

Mindfulness-of-breathing exercise modulates EEG alpha activity during cognitive performance

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Abstract

The present study investigated whether engaging in a mindful breathing exercise would affect EEG oscillatory activity associated with self-monitoring processes, based on the notion that mindfulness enhances attentional awareness. Participants were assigned to either an audio exercise in mindful breathing or an audio control condition, and then completed a Stroop task while EEG was recorded. The primary EEG measure of interest was error-related alpha suppression (ERAS), an index of self-monitoring in which alpha power is reduced, suggesting mental engagement, following errors compared to correct responses. Participants in the mindful-breathing condition showed increased alpha power during the listening exercise and enhanced ERAS during the subsequent Stroop task. These results indicate enhanced error-monitoring among those in the mindful-breathing group.

Descriptors: Mindfulness, Attention, Self-monitoring, Error-monitoring, EEG, Alpha

Recent years have seen a rapid growth in research on psychological and physical aspects of mindful meditation. Originally derived from contemplative religious traditions, the concept of mindfulness has been adapted to secular contexts and examined from scientific perspectives. Mindfulness, as articulated by a key proponent, involves “the awareness that emerges through paying attention on purpose, in the present moment, and nonjudgmentally to the unfolding of experience moment by moment” (Kabat-Zinn, 2003, p. 145). Literature reviews suggest that training in mindful practices may be beneficial in coping with numerous psychological and physical conditions, including depression, anxiety, cancer, chronic pain, and hypertension (e.g., Bishop et al., 2004; Brown & Ryan, 2003; Brown, Ryan, & Creswell, 2007; Chiesa & Serretti, 2010; Ivanovski & Malhi, 2007; Keng, Smoski, & Robins, 2011).

Despite increasing evidence of the widespread benefits of mindfulness for well-being, its mechanisms of action are less well understood. As prior reviewers of the literature have pointed out (e.g., Bishop et al., 2004; Cahn & Polich, 2013; Tang, Hölzel, & Posner, 2015), difficulties in pinning down precise mechanisms may be due to the elusiveness and breadth of the concept of mindfulness as well as the varied ways in which mindfulness has been operationalized in research studies, including those that consider transient, state-related effects of meditation as well as those that consider longer-term changes in mental outlook induced by extensive meditative practice. It is also difficult to disentangle psychological characteristics specific to mindful meditation from those

shared with other experiential training approaches such as transcendental or concentrative meditation or relaxation training.

One possible mechanism of the psychological effects of mindfulness practice involves attention (e.g., Hölzel et al., 2011; Malinowski, 2013). As articulated by its proponents, mindfulness involves changes in attentive awareness, including an emphasis on observing and noticing without judging (Bishop et al., 2004; Kabat-Zinn, 2003). Indeed, numerous studies have found that mindfulness is associated with improved performance on cognitive tasks of attentional awareness, focus, and orienting (e.g., Chiesa, Calati, & Serretti, 2011; Hodgins & Adair, 2010; Jha, Krompinger, & Baime, 2007; Malinowski, 2013; van den Hurk, Gionmi, Giesen, Speckens, & Barendregt, 2010). Enhanced attentional control may improve the ability to regulate emotional responses to events (Teper, Segal, & Inzlicht, 2013). The possible role of attentional control in the mechanisms of mindfulness is further supported by evidence that mindfulness alters activity in frontal-lobe regions important in attentional control (e.g., Allen et al., 2012; Froeliger, Garland, Modlin, & McClernon, 2012; Hasenkamp & Barsalou, 2012; for review, see Tang et al., 2015).

The present study focuses on a particular aspect of attention, namely, attention to one’s own performance, which is often referred to as self-monitoring or error monitoring. The ability to adaptively meet one’s goals depends on noticing and correcting errors in thought or performance. Maladaptive self-monitoring could occur either when people fail to notice their errors, when they notice errors but fail to engage in appropriate corrective actions, or when they are overattentive to errors, as occurs in conditions such as obsessive-compulsive disorder (Olvet & Hajcak, 2008). Because optimal self-monitoring requires both awareness of errors and noncatastrophic reactions to them, self-monitoring may

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be particularly sensitive to manipulations of mindfulness, which promotes nonjudgmental awareness.

Prior studies have investigated the influence of mindfulness upon self-monitoring during cognitive performance. In one study, Teper and Inzlicht (2013) compared experienced meditators to naïve participants during a Stroop task while EEG was recorded. The authors examined the error-related negativity (ERN), an ERP that peaks within 100 ms of error commission and is thought to reflect an internal error detection process (Gehring, Liu, Orr, & Carp, 2012; Holroyd & Coles, 2002; Simons, 2010). Experienced meditators exhibited a more pronounced ERN than controls, indicating superior error detection. A second study (Larson, Steffen, & Primosch, 2013) examined neural markers of error monitoring in meditation-naïve participants who were randomly assigned to a brief mindfulness-of-breathing exercise or a control condition. Unlike Teper and Inzlicht (2013), Larson et al. (2013) did not find group differences in the ERN, but they did find that those in the mindfulness group displayed reduced amplitudes of the error positivity (Pe), another error-specific ERP that is thought to reflect the motivational salience of an error (Arbel & Donchin, 2009; Overbeek, Nieuwenhuis, & Ridderinkhof, 2005; Ridderinkhof, Ramautar, & Wijnen, 2009). Therefore, while both studies found mindfulness effects on neural signals of self-monitoring in response to errors, the studies differed in the direction of their findings and the specific neural markers that showed group differences. The most likely reason for discrepant findings is that one study compared preexisting groups (experienced meditators vs. controls) whereas the other study experimentally manipulated states of mindfulness with a brief exercise in naïve participants.

The present study extends these prior investigations by examining the influence of a mindfulness manipulation on another neural measure of self-monitoring, namely, error-related alpha suppression (ERAS). ERAS refers to a phenomenon in which oscillatory EEG activity in the alpha frequency band is suppressed following performance errors, compared to correct responses (Carp & Compton, 2009). Prior studies have found alpha suppression in response to attentional cues, presumably because such cues increase arousal and attention to task-relevant events, thereby reducing alpha power, which is correlated with relaxation or internally focused attention (Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998; Sauseng et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; see also Bollimunta, Mo, Schroeder, & Ding, 2011; Min & Park, 2010). Similarly, alpha suppression following errors may reflect greater arousal or attentional engagement following errors compared to correct responses. Independent confirmation of reduced alpha power in the intertrial interval (ITI) following error trials compared to correct trials has been obtained from several labs using varied tasks, confirming a robust phenomenon (Carp & Compton, 2009; Compton, Arnstein, Freedman, Dainer-Best, & Liss, 2011; Compton, Bissey, & Worby-Selim, 2014; Navarro-Cebrian, Knight, & Kayser, 2013; van Driel, Ridderinkhof, & Cohen, 2012). ERAS appears to be partially independent of the error-specific ERP signals (the ERN and Pe), indicating a phenomenon worthy of study in its own right (Compton, Hofheimer, & Kazinka, 2013; Compton et al., 2014).

ERAS can also be distinguished from another error-related oscillatory phenomenon that occurs in the theta range of the EEG. Prior research has shown increases in EEG activity in the theta range (approximately 4–7 Hz) following error responses compared to correct responses (e.g., Luu, Tucker, & Makeig, 2004; see Cavanagh & Frank, 2014, for review). The error-related theta effect is

most pronounced frontally, rather than posteriorly like ERAS, and it disappears within a few hundred milliseconds of the response, unlike ERAS, which persists throughout the ITI. Because the ERN also has a frontal midline scalp distribution and peaks early in the ITI, researchers have debated whether the ERN and the error-related theta effect are functionally distinct or simply two manifestations of the same underlying process (Cavanagh, Zambrano-Vazquez, & Allen, 2012; Hajihosseini & Holroyd, 2013; Yeung, Bogacz, Holroyd, Nieuwenhuis, & Cohen, 2007). Regardless, error-related theta activity is distinct from ERAS in frequency, timing, and location on the scalp, and preliminary findings suggest that it may differ functionally as well, with alpha more sensitive than theta to error-related lapses in sustained attention (van Driel et al., 2012).

