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RESEARCH REPORT

Acute effects of meditation training on the waking and sleeping brain: Is it all about homeostasis?

Daniela Dentico[1,2,3,4] | **David Bachhuber**[1,2,3] | **Brady A. Riedner**[4] | **Fabio Ferrarelli**[4] | **Giulio Tononi**[4] | **Richard J. Davidson**[1,2,3] | **Antoine Lutz**[5]

[1]Center for Healthy Minds, University of Wisconsin-Madison, Madison, Wisconsin

[2]Waisman Laboratory for Brain Imaging and Behavior, University of Wisconsin-Madison, Madison, Wisconsin

[3]Department of Psychology, University of Wisconsin-Madison, Madison, Wisconsin

[4]Department of Psychiatry, University of Wisconsin-Madison, Madison, Wisconsin

[5]Lyon Neuroscience Research Center INSERM U1028, CNRS, UMR5292, Lyon 1 University, Lyon, France

Correspondence

Daniela Dentico, Center for Healthy Minds, University of Wisconsin-Madison, Madison, WI.

Email: dentico@wisc.edu

and

Antoine Lutz, Centre de Recherche en Neurosciences de Lyon (INSERM U1028, CNRS UMR5020) – Équipe Dynamique Cérébrale et Cognition (DYCOG), Centre Hospitalier Le Vinatier, Bron, France.

Email: antoine.lutz@inserm.fr

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Abstract

Our recent finding of a meditation-related increase in low-frequency NREM sleep EEG oscillatory activities peaking in the theta-alpha range (4–12 Hz) was not predicted. From a consolidated body of research on sleep homeostasis, we would expect a change peaking in slow wave activity (1–4 Hz) following an intense meditation session. Here we compared these changes in sleep with the post-meditation changes in waking rest scalp power to further characterize their functional significance. High-density EEG recordings were acquired from 27 long-term meditators (LTM) on three separate days at baseline and following two 8-hr sessions of either mindfulness or compassion-and-loving-kindness meditation. Thirty-one meditation-naïve participants (MNP) were recorded at the same time points. As a common effect of meditation practice, we found increases in low and fast waking EEG oscillations for LTM only, peaking at eight and 15 Hz respectively, over prefrontal, and left centro-parietal electrodes. Paralleling our previous findings in sleep, there was no significant difference between meditation styles in LTM as well as no difference between matched sessions in MNP. Meditation-related changes in wakefulness and NREM sleep were correlated across space and frequency. A significant correlation was found in the EEG low frequencies (<12 Hz). Since the peak of coupling was observed in the theta-alpha oscillatory range, sleep homeostatic response to meditation practice is not sufficient to explain our findings. Another likely phenomenon into play is a reverberation of meditation-related processes during subsequent sleep. Future studies should ascertain the interplay between these processes in promoting the beneficial effects of meditation practice.

Abbreviations: a, anterior; C3, C4, central electrodes 3 and 4 in the international 10–20 system; DC, direct current; EC, eyes-closed; EO, eyes open; ESS, Epworth Sleepiness Scale; F3, F4, frontal electrodes 3 and 4 in the international 10–20 system; FA, focused attention meditation; FSS, Fatigue Severity Scale; hd-EEG, high-density electroencephalography; ICA, independent component analysis; ISI, Insomnia Severity Index; LK, loving-kindness-and-compassion meditation; L, left; LTM, long-term meditators; M, midline; MNP, meditation-naïve participants; *N*, number of data points forming the significant cluster; NREM, non-REM; O1, O2, occipital electrodes 1 and 2 in the international 10–20 system; OM, open monitoring meditation; p, posterior; PSG, polysomnography; REM, rapid eye movement; R, right; *SD*, standard deviation; SnPM, statistical non-parametric mapping; SWA, slow wave activity; α, alpha; β^*, high-beta; β, low-beta; γ, gamma; δ, delta; θ, theta; σ, sigma.

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KEYWORDS
cross-frequency coupling, high-density EEG, mindfulness and compassion-and-loving-kindness meditation, NREM sleep, plasticity, resting wakefulness

1 | INTRODUCTION

Meditation has received increasing attention as a non-pharmacologic intervention to provide health-related benefits, both to promote general wellness and to alleviate symptoms of a variety of medical conditions (Kabat-Zinn, 1982; Kabat-Zinn et al., 1992; Nagendra, Maruthai, & Kutty, 2012; Sephton et al., 2007; Teasdale et al., 2000). Meditation presumably mediates its effects on health via associated changes in behavior and mental states, as well as through short-term (i.e., within session) and long-lasting (i.e., across multiple sessions) plastic changes in the brain. This basic stance is consistent with ongoing research on neuroplasticity, broadly defined as the investigation on how the experience changes the brain (Holtmaat & Svoboda, 2009; Lledo, Alonso, & Grubb, 2006).

Research in cognitive science has just started to document promising meditation-related training effect on brain structure (e.g., Hölzel et al., 2011; Lazar et al., 2005; Luders, Clark, Narr, & Toga, 2011), or on behavioral and neuroimaging markers of attention, and emotion regulation (e.g., Farb, Segal, & Anderson, 2013; Lutz, Slagter, Dunne, & Davidson, 2008; Zanesco, King, Maclean, & Saron, 2013). Effects on brain functions induced by meditation practice are likely to reflect neuroplastic changes consequent to the training of cognitive and emotional skills, but might also arise from changes merely in conscious effort or motivation resulting from demand characteristic (Jensen, Vangkilde, Frokjaer, & Hasselbalch, 2012). A promising alternative approach to identify meditation-related plastic changes in brain function is to investigate spontaneous brain activity, at rest or especially during sleep following training.

Increasing evidence suggests that meditation practice changes spontaneous oscillatory brain activity both during resting wakefulness and sleep (Cahn, Delorme, & Polich, 2013; Dentico et al., 2016; Ferrarelli et al., 2013). An increase in gamma oscillatory activity (25–40 Hz) was established in experienced meditators during resting wakefulness and NREM (non-rapid eye movement) sleep (Ferrarelli et al., 2013; Lutz, Greischar, Rawlings, Ricard, & Davidson, 2004). Furthermore, after an intense meditation session, experienced practitioners showed an increase in EEG low-frequency oscillatory activities, which peaked around 7–8 Hz during the first NREM sleep cycle, involved slow wave activity (SWA, 1–4 Hz) during the second cycle, and extended to the gamma range at the end of the night (Dentico et al., 2016).

