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Expanding the Circle of Care: An EEG Spectral and Microstate Analysis of Compassion Meditation and Rest during an Intensive Meditation Retreat

By

ALEA CORIN SKWARA DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

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of the

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Abstract

Humans have a remarkable capacity to feel and enact care for others. But this capacity is not universally expressed: decades of research have elucidated the contextual, social, cognitiveaffective, and relational factors that limit the tendency to experience empathy and engage in prosocial action. Buddhist contemplative traditions have long been concerned with the alleviation of suffering and expanding the boundaries of those who we hold in our circle of care. Recent years have seen a growth of interest in contemplative approaches to cultivating compassionate responses to suffering. This dissertation explores contemplative approaches to training compassion, focusing on the question of whether we can, with volitional training, expand the boundaries of our circle of care.

Chapter 1 draws on contemporary research from cognitive, affective, and social psychology to provide an integrative review of empirical studies of compassion training. I consider what constitutes compassion training and offer a summary of current meditation-based approaches. I then provide an overview of the empirical evidence for a relationship between compassion training and changes in socioemotional processes, prosocial behavior, and physiological stress responses to the perception of others' suffering. I further address challenges in interpreting data from these studies, considering training-related mechanisms of change and how compassion-relevant processes might develop over time. I conclude by outlining key theoretical challenges for future research.

Chapters 2 and 3 empirically investigate two key issues in contemplative approaches to training compassion: the generalization of training effects, and the volitional expansion of the circle of care. Leveraging EEG data collected as part of the Shamatha Project—a multimethod study of the psychobiological effects of intensive meditation retreat training—these chapters

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work to contribute to the understanding of the neurocognitive consequences of intensive contemplative training.

Establishing whether effects instantiated through meditation training generalize to other, non-meditative states is an essential link in understanding how contemplative training may influence behavior—including responses to suffering—outside of the meditative context. In Chapter 2, I examine retreat-related changes in the resting brain. I show that rest is not a static baseline but rather indexes behaviorally meaningful effects of retreat training. Notably, the training-related changes in the resting brain observed in Chapter 2 closely mirror patterns of change observed in these same participants when they actively practiced mindfulness of breathing meditation. This offers support for the idea that changes instantiated during meditation practice may generalize to other, non-meditative contexts, providing key evidence for the generalization of meditation-related change.

In Chapter 3, I explore whether brain activity recorded during compassion meditation provides evidence that contemplative training can extend the circle of care. Using microstate analysis, I first show that the general patterns of retreat-related change observed during compassion meditation are similar to those of the resting brain. This finding establishes global shifts in brain dynamics as a core consequence of intensive meditation training. I next use sequence analysis to compare temporal patterns of brain activity during compassion meditation when a close other, a difficult other, and all others are taken as the object of compassion. I hypothesize that the mental representations of these various others—reflected in the ongoing activity of the brain—should become more similar with training. I find consistent differences in microstate sequences as a function of the target of compassion. I do not, however, find any evidence that these sequences become more similar with training. Thus Chapter 3 establishes

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microstate sequence analysis as a viable method for distinguishing target-based differences in brain activity during compassion meditation, but does not offer evidence for the extension of the circle of care.

As a whole, this dissertation grapples with how we can understand and measure the consequences of contemplative practice. The empirical studies offer two small contributions to the greater project of understanding if and how we can collectively expand our circles of care.

In grateful memory of the life and teachings of H. H. Getse Rinpoche, for the benefit of all. "Ground your practice in compassion. The rest will follow..."

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Chapter 1

Studies of Training Compassion: What Have We Learned; What Remains Unknown?

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Introduction

We live in a world that is increasingly interconnected—through our economic and trade systems, our environmental policies, ease of travel and communication, and global media reach. This confluence of factors places humans in an unprecedented situation wherein we are ever more aware of the suffering occurring around the world. We can immerse ourselves in the stories of refugees through virtual reality, view personal cellphone videos of war, and watch cities crumble in earthquakes and tsunamis or reel from terrorist attacks. We cannot escape the evidence of how our consumption choices affect the lives of countless other species. This increased global exposure to the suffering of others presents us with a challenge: we can—in despair—become disillusioned and overwhelmed by our own powerlessness in its wake, or we can focus on building capacities that allow us to engage with this onslaught skillfully and adaptively. Increasing our capacity for compassion is one such way to alter how we engage with suffering.

Contemplative traditions have long been concerned with questions of human suffering and the development of compassion (e.g., Salzberg, 2004; Wallace, 1999). More recently, researchers and clinicians in Western psychological traditions have incorporated aspects of these contemplative traditions into their evolving understanding of compassion. The potential for drawing on contemplative traditions—particularly meditation practices—to *train* compassion has been of special interest. While this area of research is rapidly growing, the field is still in its infancy and many core questions remain unanswered. This chapter, and the *Handbook* section that follows, will explore some of what we know, and what we do not, about the training of compassion using contemplative approaches.

First, we consider what constitutes compassion training and offer an overview of current research approaches to investigating the training of compassion. Next, we provide an introductory overview of the empirical evidence for the relationship between compassion training and compassion-relevant processes in psychological research contexts, with a consideration of how these processes might develop over time and a focus on addressing challenges of interpretation. Lastly, we outline two core issues with which the field has yet to grapple: characterizing subtle forms of suffering, and the possibility of compassion without action.

What Constitutes Compassion Training?