The primary purpose of the present study was to examine whether induction into a mindful state has effects on the ERAS phenomenon. If mindfulness increases awareness and attentional engagement toward relevant events, ERAS may be more pronounced in participants characterized by a more mindful mental state. As a first step in addressing this hypothesis, the present study experimentally manipulated state mindfulness in two groups of participants, a group that engaged in an audio-based mindful breathing exercise and a control group that listened to the same narrator describe key concepts of mindfulness. Individual differences in trait levels of mindfulness and prior experience with mindful practice were also quantified in order to ensure that group comparisons were not confounded by these factors. All participants subsequently completed a Stroop task that has elicited ERAS in prior studies (e.g., Carp & Compton, 2009; Compton et al., 2013). The key question of the study was whether induction into a mindful state would alter neural activity associated with self-monitoring, as operationalized primarily by the ERAS pattern of alpha oscillations during the Stroop task. The ERN, Pe, and theta activity were examined as secondary measures of interest. EEG activity during the mindfulness manipulation itself was also quantified to assess whether the manipulation altered concurrent mental state.

Method

Participants

Participants were undergraduate students ($n = 44$; 14 male), divided into two experimental conditions, mindfulness ($n = 23$; 9 male) and control ($n = 21$; 5 male). Two participants were excluded from Stroop behavioral and EEG data analysis due to excessively high error rate that indicated misunderstanding of the task instructions, and five participants were excluded from Stroop EEG analysis due to technical difficulties.

Procedure

Before coming into the lab for the main experiment, participants completed a brief prescreening questionnaire assessing trait mindfulness and trait anxiety. Trait mindfulness was assessed using the 39-item Five Facet Mindfulness Questionnaire (FFMQ; Baer et al., 2008), and trait anxiety was assessed with the 16-item Penn State Worry Questionnaire (PSWQ; Meyer, Miller, Metzger, & Borkovec, 1990).

In the main experiment, participants were run in individual testing sessions following a procedure that was identical for mindfulness and control conditions except for the audio exercise that manipulated mindfulness. After completing informed consent,

participants were fitted with the electrode EEG cap. Next, participants engaged in either a mindfulness meditation exercise or a control listening exercise (described below) while EEG was recorded. Immediately following the audio exercise, participants completed the 20-item state anxiety scale of the State Trait Anxiety Inventory (STAI; Spielberger, 2010). Next, participants completed the Stroop task while EEG was recorded. Finally, participants completed a single-item survey assessing prior familiarity and experience with mindfulness meditation techniques on a scale of 1 to 10, 1 denoting “never heard of mindfulness meditation previously” and 10 indicating “prior experience engaging in mindfulness meditation practices.”

Mindfulness and Control Exercises

Mindfulness and control condition exercises were chosen from Jon Kabat-Zinn’s *Mindfulness for Beginners* two-disc CD set, following methods outlined by Larson et al. (2013). Participants in the mindfulness condition engaged in a *Mindfulness of Breathing* audio exercise (time = 14:33 min), focused on attending to breath and being mindful in the moment. Control participants listened to two instructional CD sections on mindfulness, including *Awareness, A Sixth Sense* (time = 7:41 min) and *An Ethical Foundation* (time = 6:38 min), presented consecutively. These clips included educational information on environmental awareness and ethical behavior, though they did not involve any mindfulness meditation practice. Audio clips for the two conditions were read by the same narrator.

Stroop Task

Participants completed a six-option Stroop test modeled after Compton et al. (2013). A six-choice task was used to increase the probability of errors and Stroop interference. The task included a series of color words, each presented in a font color that either matched (congruent trial) or did not match (incongruent trial) the semantic meaning of the word. The task also incorporated words unrelated to color, such as “dog,” which comprised the neutral trials. Participants were instructed to indicate the font color of each word by a keystroke response. The six possible responses included red, orange, yellow, green, blue, and purple, which were mapped from left to right across the keyboard. Responses were elicited by the first three fingers of each hand, with corresponding keys mapped to one of the six color options.

Each trial involved presentation of a stimulus word against a black background for 150 ms, followed by a blank screen until the participant made a response or for a maximal duration of 2,000 ms. Once a response was elicited, a blank screen was displayed for a 1,280-ms ITI before onset of the next trial. Participants completed 24 practice trials, in which they received explicit accuracy feedback to ensure they understood the instructions and the stimulus-response keystroke mapping. No such explicit feedback was provided on the remainder of the experimental trials. After the practice trial set, participants completed eight experimental trial blocks with 90 trials per block (30 each of congruent, incongruent, and neutral trials, in random order), creating a total of 720 experimental trials per participant.

Electrophysiological Recording and Processing

Electrodes were applied using an elastic cap (Quik-Cap) embedded with sintered Ag/AgCl electrodes. EEG was continuously recorded

from four midline scalp sites (Fz, FCz, Cz, Pz), as well as three pairs of lateral sites (F3/4, C3/4, P3/4). Electrical signals were amplified using a NuAmps amplifier controlled by NeuroScan software, with a sampling rate of 1000 Hz and a band-pass of 0.1–40 Hz (−3 dB). The right mastoid site was used as an online data reference point, and data were digitally rereferenced offline to the average of left and right mastoid sites. Eye movements were monitored by electrodes placed above and below the left eye and at the outer canthus of each eye. Recordings from these facial sites were used to compute bipolar horizontal and vertical electrooculogram channels offline.

Artifacts were attended to offline in a series of steps. Initially, the EEG record was visually examined for portions with large non-blink artifacts, and these sections were manually excluded. Next, NeuroScan software’s regression-based algorithm for ocular artifact rejection was employed to decrease the influence of blinks on EEG data. Any remaining artifacts were identified using a ± 150 μ V threshold, and the epochs corresponding to these artifacts were excluded.

Alpha power was computed for three main periods of interest during the procedure, one of which was during the audio exercise and two of which were during the Stroop task. First, alpha power was computed throughout the audio listening exercise, to quantify the effect of the breathing exercise on concurrent EEG activity. Data from the first minute of the audio exercise were discarded to eliminate effects related to transitioning to the task, and data from the next 12 min of the audio exercise were broken into consecutive 256-ms epochs for analysis. Second, to assess EEG activity during stimulus processing in the Stroop task, alpha power was computed for two 256-ms intervals (total of 512 ms) immediately following each stimulus onset. Third, to assess EEG activity following overt responses, alpha power was extracted from five 256-ms epochs following each keystroke response, thereby covering the 1,280-ms ITI between trials. Postresponse alpha power was quantified separately following correct and error responses. Each of these analyses was conducted on data from nine electrode sites, located at left, midline, and right locations in frontal, central, and parietal regions (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4).

In each of these segments of interest, power spectra were computed via the fast Fourier transform (FFT) using a cosine windowing method. Under the FFT approach, frequency ranges are constrained by the epoch length. Because the epoch length was set at 256 ms (to allow investigation of changes in oscillatory power across the ITI), the FFT yields estimates for frequency bands with approximately 4 Hz precision. Bands of interest were centered at 3.91 Hz (2–6 Hz band, hereby labeled *theta*), 7.81 Hz (6–10 Hz band, hereby labeled *low alpha*), and 11.72 Hz (10–14 Hz band, hereby labeled *alpha*). Because prior research has suggested somewhat different functions associated with low and high alpha within the extended alpha range (Klimesch, 1999; Klimesch, Sauseng, & Hanslmayr, 2007), we examined low and high alpha sub-bands separately. However, exploratory analyses of the low alpha band did not yield any effects related to mindfulness, and otherwise its pattern mirrored that of the higher alpha range, so it is not further considered in this report.

Because of limits on the precision of the FFT in frequency and time dimensions, we also calculated time-frequency representations across the ITI in the Stroop task as a supplementary means of representing the data. The time-frequency analyses used a Morlet wavelet analysis implemented in EEGLAB (maximum frequency = 40 Hz; wavelet cycles setting 3, 0.5). The resulting plots depict event-related spectral perturbation, namely, changes in

Table 1. Descriptive Statistics for Self-Report Measures

Measure	Mean (<i>SEM</i>)	Range
FFMQ nonreactivity	20.9 (0.6)	14–29
FFMQ observing	25.2 (0.9)	15–37
FFMQ awareness	20.7 (1.0)	11–40
FFMQ describing	23.7 (0.5)	15–29
FFMQ nonjudging	21.8 (1.0)	12–40
Mindfulness experience	5.6 (0.4)	1–10
STAI	32.3 (1.5)	20–63
PSWQ	51.2 (1.7)	29–73

activity over time and across frequencies relative to the prereponse baseline.