Slow wave activity is traditionally assumed to be a marker of sleep homeostasis (Borbély, 2001) and to mediate neuroplasticity (Gorgoni et al., 2013). Further, it has been shown that experience-dependent plasticity can reflect in changes extending to a broader low-frequency range (1–11 Hz, Hung et al., 2013) than SWA. Still, our finding is somewhat surprising because it mainly involves oscillations peaking at the boundary between the theta (4–8 Hz) and alpha (8–12 Hz) ranges. In light of a consolidated body of research on sleep homeostasis (Borbély, 2001; Huber, Ghilardi, Massimini, & Tononi, 2004; Nir et al., 2011; Vyazovskiy et al., 2011), we would have predicted a topographically specific increase in NREM sleep low frequencies, with a dominant SWA component. An increase in SWA was indeed found in the second sleep cycle, as previously reported for plastic changes induced by experiences not immediately preceding sleep (Määttä et al., 2010). However, the dominant theta-alpha component of the acute changes, that we observed during sleep echoes a large body of literature pointing to a meditation-induced increase in (pre)frontal theta-alpha activity during wakefulness (Cahn & Polich, 2006). In other words, our electrophysiological findings suggest the possibility of a reactivation during sleep of the circuitry engaged by experienced practitioners during meditation practice in the day preceding the sleep recording.

Here we measured changes in brain oscillatory activity in the same long-term meditators during the post-meditation resting wakefulness relative to baseline. Based on previous reports (Cahn & Polich, 2006), we predicted an increased oscillatory activity over prefrontal and centro-parietal electrodes in the theta-alpha and beta-gamma ranges. Hence, we investigated the coupling between the changes in waking EEG and changes occurring during the following sleep. A topographically specific mapping of waking changes onto SWA would favor the hypothesis of a homeostatic response during sleep to meditation practice (Borbély, 2001). On the contrary, a mapping of waking changes onto theta-alpha (and potentially higher) NREM sleep frequencies would suggest that other phenomena might be involved, possibly processes reverberating waking meditation experience during sleep (Cahn & Polich, 2006).

2 | METHODS AND MATERIALS

2.1 | Participants

We recruited 29 right-handed long-term meditators (LTM, mean age = 50.7 ± 10.4, 15 female) with a history of daily meditation practice of at least 3 years and a minimum of 3 one-week intensive retreats. Mean duration of meditation training was 15.6 years (±7.8, *SD*). All participants were familiar with meditation practices as taught in the Theravada and/or Tibetan Buddhist traditions. These meditations practices aim at cultivating emotion regulation, attention balance, and well-being. In these traditions, attention-based meditations, like Vipassana or Insight meditation (Goldstein, Kornfield, Lama, & Robert K. Hall, 2001), include two common styles of practice: focused attention meditation (FA) and open monitoring meditation (OM, Lutz, Slagter, et al., 2008). FA meditation involves sustaining the attention on a specific object, like the breath, without being distracted. OM meditation, in contrast, aims to monitor the spontaneous flow of cognitive and emotional patterns without being taken away or reacting to them (Lutz, Slagter, et al., 2008). Complementary to these practices are emotion-based meditations such as Metta or loving-kindness-and-compassion (LK) meditation, which aim to reduce self-centered tendencies and foster altruistic behaviors. Metta meditation specifically trains loving-kindness, or the wish of happiness toward ourselves and others, as well as compassion, the wish for all beings to be free from suffering (Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008). The long-term meditators underwent three sets of resting waking and whole night sleep high-density EEG (hd-EEG) recordings: at baseline, following a full day of Vipassana practice, and following a full day of Metta meditation practice. Two participants did not complete the Vipassana meditation day of practice. Moreover, three participants were excluded from the analyses of the sleep data due to sleep disturbances (details can be found in [Dentico et al., 2016]). We also recruited 38 age and gender matched control participants, with no prior experience with meditation or mind-body techniques (mean age = 47.91 ± 10.3, 26 female). Resting waking and whole night sleep hd-EEG recordings were acquired for each of these three time points. Two female participants dropped after the baseline session and an additional five individuals (four females) did not complete the third time point. Eventually, 24 age and gender matched meditation-naïve participants (MNP) were selected for the correlation study between sleep and waking data. After an initial phone screening to collect medical and psychiatric history, each study participant underwent a thorough in-person screening. Sleep-disordered breathing and sleep-related movement disorders were also established/excluded with in-laboratory polysomnography (Dentico et al., 2016). All subjects provided written informed consent. This study was reviewed and approved by the Institutional Review Board of the University of Wisconsin-Madison.

2.2 | Study design

The experimental design consisted of three visits, separated by a 4–6 month interval. After a baseline session, the LTM completed 2 days of practice of Vipassana and Metta meditations respectively, in a randomized order. The 2 days of practice started at 7:30 a.m. and reproduced the structure of a meditation retreat. After being offered an overview and general instructions, the meditators attended six 45-min sessions of sitting meditation, three in the morning, three in the afternoon, which were separated by four 30-min sessions of walking meditation. The first session in the morning started with a short, guided meditation and the first afternoon session was introduced by a 30-min meditation inspirational talk. There was a 1-hr lunch break. The MNP completed a baseline session, 2 days of leisure which matched structurally the days of practice for the LTM, in terms of length, and physical activity. The sitting sessions involved activities such as reading, playing computer games, and watching documentaries. The participants were given instructions to walk outside or around the lab during the walking sessions. No social interaction took place between participants and administration of food and drink was held constant for both groups. Participants arrived at the sleep laboratory 5 hrs before their usual bedtime for EEG set-up and waking recordings that comprised resting state baseline and cognitive and emotional tasks. Within 1 hr of their usual bedtime, participants completed a Stanford Sleepiness Scale (MacLean, Fekken, Saskin, & Knowles, 1992) and were allowed to sleep undisturbed in the laboratory. We collected sleep EEG recordings with a 256 channel hd-EEG system (Electrical Geodesics Inc., Eugene, OR) for each of those three visits and additional measures were collected the next day.

