., 2003; Yeung et al., 2004). The ACC is believed to be involved in the executive control of actions, such as in monitoring conflicting response demands, detecting errors, and evaluating the emotional significance of events (Bush, Luu, & Posner, 2000; Luu et al., 2003). Relating high executive control brain generators, such as the ACC, to high cognitive processes that follow the Weber–Fechner and Stevens’ Laws further supports the idea that certain high cognitive and low perceptual or sensory processes share similar fundamental mechanisms and neural coding schemes.

Therefore, the present study suggests that the generic mechanism for error detection and evaluation processes proposed in our previous studies (Tzur & Berger, 2007, 2009) might share similar fundamental neural schemes with primary cognitive and sensory or perceptual processes, which are directly involved in processing the specific type of input. In the case of arithmetical equations, when the solution is presented, it is evaluated based on prior expectations and knowledge. A process comparing the “expected” solution to the “perceived” one begins. The estimation of the degree of deviation of the perceived solution from the expected one involves parietal activity, similar to other magnitude or quantity estimations. This basic information is transferred to frontal areas including the ACC, where the actual “error or violation” signaling occurs. It is possible that the ACC detects the presence of a conflict or error and alerts other areas to resolve it. In other words, the ACC might be responsible for detecting error or conflict and conveying this information to brain regions directly responsible for the control of cognitive processing (e.g., lateral prefrontal regions; Botvinick, Braver, Barch, Carter, & Cohen, 2001; van Veen & Carter, 2006; Yeung et al., 2004). What is being detected by the ACC? Is it conflict between responses (Botvinick et al., 2001; Carter et al., 1998; Yeung et al., 2004), error detection (Coles, Scheffers, & Holroyd, 2001; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Gehring et al., 1993; Scheffers & Coles, 2000), or evaluation of the motivationally significant information concerning rewards and punishments (Holroyd & Coles, 2002; Nieuwenhuis, Yeung, & Holroyd, 2004; Yeung, Holroyd, & Cohen, 2005)? We have suggested (Tzur & Berger, 2007, 2009) an integrative view by which

Table 2. Modeled Power Functions and Simple Comparison Analyses of the Parietal Maximum Peak Amplitude Effects in Time Windows 1 and 2

Frequency	Comparison (A vs. B)	Maximum peak amplitude		Incorrect conditions	
		<i>F</i> value	<i>p</i> value	Power function	<i>R</i> ²
Time window 1	L1 vs. (L3, L5, L7)	1.535	.229	$1.982 \times (S)^{100}$.804
	L3 vs. (L5, L7)	0.002	.968		
Time window 2	L1 vs. (L3, L5, L7)	5.713	.026*	$2.996 \times (S)^{097}$.962
	L3 vs. (L5, L7)	0.192	.666		

*Statistically significant effects ($p < .05$), $A < B$.

the medial-frontal theta activity found emanating from the ACC in tasks involving monitoring is connected to a generic evaluation process that compares and analyzes the similarities and differences between an expected stimulus or action (e.g., feedback, a solution of a mathematical equation, or performing an incorrect action or response) and a presented or performed stimulus or action. Interpreting these processes as a violation of expectation processes is in line with the idea that even infants distinguish between correct and erroneous information by using violation of expectation processes (Baillargeon, 1987; Wynn, 1996) that express a similar theta activity signature (Berger et al., 2006) as found in adults in this study. This implies that the proposed generic mechanism accompanies us from early childhood and has an important role in our adjusting and interacting with our surroundings.

The findings of the present study contradict the idea that the ACC theta activity reflects the amount of effort dispensed, as this would have predicted finding larger activity when the salience of the error was small. At least in the context of the task used, the opposite occurs. This relation between larger amplitudes for easier conditions that show shorter RT can be seen in other ERP components, for example, P300 (Cohen Kadosh, Cohen Kadosh, Linden, et al., 2007). It is plausible to hypothesize that extra effort and more computation leads to lower synchrony in the firing of neurons and this is reflected in smaller amplitudes in the ERP that averages the activity over neuronal communities and over trials.