Finally, the ERPs, ERN and Pe, were extracted from response-locked epochs that began 200 ms before the response and extended to 600 ms postresponse. Epochs were baseline-corrected, with the baseline defined as voltages in an interval ranging from 200 to 100 ms prereponse, and were separately averaged for correct and error trials. The most negative value between –50 and 100 ms surrounding a button press response was used to define the ERN. The Pe was defined as the mean amplitude between 100 and 300 ms postresponse. Analysis of the ERN and Pe data focused on the midline sites (Fz, FCz, Cz, Pz) where these phenomena are most reliably observed.

Statistical analysis relied upon *t* tests for self-report variables and mixed-factorial analysis of variance (ANOVA) for the performance and EEG data. For all ANOVAs of EEG data, the Greenhouse-Geisser correction was applied to correct for violations of sphericity. Partial eta-squared (η_p^2) values are presented to quantify effect sizes for significant effects ($ps < .05$).

Results

Self-Report Data

Means for self-report data (FFMQ, PSWQ, STAI, mindfulness experience) are presented in Table 1. Participants in the mindful and control conditions did not differ on any of the self-report measures ($-1.5 < ts < 1.2$, $ps > .14$). Because these variables were not correlated with behavioral or EEG measures, they are not considered further.

Performance Data

Accuracy (proportion correct) and reaction time (RT; on correct trials only) during the Stroop task were submitted to ANOVAs with the between-subjects factor condition (mindful, control) and the repeated measures factor trial type (congruent, incongruent, neutral). For both dependent variables, expected Stroop congruency effects emerged. The main effect of trial type on accuracy, $F(2,80) = 18.24$, $p < .001$, $\eta_p^2 = .31$, was due to lower accuracy (Bonferroni post hoc, $ps < .001$) on incongruent trials ($M = 0.88$, $SEM = 0.02$) than either congruent trials ($M = 0.91$, $SEM = 0.02$) or neutral trials ($M = 0.92$, $SEM = 0.02$), which did not differ. Likewise, in the RT data, the main effect of trial type, $F(2,80) = 121.50$, $p < .001$, $\eta_p^2 = .75$, was due to slower responses (Bonferroni post hoc, $ps < .001$) on incongruent trials ($M = 688$ ms, $SEM = 20$) compared to congruent ($M = 598$ ms, $SEM = 17$) or neutral trials ($M = 588$ ms, $SEM = 17$), which did not differ. Together, these effects confirm the well-established phenomenon that color-word incongruency decreases accuracy and slows

responses. The factor condition did not affect either accuracy or RT.

Behavioral data were also examined for post-error changes in speed and accuracy, which could reflect processes of attentional control (Danielmeier & Ullsperger, 2011). Both accuracy and RT data were submitted to ANOVAs with the between-subjects factors condition and the within-subject factor previous-trial accuracy (previous trial correct vs. error). In the accuracy data, the main effect of previous-trial accuracy, $F(1,40) = 6.03$, $p < .02$, $\eta_p^2 = .13$, was due to lower accuracy following errors ($M = 0.87$, $SEM = 0.03$) compared to following correct responses ($M = 0.91$, $SEM = 0.01$). In the RT data, the main effect of previous-trial accuracy, $F(1,40) = 38.99$, $p < .001$, $\eta_p^2 = .49$, was due to slower responses following errors ($M = 678$ ms, $SEM = 23$) compared to following correct trials ($M = 617$ ms, $SEM = 19$). Thus, on the trials following mistakes, performance was both slower and less accurate than on trials following correct button presses. Neither of these effects further interacted with condition.

EEG Data

Alpha power during audio listening task. Log alpha power during the audio listening task was analyzed to compare EEG activity while engaging in either mindful breathing or the control audio exercise. The ANOVA included the between-subjects factor condition (mindful, control) and the within-subject factor site (including nine levels corresponding to each of the nine targeted electrode sites).

The main effect of condition was significant, $F(1,42) = 6.40$, $p < .02$, $\eta_p^2 = .13$, due to higher alpha power in the mindful condition ($M = 1.48 \mu V^2$, $SEM = 0.06$) than the control condition ($M = 1.27 \mu V^2$, $SEM = 0.06$). In addition, regional differences in alpha power were evident in the main effect of site, $F(8,336) = 54.16$, $p < .001$, $\eta_p^2 = .56$, and the Condition \times Site interaction, $F(8,336) = 2.95$, $p < .05$, $\eta_p^2 = .06$. As illustrated in Figure 1, posterior scalp sites tended to have higher alpha power and to better differentiate between mindful and control groups. No other effects were significant. In sum, the alpha power data were consistent with the expectation of greater mental relaxation (and thus higher alpha power) during the mindfulness-of-breathing exercise.

Alpha power during Stroop stimulus processing. Alpha power in the 512-ms interval immediately following each stimulus presentation was analyzed to address whether the mindfulness manipulation affected alpha power during stimulus processing. While the main question of interest involved alpha power during response processing, patterns of alpha activity during stimulus processing can help provide a context for evaluating whether any response-related group differences are evident throughout the task or only during response-monitoring epochs. Stimulus-locked data were examined by an ANOVA with between-subjects factor condition and within-subject factors site and epoch (beginning at 0 ms and 256 ms following stimulus onset, respectively). A preliminary analysis that separated data by trial type (congruent, incongruent, neutral) found no significant effects involving the trial type factor, so the data were collapsed across this factor for simplicity.

No effects of condition were significant. The main effect of epoch, $F(1,35) = 116.99$, $p < .001$, $\eta_p^2 = .77$, was due to higher alpha in the first poststimulus epoch ($M = 1.39 \mu V^2$, $SEM = 0.05$) than the second epoch ($M = 1.15 \mu V^2$, $SEM = 0.04$). The main effect of site, $F(8,280) = 40.81$, $p < .001$, $\eta_p^2 = .54$, reflected the

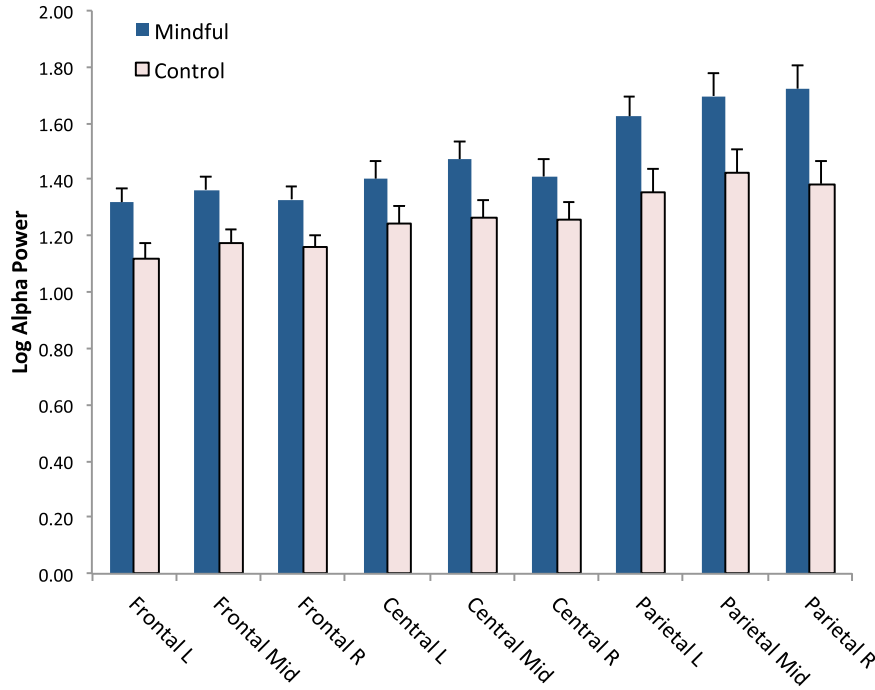


Figure 1. Log alpha power (in μV^2) during the audio listening exercise for participants in the mindful and control groups. L = left hemisphere; R = right hemisphere; Mid = midline site.

typical posterior distribution of alpha power (see means in Table 2). Moreover, the Site \times Epoch interaction, $F(8,280) = 11.99$, $p < .001$, $\eta_p^2 = .26$, revealed a pattern in which regional differences in alpha power were more pronounced at the earlier epoch (see Table 2). In sum, although expected regional effects on alpha power were evident, the mindfulness manipulation did not affect alpha power during stimulus processing.