2.3 | Self-reported measures

The socioeconomic status (Hollingshead, 1957) was administered using the Two Factor Index of Social Position to measure the level of education. The presence of depression and other mental health issues were evaluated through the Quick Inventory of Depressive Symptoms (Rush et al., 2003) and the Symptom Checklist-90-Revised (Derogatis & Cleary, 1977). Symptoms of common sleep disorders, such as restless leg syndrome and obstructive sleep apnea were measured using validated sleep rating scales, comprising the Insomnia Severity Index (ISI, Bastien, Vallières, & Morin, 2001), the Fatigue Severity Scale (FSS, Valko, Bassetti, Bloch, Held, & Baumann, 2008), the Epworth Sleepiness Scale (ESS, Johns, 1991), a sleep history questionnaire, and the Stanford Sleepiness Scale (MacLean et al., 1992). Cutoff for exclusion were an ISI > 10 and/or an FSS > 4 and/or an ESS > 9. We also assessed for LTM the perceived effect of 1 day of intensive meditation on common phenomenological features. As expected, all LTM reported changes in their experience as the results of the days of practice in “feelings of calm abiding, concentration, mindfulness, or equanimity” after the day of mindfulness meditation, and enhanced "feelings of compassion, self-compassion, or sympathetic joy" after the day of metta meditation (either +1, or +2, on a 5-point scale from −2 to +2 measuring change compared to the baseline session).

2.4 | Meditation practice

The total amount of lifetime hours of practice and the contribution of different meditation styles to the overall training were assessed based on self-reported retreat time and hours of formal (sitting and walking) meditation training per week. The total amount of lifetime hours of practice ranged from 1,526 to 32,349 hrs and the average across the 24 practitioners included in this work was 9,136 ± 7,461, *SD*. The specific contribution of meditation styles to their training were expressed in terms of percentage over the total of daily sitting meditation practice (3,890 hrs ± 2,351, *SD*). Specifically, participants were highly proficient in OM (51.2% ± 23.5%, *SD*), followed by FA (32.9% ± 22.7%, *SD*) and LK (14.5% ± 12.5%, *SD*).

2.5 | Sleep polysomnographic (PSG) assessment and hd-EEG data analysis

Six mastoid-referenced channels (F3, F4, C3, C4, O1, and O2), as well as a sub-mental electromyogram and an electrooculogram were used to assess sleep staging, in 30-s epochs according to standard criteria (Silber et al., 2007) using Alice® Sleepware (Philips Respironics, Murrysville, PA, USA). Sleep EEG recordings were scored by a registered polysomnographic technologist who was blind to the experimental conditions and reviewed by a board certified sleep medicine physician to exclude sleep disorders during the baseline session. Two participants with sleep-related movement disorders (periodic limb movement arousal index > 10/hr), and one with sleep-disordered breathing (apnea–hypopnea index > 10/hr), were excluded from the analyses. Baseline and whole-night sleep hd-EEG recordings were collected at a sampling frequency of 500 Hz with vertex-referencing, using a NetAmps 300 amplifier and NetStation software (Electrical Geodesics Inc., Eugene, OR, USA). The EEG waking baseline consisted of two 2-min eyes-closed (EC) blocks, and one 6-min eyes open (EO) block (order EC-EO-EC). EEGLAB (Delorme & Makeig, 2004) and MATLAB (MathWorks) were used for offline EEG data processing. After applying a first-order high-pass filter (Kaiser type, 0.1 Hz) to eliminate the DC shift, data were bandpass filtered (1–50 Hz), downsampled to 256 Hz (wakefulness) or 128 Hz (sleep), and cleared of large movement-related artifacts. EEG channels in which artifacts affected most of the recording were interpolated. Following average reference, ICA as implemented in EEGLAB (Delorme & Makeig, 2004) was used to remove ocular and muscle artifacts (for a description of the method, see Delorme, Sejnowski, & Makeig, 2007). The electrodes located on the neck/face region were excluded from further analyses. Computation of the power spectral density on the remaining 185 channels was conducted on 4-s epochs (wakefulness) or on 6-s epochs (sleep) by means of a Welch's averaged modified periodogram with a Hamming window. We integrated the frequency power spectrum across 1-Hz non-overlapping frequency bins ranging from 1 to 40 Hz (Dentico et al., 2016). As there was no interaction between meditation training and either EC or EO blocks, we averaged the periodogram between EC and EO blocks. REM and NREM sleep data were analyzed with a similar approach (for details see Dentico et al., 2016). We did not report any meditation-training related effect during REM sleep, therefore we only investigate here the relationship between waking and NREM sleep EEG activity. Sleep cycles were defined according to the modified criteria (Aeschbach & Borbély, 1993) of Feinberg and Floyd (Feinberg & Floyd, 1979).

2.6 | Statistics

Differences in topographical waking and NREM sleep hd-EEG power between practice sessions and baseline were assessed with statistical non-parametric mapping (SnPM, Nichols & Holmes, 2002) in MATLAB environment. Specifically, we adopted a suprathreshold cluster method that quantifies the size of connected regions (clusters) on the thresholded statistical images (topographical maps of *t*-values) derived from the observed data and after permuting the residuals under the reduced model according to the Freedman & Lane's procedure (Anderson & Robinson, 2001). In this test, the corrected *p*-value is determined by comparing the size of each suprathreshold cluster in the observed data against the permutation distribution of the maximal suprathreshold cluster size. A set of 50,000 unique combinations for each comparison was used to approximate the actual cluster distribution. The primary threshold was set to the *t*-value corresponding to $\alpha = 0.05$ for the given degrees of freedom. Our in-house algorithm was implemented to search suprathreshold neighbors not only in the adjacent channels, but also in the adjacent frequency bins and sleep cycles, to correct at once for the multiple comparisons in the space (185 electrodes), frequency (39 bins), and time (the first three sleep cycles) dimensions (Dentico et al., 2016). The point-wise Bayes factor was computed as an indicator of the strength of the effect (Rouder, Speckman, Sun, Morey, & Iverson, 2009).