Our present study suggests that although the monitoring process may be generic, the actual data on which this process relies are probably generated by domain-specific primary processes related to the basic nature of the actual data. This would predict that in tasks involving data from domains other than numbers, the characteristics of the specific domain would be reflected in the theta activity, as it relies on the signal emanating from the relevant primary processes. For example, in the linguistic domain, when one judges semantic violations, incorrect semantic sentences should induce larger amplitudes and higher synchrony in theta activity than correct semantic sentences. Moreover, these theta effects should also depend on the context of semantic sentences, such as neutral and negative-affect context, which are related to distinct areas of the ACC (Bush et al., 2000). Indeed, preliminary results from our laboratory tend to support this notion; however, this would have to be confirmed in future research.

When considering that evaluation processes are based on violation of expectations, as suggested in this study, we should also address additional parallel cognitive processes necessary for the fulfillment of the task, such as numerical and arithmetical calculation processing, comparison processes, working memory, visual processing, and so forth. These cognitive processes often interact with each other from distant parts of the brain and therefore require synchronization and coordination. Recent studies have suggested that theta activity modulates gamma activity (Canolty et al., 2006) and that fast brain rhythms (above 20 Hz, i.e., beta and gamma bands) enable a precise functional association between specific brain regions over short as well as longer distances (Engel & Singer, 2001; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Furthermore, it seems that neural activities of fast brain rhythms (i.e., beta and gamma) are most likely related to synchronization between brain regions or processes and neural activities of slow brain rhythm (i.e., theta and alpha) are associated with memory processes (e.g., working memory, memory consolidation, encoding and retrieval; Engel & Singer, 2001; Fell et al., 2004; Mormann et al., 2005; Varela et al., 2001). Moreover, Moore, Gale, Morris, and Forrester (2006) have suggested that goal conflict in target detection tasks relates to a phase-locked theta activity that expresses communication between the hippocampal formation and neocortical areas. In this view, it is possible that the neural synchronization effects and their nonlinear patterns (see Table 1) found in low- and high-frequency bands (especially in the theta and upper gamma bands) could reflect a precise functional association between sensory or perceptual processes (involving parietal areas; Figure 5 and Table 2) and high cognitive processes (involving medial-frontal areas; Figures 1–4) that follows similar neural coding schemes. For example, the theta and the alpha activities might be related to memory (involving the hippocampal formation; Moore et al., 2006) and comparison/mismatch (involving the ACC; Carter et al., 1998; Tzur & Berger, 2007; Yeung et al., 2004) processes that evaluate the magnitude of the conflict between the presented and expected stimuli. The beta and gamma activities might involve synchronization between brain regions (Engel & Singer, 2001; Varela et al., 2001) related to these memory and comparison processes and other parallel cognitive (e.g., perceptual integration, attention selection, mathematical calculation, and response planning or execution) and affective processes (e.g., emotional evaluation; Bush et al., 2000). Still, this is a rather novel idea that should be further investigated in future studies.

REFERENCES

- Baillargeon, R. (1987). Object permanence in 3.5- and 4.5-month-old infants. *Developmental Psychology*, *23*, 655–664.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, *22*, 577–660.
- Berger, A., Tzur, G., & Posner, M. I. (2006). Infant brains detect arithmetic errors. *Proceedings of the National Academy of Sciences, USA*, *103*, 12649–12653.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*, 624–652.
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, *4*, 215–222.
- Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., et al. (2006). High gamma power is phase-locked to theta oscillations in human neocortex. *Science*, *313*, 1626–1628.
- Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, *280*, 747–749.
- Cohen Kadosh, R., Cohen Kadosh, K., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-dependent and -independent representations of numbers in the parietal lobes. *Neuron*, *53*, 307–314.
- Cohen Kadosh, R., Cohen Kadosh, K., Linden, D. E. J., Gevers, W., Berger, A., & Henik, A. (2007). The brain locus of interaction between number and size: A combined functional magnetic resonance imaging and event-related potential study. *Journal of Cognitive Neuroscience*, *19*, 957–970.
- Coles, M. G. H., Scheffers, M. K., & Holroyd, C. B. (2001). Why is there an ERN/Ne on correct trials? Response representations, stimulus-related components, and the theory of error-processing. *Biological Psychology*, *56*, 173–189.
- Dehaene, S. (2003). The neural basis of the Weber–Fechner law: A logarithmic mental number line. *Trends in Cognitive Sciences*, *7*, 145–147.

- Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences*, *21*, 355–361.
- Dehaene, S., Posner, M. I., & Tucker, D. M. (1994). Localization of a neural system for error detection and compensation. *Psychological Science*, *5*, 303–305.
- Engel, A. K., & Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness. *Trends in Cognitive Sciences*, *5*, 16–25.
- Estes, W. K., & Maddox, W. T. (2005). Risks of drawing inferences about cognitive processes from model fits to individual versus average performance. *Psychonomic Bulletin & Review*, *12*, 403–408.
- Falkenstein, M., Hohnsbein, J., Christ, S., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components: II. Error processing in choice reaction tasks. *Electroencephalography and Clinical Neurophysiology*, *78*, 447–455.
- Falkenstein, M., Hohnsbein, J., Christ, S., & Hohnsbein, J. (2000). ERP components on reaction errors and their functional significance: A tutorial. *Biological Psychology*, *51*, 87–107.
- Fell, J., Dietl, T., Grunwald, T., Kurthen, M., Klaver, P., Trautner, P., et al. (2004). Neural bases of cognitive ERPs: More than phase reset. *Journal of Cognitive Neuroscience*, *16*, 1595–1604.
- Ferree, T. C., Luu, P., Russell, G. S., & Tucker, D. M. (2001). Scalp electrode impedance, infection risk, and EEG data quality. *Clinical Neurophysiology*, *112*, 536–544.
- Fodor, J. (1975). *The language of thought*. New York: Crowell.
- Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clinical Neurophysiology*, *113*, 702–712.
- Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, *4*, 385–390.
- Greenhouse, S., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, *24*, 95–112.
- Henik, A., & Tzelgov, J. (1982). Is three greater than five? The relation between physical and semantic size in comparison tasks. *Memory and Cognition*, *10*, 389–395.
- Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, *109*, 679–709.
- Johnson, K. O., Hsiao, S. S., & Yoshioka, T. (2002). Neural coding and the basic law of psychophysics. *Neuroscientist*, *8*, 111–121.
- Kiebel, S. J., Tallon-Baudry, C., & Friston, K. J. (2005). Parametric analysis of oscillatory activity as measured with EEG/MEG. *Human Brain Mapping*, *26*, 170–177.
- Klein, T. A., Endrass, T., Kathmann, N., Neumann, J., von Cramon, D. Y., & Ullsperger, M. (2007). Neural correlates of error awareness. *NeuroImage*, *34*, 1774–1781.
- Lachaux, J. P., Rodriguez, E., Martinerie, J., & Varela, F. J. (1999). Measuring phase synchrony in brain signals. *Human Brain Mapping*, *8*, 194–208.
- Lanzara, R. G. (1994). Weber's Law modeled by the mathematical description of a beam balance. *Mathematical Biosciences*, *122*, 89–94.
- Lorch, R. F., & Myers, J. L. (1990). Regression analyses of repeated measures data in cognitive research. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *16*, 149–157.
- Luu, P., Tucker, D. M., Derryberry, D., Reed, M., & Poulsen, C. (2003). Electrophysiological responses to errors and feedback in the process of action regulation. *Psychological Science*, *14*, 47–53.
- MacKay, D. M. (1963). Psychophysics of perceived intensity: A theoretical basis for Fechner's and Stevens' laws. *Science*, *139*, 1213–1216.
- Makeig, S., Westerfield, M., Jung, T. P., Enghoff, S., Townsend, J., Courchesne, E., et al. (2002). Dynamic brain sources of visual evoked responses. *Science*, *295*, 690–694.
- Moore, R. A., Gale, A., Morris, P. H., & Forrester, D. (2006). Theta phase locking across the neocortex reflects cortico hippocampal recursive communication during goal conflict resolution. *International Journal of Psychophysiology*, *60*, 260–273.