Alpha power during Stroop response processing. To examine the effect of the mindfulness-of-breathing exercise on EEG responses to errors versus correct responses in the Stroop task, alpha power data from the ITI were submitted to an ANOVA with the between-subjects factor condition and the repeated measures factors accuracy (correct, error), epoch during the ITI (beginning 0, 256, 512, 768, and 1,024 ms postresponse), and site.

Most crucially for the present investigation, both the main effect of accuracy, $F(1,35) = 12.75$, $p = .001$, $\eta_p^2 = .27$, and the Condition \times Accuracy interaction, $F(1,35) = 4.17$, $p < .05$, $\eta_p^2 = .11$, were significant. The main effect was due to higher alpha power following correct responses ($M = 1.45 \mu V^2$, $SEM = 0.05$) compared to errors

($M = 1.39 \mu V^2$, $SEM = 0.05$), confirming an overall ERAS effect similar to prior datasets (e.g., Carp & Compton, 2009; Compton et al., 2011, 2013, 2014). The interaction effect indicated that ERAS was more pronounced in the mindfulness-of-breathing group (correct $M = 1.50 \mu V^2$, error $M = 1.41 \mu V^2$, $SEMs = 0.07$; simple main effect of accuracy, $F(1,16) = 11.28$, $p < .005$) compared to the control group (correct $M = 1.40 \mu V^2$, error $M = 1.38 \mu V^2$, $SEMs = 0.06$; simple main effect of accuracy, $F(1,19) = 1.69$, $p = .21$).

Additional effects in the omnibus ANOVA reflected variations in alpha power across electrode site and epoch. Most importantly,

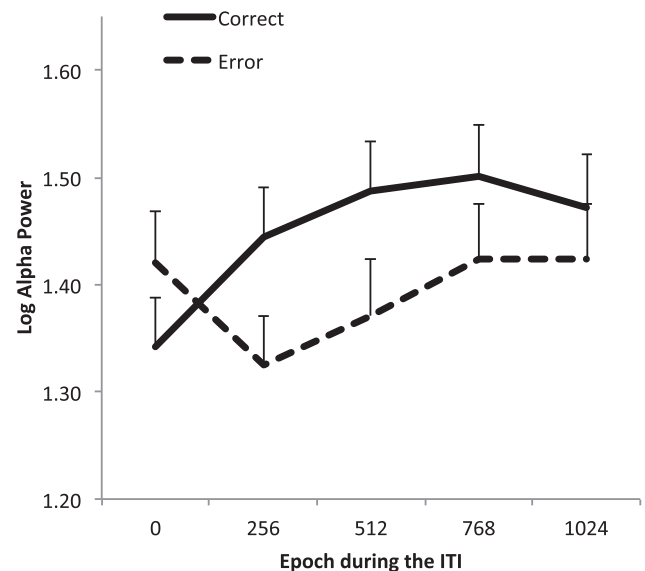


Figure 2. Log alpha power (in μV^2) across the intertrial interval (ITI) in the Stroop task, at epochs beginning at 0, 256, 512, 768, and 1,024 ms after the button press response.

Table 2. Mean (SEM) Log Alpha Power Values (in μV^2) During the First 512 ms of Stimulus Processing, as a Function of Electrode Site and Epoch

Site	Epoch 1 (0–255 ms)	Epoch 2 (256–511 ms)	Average
F3	1.26 (0.04)	1.03 (0.03)	1.14 (0.03)
Fz	1.32 (0.04)	1.08 (0.03)	1.20 (0.03)
F4	1.27 (0.04)	1.06 (0.03)	1.17 (0.03)
C3	1.33 (0.05)	1.10 (0.04)	1.21 (0.04)
Cz	1.42 (0.05)	1.20 (0.04)	1.31 (0.04)
C4	1.36 (0.05)	1.15 (0.04)	1.25 (0.04)
P3	1.47 (0.06)	1.18 (0.04)	1.32 (0.05)
Pz	1.56 (0.06)	1.31 (0.05)	1.44 (0.05)
P4	1.56 (0.06)	1.24 (0.05)	1.40 (0.05)

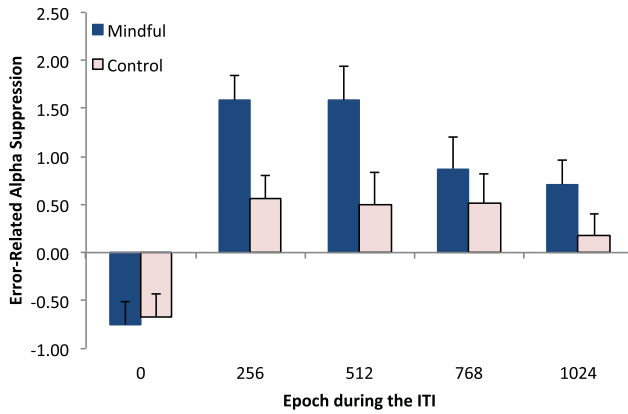


Figure 3. Error-related alpha suppression during the Stroop task, calculated as log alpha power on correct trials minus log alpha power on error trials, for five epochs during the intertrial interval (ITI). Time 0 is the time of the button press response, and each successive epoch is 256 ms in duration.

the main effect of epoch, $F(4,140) = 12.58$, $p < .001$, $\eta_p^2 = .26$, and the Accuracy \times Epoch interaction, $F(4,140) = 22.01$, $p < .001$, $\eta_p^2 = .39$, revealed the typical waxing and waning of alpha power during the ITI. (This interaction effect was also significant in each group considered separately, $F_s > 6$, $ps < .01$, indicating expected patterns of ERAS across epochs for both groups.) As illustrated in Figure 2, ERAS emerged during the epoch beginning at 256 ms, and tapered off by the end of the ITI. Effects of site, $F(8,280) = 6.41$, Accuracy \times Site, $F(8,280) = 29.47$, Epoch \times Site, $F(32,1120) = 23.87$, and Accuracy \times Epoch \times Site, $F(32,1120) = 35.18$, all $ps < .002$, are not detailed here due to low relevance to present aims, but generally depict a pattern in which parietal sites show the highest alpha power, the earliest changes during the ITI, and the greatest error-related alpha suppression.

Because of the significant changes in alpha power and ERAS across the epochs of the ITI in the group as a whole, a subsequent analysis sought to more closely examine the pattern across epochs for the mindful versus control groups. In particular, this examination can help to ascertain whether the group differences in ERAS reflect a reaction to the accuracy of the response, or whether they precede the response, as could be the case if the groups differed somehow in processes leading to an error. If group differences precede the response, they should be evident even in the earliest epoch of the ITI (e.g., beginning at Time 0). Alternatively, if group differences in ERAS were due to a reaction to the error (vs. correct trial), the group differences should emerge during the ITI.

To address these questions, an exploratory analysis examined alpha suppression scores, which were calculated for each of the five epochs by summing correct-trial alpha values across all nine sites and subtracting from that the sum of error-trial alpha values across all nine sites. The result was a set of five values for each participant, representing ERAS for each of the five epochs. These values were submitted to an ANOVA with condition and mindful experience as between-subjects factors and epoch as the single repeated measures factor. The main effect of condition was significant, $F(1,35) = 4.16$, $p < .05$, $\eta_p^2 = .11$, reflecting greater alpha suppression for the mindful versus control group, consistent with the previous analysis. The effect of epoch, $F(4,140) = 21.91$, $p < .001$, $\eta_p^2 = .39$, reflects the waxing and waning of alpha suppression over the ITI, also consistent with the pattern in the prior analysis. Although the Epoch \times Condition effect was only margin-

Table 3. Log Theta Power (in μV^2) for Correct and Error Trials as a Function of Electrode Site

Site	Correct	Error	Error minus correct
F3	1.60 (0.02)	1.68 (0.02)	0.08
Fz	1.69 (0.02)	1.78 (0.02)	0.09
F4	1.63 (0.02)	1.69 (0.02)	0.06
C3	1.54 (0.02)	1.60 (0.02)	0.06
Cz	1.64 (0.02)	1.71 (0.02)	0.07
C4	1.56 (0.02)	1.61 (0.02)	0.05
P3	1.56 (0.03)	1.59 (0.02)	0.03
Pz	1.63 (0.02)	1.66 (0.02)	0.03
P4	1.59 (0.03)	1.62 (0.03)	0.03

ally significant, $F(4,140) = 2.42$, $p = .09$, $\eta_p^2 = .07$, means for the interaction were examined to address the timing of group differences. As is evident in Figure 3, effects of condition did not emerge until the 256-ms epoch; the group means in the 0–255 ms epoch were essentially identical. This additional analysis, although exploratory, implies that the group differences emerged following the button presses rather than preceding them.