SnPM was also used to assess the relationship between post-meditation acute changes in waking spontaneous brain activity and lifetime open monitoring meditation experience, previously found to be correlated with post-meditation changes in NREM sleep low-frequency activity (Dentico et al., 2016). A practitioner was excluded from this analysis due to practice values six interquartile ranges above the median.

In order to control for the effect of time between sessions and adaptation to the lab environment, we compared with SnPM the resting state hd-EEG recordings of age and gender matched control participants collected at three different time points, corresponding to the baseline and the 2 days of meditation practice. We also assessed with the same procedure how changes with respect to baseline differed between groups.

The cross-frequency and cross-region coupling between post-meditation acute changes in NREM sleep and waking spontaneous brain activity was computed within the SnPM approach described above. Due to computational intractability (number of cross-tests equal to (185 electrodes × 39 bins)^2 × 3 sleep cycles), we reduced the electrode space to 12 groups of 15 electrodes after excluding peripheral electrodes. Likewise, we reduced the frequency space to 19 frequency bins by integrating the frequencies above 15 Hz across 5-Hz bins while keeping a 1-Hz resolution for traditional sleep rhythms (Dentico et al., 2016). We computed all the possible correlations between the 12 channels by 19 frequency bins matrix of spectral values during wakefulness and the 12 channels by 19 frequency bins by three sleep cycles matrix of spectral values during sleep (i.e., $((12*19)^2 *3)$ or 155,952 total correlations). We used SnPM to identify the significant clusters of data points.

3 | RESULTS

3.1 | Acute effects of meditation training on post-meditation resting hd-EEG

We found no Group (LTM vs. MNP) by Eyes condition (eyes opened vs. eyes closed) interaction and no Group by Eyes condition by Meditation Style (mindfulness vs. compassion meditations) interaction across the frequency bins of interest in the post-meditation EEG during resting wakefulness. We therefore averaged the power values across the Eyes condition. Next, we tested for meditation-training effects specific to each meditation style (contrast mindfulness vs. compassion meditations) across all electrodes and frequency bins. As there were no differences between meditation styles in LTM after SnPM correction ($p < 0.05$), we averaged the power values across meditation styles and investigated common training effects across the two styles of meditation.

Using the average power across meditation styles, we tested for electrode-wise and frequency-wise differences between post-meditations sessions and baseline. In LTM, but not in MNP, we found a prefrontal and left parietal increase in slow and fast oscillatory EEG activity peaking at eight and 15 Hz (Figure 1, cluster size $N = 933$ data points, $p = 0.010$; and $N = 812$, $p = 0.015$, SnPM). The 41.9% and 33.1% of these data points respectively had

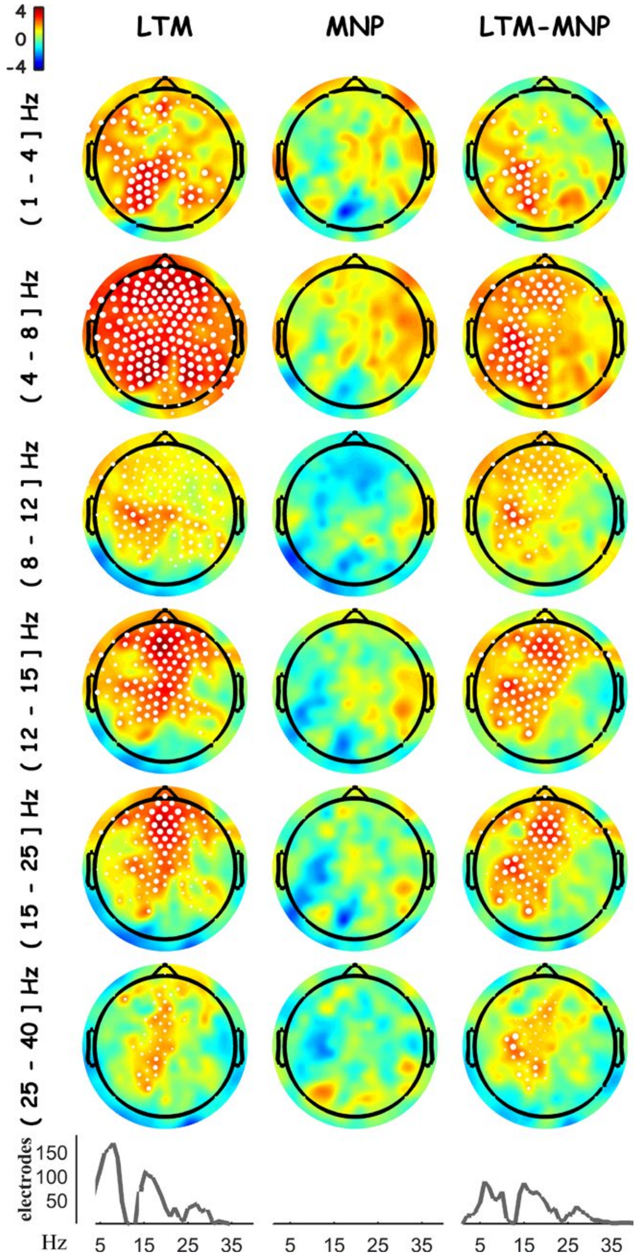

FIGURE 1 Changes in resting wakefulness after an intense meditation session. Eight hours of intense mindfulness and compassion meditation induced a prefrontal and left parietal increase in waking low and high frequency activity in long-term practitioners (LTM), but not in meditation-naïve individuals (MNP) recorded at the same time points (data pooled across practice styles). These meditation-related changes peaked at eight and 15 Hz and survived correction for the multiple comparisons ensuing from testing 185 electrodes and 39 1-Hz frequency bins (Statistical non Parametric Mapping, SnPM). The significant clusters (LTM: cluster size $N = 933$, $p = 0.010$ and $N = 812$, $p = 0.015$; LTM-MNP: $N = 1{,}168$, $p = 0.004$) are highlighted with white dots over topographical maps of t-values averaged across frequency bins for each frequency range. The size of the dots is proportional to the number of bins that is a part of a significant cluster for each electrode and frequency range. The inset at the bottom of each column shows the cluster(s) composition as number of electrodes for each frequency bin. [Colour figure can be viewed at wileyonlinelibrary.com]

Bayes factor values ranging from strong to very strong to extreme evidence for the alternative hypothesis (Supporting Information Figure S1), based on the categories reported in (Andraszewicz et al., 2015). There was no significant difference for MNP across different time points, and differential power values in LTM were significantly higher than in MNP (LTM-MNP: $N = 1168$, $p = 0.004$). The 17.0% of these data points had Bayes factor values ranging from strong to very strong to extreme evidence for the alternative hypothesis. Therefore, these meditation-related changes in LTM were not accounted for by a mere habituation effect. For purely descriptive, and not for inferential purposes, the data distribution at the peak frequencies is shown for both groups in Supporting Information Figure S2.