- Mormann, F., Fell, J., Axmacher, N., Weber, B., Lehnertz, K., Elger, C. E., et al. (2005). Phase/amplitude reset and theta-gamma interaction in the human medial temporal lobe during a continuous word recognition memory task. *Hippocampus*, *15*, 890–900.
- Moyer, R. S., & Landauer, T. K. (1967). Time required for judgments of numerical inequality. *Nature*, *215*, 1519–1520.
- Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clinical Neurophysiology*, *115*, 1760–1766.
- Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude: Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron*, *37*, 149–157.
- Nieuwenhuis, S., Yeung, N., & Holroyd, C. B. (2004). Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. *Cerebral Cortex*, *14*, 741–747.
- Nuerk, H. C., Weger, U., & Willmes, K. (2002). A unit decade compatibility effect in German number words. *Current Psychology Letters*, *7*, 19–38.
- Pascual-Marqui, R. D. (2002). Standardized low resolution brain electromagnetic tomography (sLORETA): Technical details. *Methods & Findings in Experimental & Clinical Pharmacology*, *24D*, 5–12.
- Pylyshyn, Z. (1984). *Computation and cognition: Toward a foundation for cognitive science*. Cambridge, MA: MIT Press.
- Samar, V. J., Bopardikar, A., Rao, R., & Swartz, K. (1999). Wavelet analysis of neuroelectric waveforms: A conceptual tutorial. *Brain and Language*, *66*, 7–60.
- Scheffers, M. K., & Coles, M. G. H. (2000). Performance monitoring in a confusing world: Error-related brain activity, judgments of response accuracy, and types of errors. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 141–151.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*, 701–703.
- Stevens, S. S. (1961). To honor Fechner and repeal his law. *Science*, *133*, 80–86.
- Szucs, D., & Csepe, V. (2005). The parietal distance effect appears in both the congenitally blind and matched sighted controls in an acoustic number comparison task. *Neuroscience Letters*, *384*, 11–16.
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, *3*, 154–163.
- Tzur, G., & Berger, A. (2007). When things look wrong: An ERP study of perceived erroneous information. *Neuropsychologia*, *45*, 3122–3126.
- Tzur, G., & Berger, A. (2009). Fast and slow brain rhythms in rule/expectation violation tasks: Focusing on evaluation processes by excluding motor action. *Behavioural Brain Research*, *198*, 420–428.
- Valer, J., Daisuke, T., & Ippaita, D. (2007). 10/20, 10/10, and 10/5 systems revisited: Their validity as relative head-surface-based positioning systems. *NeuroImage*, *34*, 1600–1611.
- Van Veen, V., & Carter, C. S. (2006). Conflict and cognitive control in the brain. *Current Directions in Psychological Science*, *15*, 237–240.
- Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large scale integration. *Nature Reviews Neuroscience*, *2*, 229–239.
- Wynn, K. (1996). Infants' individuation and enumeration of actions. *Psychological Science*, *7*, 165–169.
- Yeung, N., Botvinick, M. M., & Cohen, J. D. (2004). The neural basis of error detection: Conflict monitoring and the error-related negativity. *Psychological Review*, *111*, 931–959.
- Yeung, N., Holroyd, C. B., & Cohen, J. D. (2005). ERP correlates of feedback and reward processing in the presence and absence of response choice. *Cerebral Cortex*, *15*, 535–544.

(RECEIVED March 22, 2009; ACCEPTED July 19, 2009)