In sum, analyses of alpha power during the ITI found typical ERAS effects, and also found that the mindful group displayed these effects to a significantly greater extent than the control group.

Theta power during Stroop response processing. Log theta power was examined by a mixed-factorial ANOVA that paralleled the analysis for the alpha data, namely, including the between-subjects factor condition and the repeated measures factors accuracy, epoch during the ITI, and site.

A main effect of accuracy, $F(1,35) = 25.85$, $p < .001$, $\eta_p^2 = .43$, replicated prior findings by showing greater theta power following errors ($M = 1.66 \mu V^2$, $SEM = 0.02$) compared to correct responses ($M = 1.60 \mu V^2$, $SEM = 0.02$). Unlike the alpha power data, there was no Accuracy \times Condition interaction, $F < 1$.

Additional effects revealed the expected pattern of theta across the scalp sites and over time. Means for the main effect of site, $F(8,280) = 31.36$, $p < .001$, $\eta_p^2 = .47$, and the Accuracy \times Site interaction, $F(8,280) = 14.51$, $p < .001$, $\eta_p^2 = .29$, listed in Table 3, reflect the frontal maximum of the error-related theta effects. Means for the main effect of epoch, $F(4,140) = 59.96$, $p < .001$, $\eta_p^2 = .63$, and the Accuracy \times Epoch interaction, $F(4,140) = 14.40$, $p < .001$, $\eta_p^2 = .29$, are presented in Table 4 and reflect the presence of error-related theta effects only early in the ITI. The Accuracy \times Epoch \times Site interaction, $F(32,1120) = 1.97$, $p < .05$, $\eta_p^2 = .05$, is not considered further due to the large number of means involved and the irrelevance to the present aims.

In sum, analyses of activity within the theta range of the EEG found robust increases in theta following errors compared to correct trials, particularly in more frontal regions and in the first few hundred milliseconds following the erroneous response. However,

Table 4. Log Theta Power (in μV^2) for Correct and Error Trials as a Function of Epoch Within the Intertrial Interval

Epoch (ms)	Correct	Error	Error minus correct
0–255	1.65 (0.02)	1.81 (0.03)	0.16
256–511	1.63 (0.02)	1.70 (0.03)	0.08
512–767	1.61 (0.02)	1.64 (0.02)	0.02
768–1,023	1.57 (0.02)	1.58 (0.03)	0.00
1,024–1,279	1.56 (0.02)	1.56 (0.03)	0.00

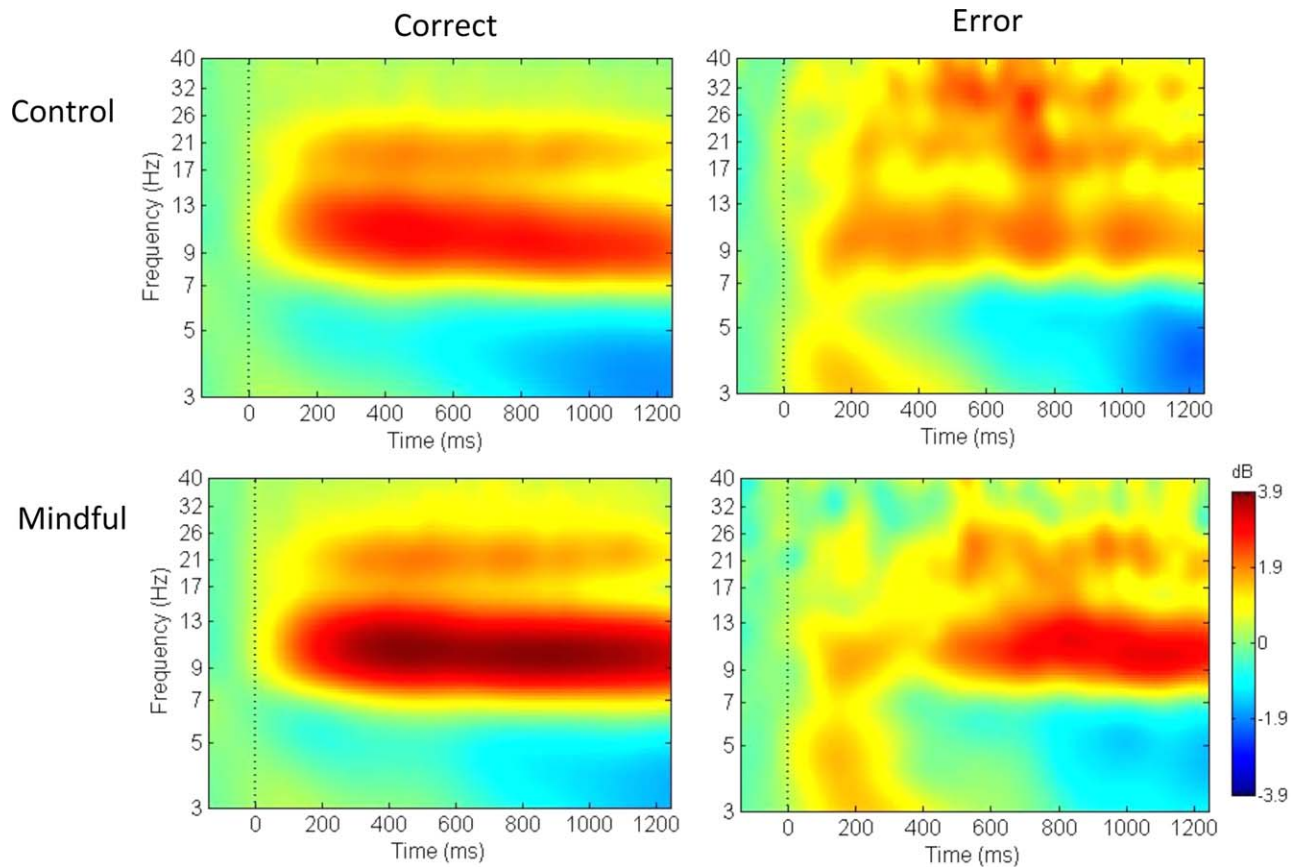


Figure 4. Time-frequency plots, presented for descriptive purposes, at the Pz site for correct trials (left) and error trials (right), separately for the control condition (top) and mindful breathing condition (bottom). Time 0 is the button press response.

unlike ERAS, these effects were not modified by mindful versus control condition.

Time-frequency analyses during Stroop response processing.

Time-frequency plots were calculated to represent response-related effects across the entire frequency spectrum. These plots are presented for descriptive purposes, to supplement and further illustrate the results that were statistically analyzed with the FFT in prior sections. Figure 4 illustrates the time-frequency plots from the Pz site separated by response accuracy (correct, error) and condition (control, mindful). The figure confirms the patterns evident in the targeted FFT analyses, specifically illustrating error-related alpha effects in the group as a whole (more activity in the alpha range following correct vs. error trials), as well as the group differences (greater correct-error difference in the alpha range for mindful vs. control groups).

ERP Data

Figure 5 illustrates response-locked waveforms for correct and error trials in the Stroop task, separately for the mindful and control conditions. ERN peak amplitudes were submitted to an ANOVA with the between-subjects factor condition and the within-subject factors accuracy (correct, error) and site (Fz, FCz, Cz, Pz). The main effect of accuracy, $F(1,36) = 24.31$, $p < .001$, $\eta_p^2 = .40$, was due to higher (more negative) amplitudes on error trials ($M = -4.68 \mu V$, $SEM = 0.41$) than correct trials ($M = -2.71 \mu V$, $SEM = 0.25$), confirming the presence of a negative-going error-

related peak. There were no significant effects involving condition (main effect, $p > .19$, Condition \times Accuracy, $F < 1$). Conclusions were unchanged when ERN mean amplitudes (in the interval 0–100 ms after the response) were analyzed as the dependent variable instead of peak amplitude (main effect of condition, $p > .23$, Condition \times Accuracy, $F < 1$).