We had also previously excluded the possibility that our findings, in particular in low-frequency band, were associated with variations in self-reported sleepiness or changes in sleep architecture (Dentico et al., 2016).

3.2 | Effects of meditation lifetime practice on post-meditation changes in resting hd-EEG

We further explored the role of lifetime open monitoring meditation training in meditating experience-dependent changes in spontaneous waking hd-EEG. We tested the hypothesis that inter-individual variability in lifetime meditation practice would correlate with post-meditation changes. Extending our earlier report of a link between lifetime open monitoring meditation and prefrontal and left parietal changes in theta-alpha power during NREM sleep (Dentico et al., 2016), we found that open monitoring meditation training also correlated with changes in waking high-frequency activity induced in the same scalp regions by the intense meditation sessions (Figure 2, $N = 657$, $p = 0.041$, SnPM, and Supporting Information Figure S3). This finding suggests that the meditators' familiarity to meditate could facilitate the occurrence of acute changes following an intense meditation session.

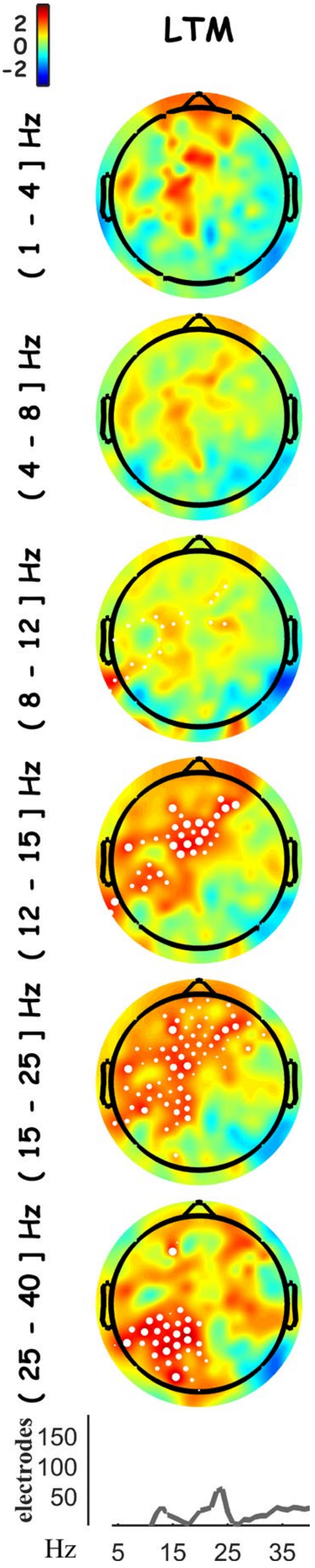

FIGURE 2 Meditation-related changes correlated with meditation experience. Lifetime open monitoring meditation experience correlated with the topography-specific changes in waking high-frequency activity following intense daylong meditation practice (data pooled across practice styles). The significant cluster ($N = 657$, $p = 0.041$, Statistical non Parametric Mapping, SnPM) is highlighted with white dots over topographical maps of *t*-values. The size of the dots is proportional to the number of 1-Hz bins that is a part of the significant cluster for each electrode and frequency range. The bottom inset shows the cluster composition as number of electrodes for each frequency bin. A participant was excluded from this analysis due to reported practice hours above six interquartile ranges from the median of practice hours across participants. [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Relationship between meditation-training related changes on waking and NREM sleep hd-EEG

We contrasted two main theoretical frames. Post-meditation changes in spontaneous waking brain activity would correlate with NREM sleep changes in SWA, indicating a homeostatic response (Borbély, 2001; Hung et al., 2013). Alternatively, post-intervention changes in wakefulness would correlate with sleep changes in the theta-alpha frequency ranges, echoing meditation-related processes (Cahn & Polich, 2006). To test these hypotheses, we investigated the cross-frequency and cross-region coupling between meditation-related changes in NREM sleep (Figure 3) and changes acutely induced by these interventions in spontaneous waking EEG. This analysis, performed on a reduced electrode and frequency space due to computational constraints (see Methods), revealed a dense pattern of cross-frequency and cross-region interactions between changes in NREM sleep and in wakefulness (cluster size $N = 14{,}138$ data points, $p = 0.026$, SnPM). Within the significant cluster, we observed a consistent mapping of waking changes to changes in sleep theta-alpha frequencies across the three sleep cycles, as it is evident from visually scanning column-wise the frequency grids in Figure 4. In contrast, the mapping of waking changes into SWA was less represented. Moreover, waking high frequencies also coupled with sleep high frequencies. The spatial composition of the same cluster is outlined in Figure 5. A row-wise visual scan of the spatial grids highlights lateral anterior scalp regions during wakefulness as the ones mainly responsible for the coupling with theta-alpha changes during NREM sleep. As for the spatial distribution during sleep, in the first and third sleep cycles, lateral scalp regions appeared to be the most engaged in coupling with waking high frequencies (peaking in the beta range), while in the second sleep cycle, anterior scalp regions were the most involved in the coupling with waking low frequencies (peaking in the theta range).

4 | DISCUSSION

In the present study, we employed hd-EEG recordings to study the effects of two intensive meditation practices (mindfulness and compassion meditation) on subsequent resting wakefulness and sleep. To our knowledge, this is the first study on meditation that combined both waking and sleep hd-EEG recordings across multiple sessions on long-term practitioners (LTM) and meditation-naïve participants (MNP). LTM exhibited an increased power compared to baseline session over midline prefrontal and left centro-parietal electrodes in several frequency bands ranging from delta to low-gamma, with the higher spatial extent in the theta range (Figure 1). These changes correlated with lifetime meditation experience (Figure 2) and overlapped with changes induced by meditation training during NREM sleep (Figure 3). These effects were absent in MNP (Figure 1), were not driven by

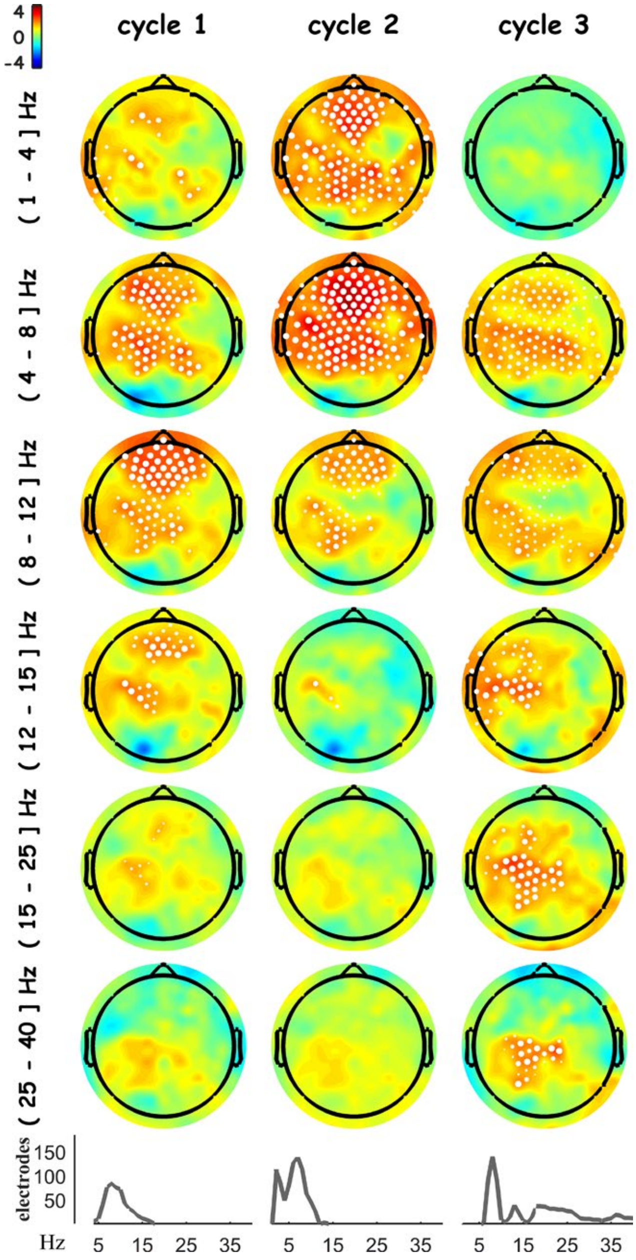

FIGURE 3 Changes in NREM sleep following an intense meditation session. The time course of NREM sleep changes occurring in long-term practitioners after 8 hrs of intense mindfulness and compassion meditation is displayed for each sleep cycle (data pooled across practice styles, Dentico et al., 2016). The significant cluster ($N = 2{,}290$, $p = 0.043$) surviving correction for the multiple comparisons ensuing from testing 185 electrodes, 39 frequency bins, and three sleep cycles, is highlighted with white dots over topographical maps of t-values (Statistical non Parametric Mapping, SnPM). The size of the dots is proportional to the number of bins that is a part of the significant clusters for each electrode and frequency range. The inset at the bottom of each column shows the cluster composition as number of electrodes for each frequency bin. [Colour figure can be viewed at wileyonlinelibrary.com]

changes in self-reported sleepiness (Dentico et al., 2016), and correlated with meditation-related changes in NREM sleep low-frequency activity, mainly in the theta-alpha range (Figures 4 and 5).

The waking EEG correlates of meditation-related effects were consistent with a large body of studies on meditation. Increase in midline frontal low-frequency (4–12 Hz) activity is reported in meditation research as a function of meditation state, or meditation trait at rest (for review see Cahn & Polich, 2006). These low frequency oscillations over frontal electrodes are also thought to be a signature of top-down processes such as working memory, focused attention, or mental effort (Klimesch, 1999). In line with this interpretation, mindfulness meditation interventions tend to produce functional and behavioral improvements on measures of attention and working memory (Cahn et al., 2013; Jha, Krompinger, & Baime, 2007; Lutz, Slagter, et al., 2008; Tang et al., 2007; Zanesco et al., 2013). By contrast, another EEG study on meditation reported an increase in fronto-parietal fast-frequency (25–42 Hz) activity, and enhanced phase-synchrony between frontal and parietal electrodes during compassion meditation, and after meditation compared to the initial resting baseline (Lutz et al., 2004). The combined increase of fast and low frequencies in this study can been seen in light of their complementary role observed in