Pe data were likewise submitted to an ANOVA with condition, accuracy, and site as factors. The main effect of accuracy, $F(1,35) = 5.87$, $p < .05$, $\eta_p^2 = .14$, was due to higher amplitudes on

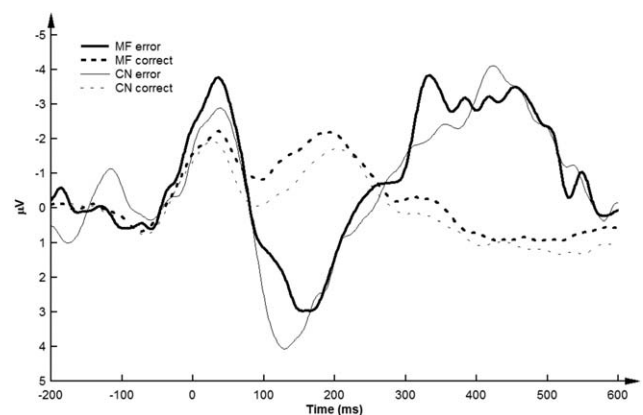


Figure 5. Response-locked waveform at the FCz site for error and correct trials in the Stroop task, separately for mindful (MF) and control (CN) groups.

error trials ($M = 1.92 \mu\text{V}$, $SEM = 0.22$) than correct trials ($M = 1.48 \mu\text{V}$, $SEM = 0.08$), confirming the presence of a positive-going error-related peak. The main effect of site, $F(3,105) = 3.51$, $p < .05$, $\eta_p^2 = .09$, was due to the fact that overall Pe values were lower at frontal sites. (Fz, $M = 1.58 \mu\text{V}$; FCz, $M = 1.74 \mu\text{V}$; Cz, $M = 1.74 \mu\text{V}$; Pz, $M = 1.74 \mu\text{V}$). There were no significant effects involving condition.

Discussion

The main goal of the study was to examine the effects of a briefly induced mindful state on neural signals of self-monitoring, particularly oscillatory EEG changes in the intervals between trials. The relatively brief mindfulness-of-breathing audio exercise increased overall alpha power simultaneously during the exercise itself (compared to a control condition), and also impacted self-monitoring during the subsequent Stroop task. Specifically, participants in the mindful condition showed an enhanced ERAS index of error-related self-monitoring. These results add to prior literature indicating that even brief mindful interventions may enhance aspects of attentional control and self-regulation.

Consistent with expectations, engaging in a mindfulness-of-breathing exercise altered concurrent EEG activity, increasing power in the alpha frequency band compared to the control group. The control group listened to the same narrator discuss theoretical aspects of mindfulness, so group differences are likely to be due to the breathing exercise itself rather than to auditory stimulation or merely thinking about concepts of mindfulness. The increase in alpha power during the mindfulness-of-breathing exercise supports theoretical conceptions that consider greater alpha power to reflect a mental state that is relaxed or characterized by inward focus of attention (e.g., Cooper, Croft, Dominey, Burgess, & Gruzeli, 2003). While alpha power changes during this specific breathing exercise have not been previously reported, a prior study reported significant decreases in systolic blood pressure during the mindfulness-of-breathing exercise, also consistent with a state of relaxation (Larson et al., 2013). Furthermore, the pattern of increased alpha during the breathing exercise fits with prior findings of increased alpha during various meditative experiences (e.g., Fan, Tang, Tang, & Posner, 2014; Lagopoulos et al., 2009; Takahashi et al., 2005; see Cahn & Polich, 2013, for review).

More relevant to the study's primary aims, the mindfulness-of-breathing exercise resulted in changes in alpha power activity during the subsequent Stroop task. Specifically, participants who engaged in the breathing exercise demonstrated more dynamic changes in alpha power during the segments of the Stroop task that involved self-monitoring of performance. Participants in the mindful condition showed differences in alpha power in the ITI following correct versus error responses to a significantly greater extent than controls. The presence of greater ERAS in the mindful group indicates that, at least by this measure, the mindful group was more responsive to the accuracy of their own performance, indicating enhanced self-monitoring. The fact that the groups did not differ in alpha power during epochs of Stroop stimulus processing suggests that the group differences were specific to self-monitoring processes rather than reflecting general differences in externally driven alpha reactivity or overall alpha power. Furthermore, the response-related group differences in alpha power did not emerge until 256 ms after the button press, supporting the conclusion of group differences in processes that monitor and evaluate performance as opposed to processes that cause a correct versus error response.

While the present study is the first to show mindfulness-induced changes in alpha reactivity during response-monitoring processes, other studies have demonstrated effects that show some conceptual similarities. For example, Kerr and colleagues (2011) found that participation in a mindfulness-based stress reduction program altered alpha power modulation in response to cues predicting upcoming somatosensory stimulation. Specifically, suppression of alpha over the hand region of somatosensory cortex in response to a "hand" cue (versus a "foot" cue) was enhanced among the meditation group, a result the authors take to indicate enhanced control of attention in the meditation group. Somewhat similarly, Cahn, Delorme, and Polich (2013) reported that experienced meditators showed enhanced modulation of alpha power in response to auditory oddball stimuli. While the specific tasks and participant characteristics differ notably across these two prior studies and the present one, what the three share in common is a finding that mindfulness is associated with greater dynamic alteration of alpha power in response to attentionally relevant task events (i.e., error vs. correct trial, sensory cue, distractor stimulus). This general pattern fits with the notion that mindful awareness enhances aspects of attention and is worthy of further exploration in future studies.

The present results have implications for theoretical conceptions of ERAS that link the phenomenon to arousal. Prior work from our lab has proposed that ERAS may reflect an arousal response to errors, perhaps mediated by a brainstem locus coeruleus response that sends norepinephrine stimulation throughout the forebrain (Carp & Compton, 2009; see also Compton et al., 2014). This conception fits with other theoretical views that norepinephrine input to the cortex can fine-tune attentional selectivity (e.g., Aston-Jones & Cohen, 2005; Bouret & Sara, 2005; Dayan & Yu, 2006). While an arousal-based conception of ERAS is plausible, it seems potentially paradoxical that a mindful group, presumably more mentally "relaxed," would show a stronger arousal response to errors (i.e., greater ERAS).

One possible resolution to this apparent paradox is to distinguish between tonic and phasic modes of arousal. Participants in the mindful condition may be more tonically relaxed (as suggested by increased alpha power throughout the audio listening task) and yet still able to phasically increase arousal as needed in response to task-relevant events, such as a stimulus onset or error detection. Closer examination of the mean alpha power values in response to correct and error trials for the two groups supports and extends this interpretation. Upon close inspection, the difference between groups is better described as higher alpha power following correct trials in the mindful versus control group, rather than lower alpha power following error trials in the mindful versus control group (though neither of the pairwise comparisons was significant on its own). In other words, it may be more accurate to describe the mindful group as more relaxed following correct trials, rather than more aroused following errors. Because the statistical group difference was restricted to the difference between correct and error trials and could not be unambiguously attributed to either correct or error trials individually, this interpretation must be considered tentative. Nevertheless, regardless of which trial type is driving the effect, the conclusion still remains that alpha power in the mindful group better differentiated between the correct and error trials, consistent with a concept of enhanced self-monitoring.

While group differences were significant for the ERAS measure, they failed to reach significance for the ERN and Pe measures of self-monitoring. Group differences were also not evident for the error-related theta activity, despite the fact that, as for the ERN and

Pe, robust error-related theta effects were evident in the sample as a whole, demonstrating sufficient preconditions for examining potential effects of condition. This pattern is broadly consistent with a theme that ERAS, error-related theta, ERN, and Pe reflect somewhat dissociable neural markers of error monitoring, as the measures do not always respond similarly to experimental manipulations (see Compton et al., 2013, 2014; van Driel et al., 2012).

The null findings for the ERN and Pe are only somewhat consistent with prior studies of mindfulness using similar paradigms. Our null results for the ERN concur with the findings of Larson et al. (2013), who used a similar experimental manipulation and also found no influence of mindfulness-of-breathing on the ERN component. Although the means (Figure 5) might suggest higher-amplitude ERN for those in the mindful group, similar to a pattern evident in Figure 4 from Larson et al. (2013), the effect did not reach significance in either study. Indeed, in the present study, the Condition \times Accuracy interaction for the ERN did not even approach significance ($F < 1$), suggesting that the modest sample size is unlikely to be a key reason for the null effect. In addition, we found no evidence of effects of mindfulness induction on the Pe marker, contrary to the findings of Larson et al. (2013).

Future research will be necessary to address whether differences across studies in the association between mindfulness and the ERN and Pe reflect systematic factors related to the varied sample characteristics (e.g., expert vs. naïve meditators) or implementations of mindfulness (e.g., brief induction vs. sustained training), or, alternatively, whether they suggest that effects of mindfulness on the ERN and Pe are unreliable. It is possible that oscillatory error-related measures such as ERAS will produce more consistent results, due to the long-known associations between alpha activity and meditative states (e.g., Fan et al., 2014; Lagopoulos et al., 2009; Takahashi et al., 2005; see also Berman & Stevens, 2015; Hinterberger, Schmidt, Kamei, & Walach, 2014); however, that speculation can only be confirmed by future replications.

While the present study implies that a brief mindfulness-of-breathing exercise enhances neural markers of self-monitoring, at least as indexed by the ERAS measure, several limitations should be acknowledged. First, because the mindfulness induction was brief, it is unknown whether similar results would be obtained in response to long-term meditative practice. A study of participants trained in the practice of mindful awareness over the long-term would be an appropriate next step. Likewise, the participant group was generally meditation-naïve, and the measurement of prior mindful experience may not have been optimized to assess individual differences in the amount and nature of prior mindfulness training.

A second limitation is that the group differences in ERAS were evident despite the fact that there were no group differences in performance, including overall accuracy and reaction time, Stroop interference, and behavioral measures of post-error adjustment (cf. Larson et al., 2013). The lack of behavioral differences may be due to the brevity of the manipulation. While it may be seen as a strength that group differences in ERAS are not confounded by performance differences such as error frequency, on the other hand, the lack of behavioral differences between groups raises the question of whether the mindfulness-induced neural changes reflected in ERAS have functional consequences for performance. This question, too, could be taken up by future research, perhaps using more demanding cognitive tasks as more sensitive probes of performance.

Despite these limitations, the present results contribute to existing literature on the effects of mindfulness on neural function by providing evidence of increased dynamic changes in oscillatory EEG activity following mindful breathing. Specifically, participants who engaged in the mindful breathing exercise exhibited greater evidence of self-monitoring, as measured by alpha suppression following errors, during a subsequent cognitive performance task. Results imply that future studies of self-monitoring in mindfulness would do well to include measures of oscillatory alpha activity as well as more traditional ERP measures.

References

- Allen, M., Dietz, M., Blair, K. S., van Beek, M., Rees, G., Vestergaard-Poulsen, P., . . . Roepstorff, A. (2012). Cognitive-affective neural plasticity following active-controlled mindfulness intervention. *Journal of Neuroscience*, 32, 15601–15610. doi: 10.1523/JNEUROSCI.2957-12.2012
- Arbel, Y., & Donchin, E. (2009). Parsing the componential structure of post-error ERPs: A principal components analysis of ERPs following errors. *Psychophysiology*, 46, 1179–1189. doi: 10.1111/j.1469-8986.2009.00857.x
- Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, 28, 403–450. doi:10.1146/annurev.neuro.28.061604.135709
- Baer, R. A., Smith, G. T., Lykins, E., Button, D., Krietemeyer, J., Sauer, S., . . . Williams, J. M. G. (2008). Construct validity of the five facet mindfulness questionnaire in meditating and nonmeditating samples. *Assessment*, 15, 329–342. doi: 10.1177/1073191107313003
- Berman, A. E., & Stevens, L. (2015). EEG manifestations of nondual experiences in meditators. *Consciousness and Cognition*, 31, 1–11. doi: 10.1016/j.concog.2014.10.002
- Bishop, S. R., Lau, M., Shapiro, S., Carlson, L., Anderson, N. D., Carmody, J., . . . Devins, G. (2004). Mindfulness: A proposed operational definition. *Clinical Psychology: Science and Practice*, 11, 230–241. doi: 10.1093/clipsy.bph077
- Bollimunta, A., Mo, J., Schroeder, C. E., & Ding, M. (2011). Neuronal mechanisms and attentional modulation of corticothalamic alpha oscillations. *Journal of Neuroscience*, 31, 4935–4943. doi: 10.1523/JNEUROSCI.5580-10.2011
- Bouret, S., & Sara, S. J. (2005). Network reset: A simplified overarching theory of locus coeruleus noradrenaline function. *Trends in Neurosciences*, 28, 574–582. doi: 10.1016/j.tins.2005.09.002
- Brown, K. W., & Ryan, R. M. (2003). The benefits of being present: Mindfulness and its role in psychological well-being. *Journal of Personality and Social Psychology*, 84, 822–848. doi: 10.1037/0022-3514.84.4.822
- Brown, K. W., Ryan, R. M., & Creswell, J. D. (2007). Mindfulness: Theoretical foundations and evidence for its salutary effects. *Psychological Inquiry*, 18, 211–237. doi: 10.1080/10478400701598298
- Cahn, B. R., Delorme, A., & Polich, J. (2013). Event-related delta, theta, alpha and gamma correlates to auditory oddball processing during Vipassana meditation. *Social Cognitive and Affective Neuroscience*, 8, 100–111. doi: 10.1093/scan/nss060
- Cahn, B. R., & Polich, J. (2013). Meditation states and traits: EEG, ERP, and neuroimaging studies. *Psychology of Consciousness: Theory, Research, and Practice*, 1, 48–96. doi: 10.1037/2326-5523.1.s.48
- Carp, J., & Compton, R. J. (2009). Alpha power is influenced by performance errors. *Psychophysiology*, 46, 336–343. doi: 10.1111/j.1469-8986.2008.00773.x
- Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, 18, 414–421. doi: 10.1016/j.tics.2014.04.012
- Cavanagh, J. F., Zambrano-Vazquez, L., & Allen, J. J. (2012). Theta lingua franca: A common mid-frontal substrate for action monitoring processes. *Psychophysiology*, 49, 220–238. doi: 10.1111/j.1469-8986.2011.01293.x
- Chiesa, A., Calati, R., & Serretti, A. (2011). Does mindfulness training improve cognitive abilities? A systematic review of neuropsychological