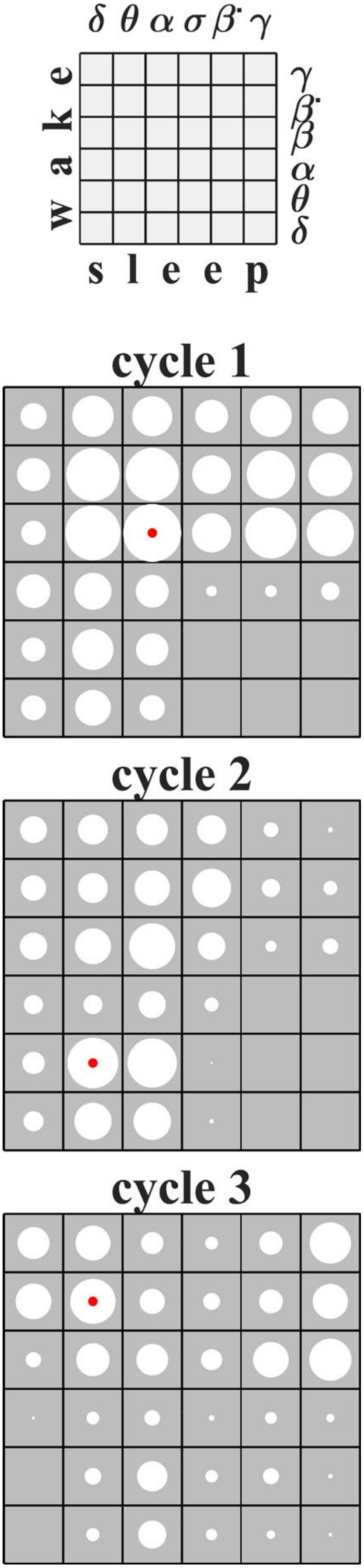

FIGURE 4 Frequency coupling between waking and NREM sleep EEG. Meditation-related changes in resting wakefulness correlated across space and frequency with meditation-related changes in NREM sleep, and this correlation peaked in the sleep theta-alpha (θ-α) frequency ranges. Frequency and temporal composition of the significant cluster ($N = 14{,}138$, $p = 0.026$, Statistical non-Parametric Mapping, SnPM) surviving correction for the multiple comparisons ensuing from computing all the possible correlations between the 12 channels by 19 frequency bins matrix of spectral values during wakefulness and the 12 channels by 19 frequency bins by three sleep cycles matrix of spectral values during sleep (i.e., $((12*19)^2 *3)$, 155,952 total correlations). More specifically, these 12 scalp channels were derived by averaging a set of 180 electrodes across groups of 15, as depicted in Figure 5. We reduced the frequency space by integrating the frequencies above 15 Hz across 5-Hz bins while keeping a 1-Hz resolution for traditional sleep rhythms, according to (Dentico et al., 2016). The three square grids represent mapping of waking to sleep frequency ranges for each of the first three sleep cycles. The axes legends are reported in the top inset: δ, (1–4] Hz; θ, (4–8] Hz; α, (8–12] Hz; β and σ, (12–15] Hz; β^*, (15–25] Hz; γ, (25–40] Hz. The dot size is proportional to the number of bins belonging to the significant cluster for each cross-frequency coupling, averaged across channel coupling. For each cycle, a red mark indicates the peak of the cross-frequency coupling. This layout was designed so that the density of dots along the columns of the frequency grids allows for an immediate representation of the sleep frequencies more involved in the waking to sleep cross-frequency coupling. The spatial dimension is absent from this graph for display purposes. [Colour figure can be viewed at wileyonlinelibrary.com]

animal research: top-down influence are associated with low-frequency activity whereas bottom-up influences are associated with fast-frequency activity (Buffalo, Fries, Landman, Buschman, & Desimone, 2011). Based on this literature, and with the caveats that we did not have any behavioral markers of attention in this study, and that one cannot infer the spatial origin of EEG oscillations from their spatial locations on the scalp, we speculate that these changes in low and fast frequency oscillations over prefrontal and left centro-parietal electrodes could reflect the recruitment during meditation of fronto-parietal attentional networks. Consistent with this interpretation, we reported here that the magnitude of lifelong training in open monitoring meditation, an attention-based practice, was associated with the magnitude of changes in wakefulness (and NREM sleep, Dentico et al., 2016) over frontal and parietal electrodes (Figure 2). This result suggests that our study captured the common attention-based mechanisms shared by mindfulness and compassion meditations. The finding of a positive correlation is important, as an alternative possibility would have been that the magnitude of lifelong daily practice reduced the extent of changes acutely occurring after a day of training (i.e., a negative correlation would manifest as a consequence of meditation experience). This finding is of clinical relevance and suggests that a daily meditation practice might be required to maintain some of the alleged positive effects of meditation training on stress or well-being.

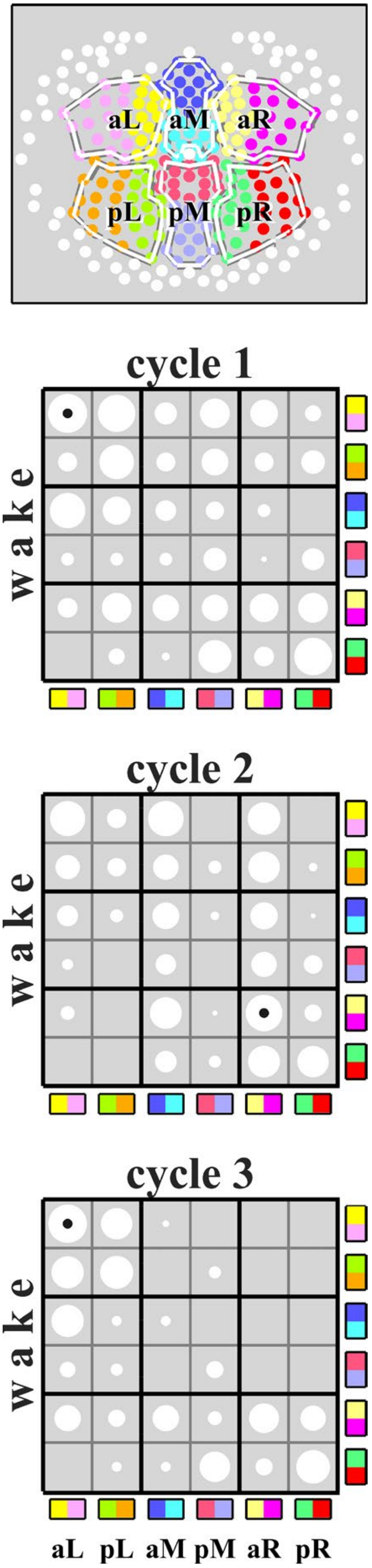

FIGURE 5 Spatial coupling between waking and NREM sleep EEG. The spatial representation of the significant cluster depicted in Figure 4 revealed a complex pattern of cross-region correlations. The top inset displays the reduced channel layout employed to decrease the data dimensionality. After excluding peripheral electrodes, the inner 180 electrodes were grouped in 12 sets of 15, following an anteroposterior criterion and a mediolateral criterion. For each cycle, the spatial composition of the significant cluster is shown at the peak of the cross-frequency coupling, indicated by a red mark in Figure 4. For each cross-channel coupling, the dot size is proportional to the number of bins belonging to the significant cluster for the given cross-frequency coupling peak. The thickest gridlines separate left (L), midline (M), and right (R) scalp regions. Within each region, and only for display purposes, data are shown averaged across anterior channels (a) and across posterior ones (p). A black mark indicates the spatial coupling peak for the given frequency coupling. Visually scanning the grid layout row-wise, it appears that the *waking* meditation-related changes in the *lateral anterior* scalp regions were the most involved in cross-frequency and cross-region interactions with meditation-related changes in NREM sleep. Specifically, a column-wise visual scan of the grid layout reveals that waking high frequencies changes mainly coupled with theta-alpha changes in *left* scalp regions in the *first and third sleep cycles*, while waking low frequencies changes mainly coupled with theta-alpha changes in *anterior* scalp regions in the *second sleep cycle*. The frequency dimension is absent from this graph for display purposes. [Colour figure can be viewed at wileyonlinelibrary.com]

Our main research question was to investigate the relationship between waking and sleep findings in order to shed further light onto the functional significance of the electrophysiological changes we acutely observed during NREM sleep (Dentico et al., 2016). A strong line of evidence supports the role of NREM sleep low frequency activity in mediating task-related region-specific neuroplastic changes after several forms of training (Huber et al., 2004; Hung et al., 2013; Määttä et al., 2010) as well as forced inactivity (Huber et al., 2006). Though most of these studies focused on measuring SWA, when theta and alpha frequencies have been reported, it appears that experience-dependent plasticity leaves traces in the sleeping brain in a broader range of low-frequencies including theta and alpha (Hung et al., 2013). Moreover, it is well-known that the range of low frequencies homeostatically regulated across the sleep cycles extends from 0.25 up to 12 Hz (Aeschbach & Borbély, 1993). Finally, an increase in SWA in the second cycle after meditation training relative to baseline is consistent with homeostatic patterns of activation following training not immediately preceding the sleep night (Määttä et al., 2010). Thus, the predominant increase in the theta-alpha range during sleep might still be a part of a broad homeostatic response. This interpretation is hampered in this study by the lack of a behavioral marker indexing neuroplasticity.

Another possibility is a reenactment of the waking patterns activated by meditation training during wakefulness. The bimodal distribution of the increase in low-frequency activity in the second cycle, with distinct peaks in SWA and in the theta-alpha range respectively (Figure 3, second column, bottom inset), hints to distinct phenomena into play. In support of this interpretation, our whole brain analysis revealed a complex pattern of cross-frequency and cross-region interactions. Interestingly, waking low-frequencies coupled with sleep low frequencies with a peak in theta-alpha in the second cycle and a fronto-prefrontal distribution. Waking high frequencies coupled with both sleep high and low-frequencies with a peak in theta-alpha in the first cycle and a spatial distribution extending to temporo-parietal regions. The mapping of a broad range of waking frequencies onto NREM sleep theta-alpha across all cycles would hint to a more specific role for the activity in the theta-alpha range during sleep on top of the homeostatic regulatory function shared with SWA. A continuity between waking and sleep electrophysiological changes could potentially subtend the retention of certain aspects of waking mentation during sleep (Marzano et al., 2011). It would be interesting in future work to broaden the research focus to a wider spectrum of low-frequencies in order to establish whether the dynamics we observed in long-term practitioners are specific for meditation training or might be as well induced by other forms of waking experience.

An important takeaway is that homeostatic regulation may not be the only (or main) key for understanding the electrophysiological changes we observed in the sleeping brain of long-term meditators. While homeostasis aims at restoring a fixed set point, learning is an allostatic, plastic phenomenon that shifts the system balance toward a new set point (Ramsay & Woods, 2014). It is worth mentioning that two contrasting mechanistic models respectively link SWA to homeostatic changes in the form of synaptic downscaling (Tononi & Cirelli, 2006) or allostatic changes in the form of synaptic upscaling (Chauvette, Seigneur, & Timofeev, 2012). Synaptic downscaling aims at renormalizing synaptic weights increased after a waking episode in order to prepare the brain to receive new information during the subsequent wakefulness. Synaptic upscaling has been linked to memory consolidation and long-term plasticity. Certainly, the present investigation does not allow for achieving insights into the microscale of the phenomenon. However, at the macroscale level, the frequency patterns observed after intense meditation in the waking and sleeping brain, together with their characteristic coupling, suggest the possibility of a maintenance during sleep of electrophysiological patterns trained during wakefulness. Meditation training would therefore entail a progressive shift toward a new set point, possibly characterized by qualitative and quantitative changes in conscious experience and in the level of connectedness with the environment. The investigation of the functional significance of these meditation-related plastic changes in terms of sleep mentation is undoubtedly a fascinating avenue to explore. Besides, our findings call for a more thorough investigation of the effect of training on sleep low frequencies beyond SWA and how these couple with electrophysiological markers of waking experience.

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CONFLICT OF INTEREST

Dr. Richard J. Davidson is the founder, president, and serves on the board of directors for the non-profit organization, Healthy Minds Innovations, Inc. In addition, Dr. Davidson serves on the board of directors for the Mind and Life Institute. No donors, either anonymous or identified, have participated in the design, conduct, or reporting of research results in this manuscript.

DATA ACCESSIBILITY

Data are available upon request because of IRB restrictions on human data. Readers are welcome to send their request to Antoine Lutz at antoine.lutz@inserm.fr.

AUTHOR CONTRIBUTIONS

Daniela Dentico: analyzed data, contributed analysis tools, wrote manuscript. David Bachhuber: collected data, analyzed data. Brady A. Riedner: analyzed data, wrote manuscript. Fabio Ferrarelli: analyzed data, wrote manuscript. Giulio Tononi: designed study. Richard J. Davidson: designed study. Antoine Lutz: designed study, analyzed data, wrote manuscript.

ORCID

Daniela Dentico http://orcid.org/0000-0003-1050-0327

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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