- findings. *Clinical Psychology Review*, 31, 449–464. doi: 10.1016/j.cpr.2010.11.003
- Chiesa, A., & Serretti, A. (2010). A systematic review of neurobiological and clinical features of mindfulness meditations. *Psychological Medicine*, 40, 1239–1252. doi: 10.1017/S0033291709991747
- Compton, R. J., Arnstein, D., Freedman, G., Dainer-Best, J., & Liss, A. (2011). Cognitive control in the inter-trial interval: Evidence from EEG alpha power. *Psychophysiology*, 48, 583–590. doi: 10.1111/j.1469-8986.2010.01124.x
- Compton, R. J., Bissey, B., & Worby-Selim, S. (2014). Task motivation influences alpha suppression following errors. *Psychophysiology*, 51, 585–595. doi: 10.1111/psyp.12212
- Compton, R. J., Hofheimer, J., & Kazinka, R. (2013). Stress regulation and cognitive control: Evidence relating cortisol reactivity and neural responses to errors. *Cognitive, Affective, and Behavioral Neuroscience*, 13, 152–163. doi: 10.3758/s13415-012-0126-6
- Cooper, N. R., Croft, R. J., Dominey, S. J., Burgess, A. P., & Gruzelier, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*, 47, 65–74. doi: 10.1016/S0167-8760(02)00107-1
- Danielmeier, C., & Ullsperger, M. (2011). Post-error adjustments. *Frontiers in Psychology*, 2, 1–10. doi: 10.3389/fpsyg.2011.00233
- Dayan, P., & Yu, A. J. (2006). Phasic norepinephrine: A neural interrupt signal for unexpected events. *Network: Computation in Neural Systems*, 17, 335–350. doi: 10.1080/09548980601004024
- Fan, Y., Tang, Y. Y., Tang, R., & Posner, M. I. (2014). Short-term integrative meditation improves resting alpha activity and Stroop performance. *Applied Psychophysiology and Biofeedback*, 39, 213–217. doi: 10.1007/s10484-014-9258-5
- Froeliger, B. E., Garland, E. L., Modlin, L. A., & McClernon, F. J. (2012). Neurocognitive correlates of the effects of yoga meditation practice on emotion and cognition: A pilot study. *Frontiers in Integrative Neuroscience*, 6, 1–11. doi: 10.3389/fnint.2012.00048
- Gehring, W. J., Liu, Y., Orr, J. M., & Carp, J. (2012). The error-related negativity (ERN/Ne). In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potentials* (pp. 231–291). New York, NY: Oxford.
- Hajihosseini, A., & Holroyd, C. B. (2013). Frontal midline theta and N200 amplitude reflect complementary information about expectancy and outcome evaluation. *Psychophysiology*, 50, 550–562. doi: 10.1111/psyp.12040
- Hasenkamp, W., & Barsalou, L. W. (2012). Effects of meditation experience on functional connectivity of distributed brain networks. *Frontiers in Human Neuroscience*, 6, 1–14. doi: 10.3389/fnhum.2012.00038
- Hinterberger, T., Schmidt, S., Kamei, T., & Walach, H. (2014). Decreased electrophysiological activity represents the conscious state of emptiness in meditation. *Frontiers in Psychology*, 5, 1–14. doi: 10.3389/fpsyg.2014.00099
- Hodgins, H. S., & Adair, K. C. (2010). Attentional processes and meditation. *Consciousness and Cognition*, 19, 872–878. doi: 10.1016/j.concog.2010.04.002
- 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. doi: 10.1037/0033-295X.109.4.679
- Hölzel, B. K., Lazar, S. W., Gard, T., Schuman-Olivier, Z., Vago, D. R., & Ott, U. (2011). How does mindfulness meditation work? Proposing mechanisms of action from a conceptual and neural perspective. *Perspectives on Psychological Science*, 6, 537–559. doi: 10.1177/1745691611419671
- Ivanovski, B., & Malhi, G. S. (2007). The psychological and neurophysiological concomitants of mindfulness forms of meditation. *Acta Neuropsychiatrica*, 19, 76–91. doi: 10.1111/j.1601-5215.2007.00175.x
- Jha, A. P., Krompinger, J., & Baime, M. J. (2007). Mindfulness training modifies subsystems of attention. *Cognitive, Affective, & Behavioral Neuroscience*, 7, 109–119. doi: 10.3758/CABN.7.2.109
- Kabat-Zinn, J. (2003). Mindfulness-based interventions in context: past, present, and future. *Clinical Psychology: Science and Practice*, 10, 144–156. doi: 10.1093/clipsy.bpg016
- Keng, S. L., Smoski, M. J., & Robins, C. J. (2011). Effects of mindfulness on psychological health: A review of empirical studies. *Clinical Psychology Review*, 31, 1041–1056. doi: 10.1016/j.cpr.2011.04.006
- Kerr, C. E., Jones, S. R., Wan, Q., Pritchett, D. L., Wasserman, R. H., Wexler, A., . . . Moore, C. I. (2011). Effects of mindfulness meditation training on anticipatory alpha modulation in primary somatosensory cortex. *Brain Research Bulletin*, 85, 96–103. doi: 10.1016/j.brainresbull.2011.03.026
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, 29, 169–195. doi: 10.1016/S0165-0173(98)00056-3
- Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., & Schwaiger, J. (1998). Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters*, 244, 73–76. doi: 10.1016/S0304-3940(98)00122-0
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, 53, 63–88. doi: 10.1016/j.brainresrev.2006.06.003
- Lagopoulos, J., Xu, J., Rasmussen, I., Vik, A., Malhi, G. S., Eliassen, C. F., . . . Ellingsen, Ø. (2009). Increased theta and alpha EEG activity during nondirective meditation. *Journal of Alternative and Complementary Medicine*, 15, 1187–1192. doi: 10.1089/acm.2009.0113
- Larson, M. J., Steffen, P. R., & Primosch, M. (2013). The impact of a brief mindfulness meditation intervention on cognitive control and error-related performance monitoring. *Frontiers in Human Neuroscience*, 7, 1–12. doi: 10.3389/fnhum.2013.00308
- Luu, P., Tucker, D. M., & Makeig, S. (2004). Frontal midline theta and the error-related negativity: Neurophysiological mechanisms of action regulation. *Clinical Neurophysiology*, 115, 1821–1835. doi: 10.1016/j.clinph.2004.03.031
- Malinowski, P. (2013). Neural mechanisms of attentional control in mindfulness meditation. *Frontiers in Neuroscience*, 7, 1–11. doi: 10.3389/fnins.2013.00008
- Meyer, T. J., Miller, M. L., Metzger, R. L., & Borkovec, T. D. (1990). Development and validation of the Penn State Worry Questionnaire. *Behaviour Research and Therapy*, 28, 487–495. doi: 10.1016/0005-7967(90)90135-6
- Min, B. K., & Park, H. J. (2010). Task-related modulation of anterior theta and posterior alpha EEG reflects top-down preparation. *BMC Neuroscience*, 11, 79. doi: 10.1186/1471-2202-11-79
- Navarro-Cebrian, A., Knight, R. T., & Kayser, A. S. (2013). Error-monitoring and post-error compensations: Dissociation between perceptual failures and motor errors with and without awareness. *Journal of Neuroscience*, 33, 12375–12383. doi: 10.1523/JNEUROSCI.0447-13.2013
- Olvet, D. M., & Hajcak, G. (2008). The error-related negativity (ERN) and psychopathology: Toward an endophenotype. *Clinical Psychology Review*, 28, 1343–1354. doi: 10.1016/j.cpr.2008.07.003
- Overbeek, T. M., Nieuwenhuis, S., & Ridderinkhof, K. R. (2005). Dissociable components of error processing: On the functional significance of the Pe vis-à-vis the ERN/Ne. *Journal of Psychophysiology*, 19, 319–329. doi: 10.1027/0269-8803.19.4.319
- Ridderinkhof, K. R., Ramautar, J. R., & Wijnen, J. G. (2009). To Pe or not to Pe: A P3-like ERP component reflecting the processing of response errors. *Psychophysiology*, 46, 531–538. doi: 10.1111/j.1469-8986.2009.00790.x
- Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., . . . Birbaumer, N. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, 22, 2917–2926. doi: 10.1111/j.1460-9568.2005.04482.x
- Simons, R. F. (2010). The way of our errors: Theme and variations. *Psychophysiology*, 47, 1–14. doi: 10.1111/j.1469-8986.2009.00929.x
- Spielberger, C. D. (2010). *State-Trait Anxiety Inventory*. Hoboken, NJ: John Wiley & Sons, Inc. doi: 10.1002/9780470479216.corpsy0943
- Takahashi, T., Murata, T., Hamada, T., Omori, M., Kosaka, H., Kikuchi, M., . . . Wada, Y. (2005). Changes in EEG and autonomic nervous activity during meditation and their association with personality traits. *International Journal of Psychophysiology*, 55, 199–207. doi: 10.1016/j.ijpsycho.2004.07.004
- Tang, Y. Y., Hölzel, B. K., & Posner, M. I. (2015). The neuroscience of mindfulness meditation. *Nature Reviews Neuroscience*, 16, 213–225. doi: 10.1038/nrn3916
- Teper, R., & Inzlicht, M. (2013). Meditation, mindfulness and executive control: The importance of emotional acceptance and brain-based performance monitoring. *Social Cognitive and Affective Neuroscience*, 8, 85–92. doi: 10.1093/scan/nss045
- Teper, R., Segal, Z. V., & Inzlicht, M. (2013). Inside the mindful mind: How mindfulness enhances emotion regulation through improvements

- in executive control. *Current Directions in Psychological Science*, 22, 449–454. doi: 10.1177/0963721413495869
- Thut, G., Nietzel, A., Brandt, S.A., & Pascual-Leone, A. (2006). [Alpha]-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, 26, 9494–9502. doi: 10.1523/JNEUROSCI.0875-06.2006
- van den Hurk, P. A., Gionmi, F., Gielen, S. C., Speckens, A. E., & Barendregt, H. P. (2010). Greater efficiency in attentional processing related to mindfulness meditation. *Quarterly Journal of Experimental Psychology*, 63, 1168–1180. doi: 10.1080/17470210903249365
- van Driel, J., Ridderinkhof, K. R., & Cohen, M. X. (2012). Not all errors are alike: Theta and alpha EEG dynamics relate to differences in error-processing dynamics. *Journal of Neuroscience*, 32, 16795–16806. doi: 10.1523/JNEUROSCI.0802-12.2012
- Yeung, N., Bogacz, R., Holroyd, C. B., Nieuwenhuis, S., & Cohen, J. D. (2007). Theta phase resetting and the error-related negativity. *Psychophysiology*, 44, 39–49. doi: 10.1111/j.1469-8986.2006.00482.x

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