Approaches to studying the training of compassion within the psychological literature can be usefully divided into: (1) studies of expert or adept meditators with extensive training in compassion meditation practices (who are often compared to novice meditators on experimental outcomes of interest), and (2) longitudinal studies of individuals undergoing compassion-training interventions. Although the interventions described in this chapter and the accompanying *Handbook* section are all classified as "compassion training," extant training programs vary on a range of factors—perhaps most notably in the length and intensity of training and the pedagogical and design components they include. While many studies of compassion training emphasize procedural aspects of specific meditation techniques, these programs generally also include lectures, discussion, and the social support of a group of individuals working towards a common goal. The existence of these multiple facets of training frequently complicates interpretations of the potential mechanisms underlying any observed effects. Furthermore, for novice or beginning practitioners, the experience of undergoing such programs presumably differs greatly from the life experience of expert meditators (most frequently Buddhist monks).

Although the focus of this chapter is on training programs that incorporate compassion-based meditation practices oriented towards developing compassion for others, it is important to note that there are training approaches aimed at enhancing empathy and compassion that do not include meditation (see Weisz and Zaki, Chapter 16 in this volume for examples), programs that emphasize other types of meditation without an explicit focus on compassion (e.g., mindfulnessbased stress reduction; Kabat-Zinn, 1990), and programs that include meditation but primarily focus on cultivating compassion for one's self (mindful self-compassion; Albertson, Neff, & Dill-Shackelford, 2015; Neff & Germer, 2013; see also Neff and Germer, Chapter 27 in this volume) each of which might presumably influence the development of compassion-relevant processes (Kabat-Zinn, 2011). Finally, although our focus here is on compassion training methods drawn primarily from Buddhist traditions, the teaching of compassion appears across varied religious and secular humanist traditions (for an example from Christianity, see Rogers, 2015; for an example from secular humanism, see Becker, 2012, and other articles in that journal issue), and there exist interventions based on these traditions (e.g., gratitude; see Bono & McCullough, 2006; Gulliford, Morgan, & Kristjánsson, 2013, for reviews) that share considerable conceptual overlap with Buddhist-derived compassion-training programs.

In the section that follows, we overview current approaches to studying Buddhist-derived compassion-training programs by examining two primary dimensions on which such trainings commonly vary: (1) the length and intensity of training, and (2) the multiple training components (e.g., instructional, ethical, motivational) that comprise these programs. For illustration, we provide exemplars of several classes of studies that have been conducted; specific results will be discussed in the "Survey of Compassion Training Outcomes" section of this chapter.

Length and Intensity of Training

Many early studies on the training of compassion attempted to capitalize on the experience gained over a lifetime of practice by studying expert meditators (typically Tibetan Buddhist monks) as compared to novice or beginning meditators (e.g., Engen & Singer, 2015b; Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008; Lutz, Greischar, Perlman, & Davidson, 2009). Although these studies do not take a directed-intervention approach, they do offer insight into changes in compassion-related processes that may be cultivated through extensive training.

Other studies have employed either long-term and/or intensive training (e.g., full-time, daily practice), tracking participants over the course of a given training program. The ReSource Project, for example, is a study on the effects of contemplative training on cognitive-affective regulation and psychosocial functioning that was conducted over the course of one year (Lumma, Kok, & Singer, 2015; Singer, Kok, Bolz, Bornemann, & Bochow, 2016). The intervention included three intensive three-day retreats, which occurred at the beginning of each of three consecutive 13-week training modules; between these brief retreats, participants went about their typical day-to-day lives while practicing daily at-home meditation and attending weekly meditation groups. Another study, The Shamatha Project, was conducted by our laboratory in 2007 (with ongoing follow-up data collected through 2014), and was designed as a multi-method study on the cognitive, affective, and neurobiological effects of intensive meditation training in a formal retreat setting. Participants lived onsite at Shambhala Mountain Center, a remote retreat center in Colorado, and meditated approximately six to eight hours per day over the course of a three-month training period (e.g., Jacobs et al., 2013; MacLean et al., 2010; Rosenberg et al., 2015). Intensive and long-term designs such as these provide a higher "dosage" of training elements and thus are ostensibly more likely to yield measurable effects of training. Because of

this high dose, intensive training also increases the likelihood of obtaining measurable differences between interstitial assessment points (e.g., from the onset to the midpoint of a given training period).

In contrast to such intensive designs, the vast majority of intervention studies have employed non-intensive training protocols (i.e., typically less than one hour of practice per day; up to several hours of instruction per week), often six to nine weeks in length. The most prominent programs of this type incorporate Buddhist meditation practices that are adapted for non-religious contexts. Of the training programs that explicitly focus on compassion, the two most studied are Compassion Cultivation Training (CCT; Jinpa, 2010) and Cognitively-Based Compassion Training (CBCT; Ozawa-de Silva et al., 2012). Other compassion-focused studies employ training protocols of similar lengths that include many of the same training elements as standardized programs such as CCT or CBCT, but are customized to specific populations or study aims (e.g., Condon, Desbordes, Miller, & DeSteno, 2013). There has also been recent growth in the availability of online tools and applications (apps) for training mindfulness and compassion. Headspace (www.headspace.com), one such mindfulness training tool developed by Andy Puddicombe and his colleagues, was recently used as the training method in a study investigating the effects of mindfulness training on prosocial behavior (Lim, Condon, & DeSteno, 2015).

Currently, there is not a large enough body of work on intensive or long-term training to allow us to draw clear conclusions regarding the effects of different training lengths and intensities. As such, in the remainder of this chapter, we will collectively review findings from expert meditators, intensive interventions, and non-intensive interventions. While this approach allows for a general overview of the state of knowledge, it may also gloss over potentially

important variables that differ across training methods and with varying levels of participant meditation expertise.

Training Components

Compassion interventions often consist of multiple training components. Common features include group meditation practice, individual meditation practice, didactic instruction, group discussion, individual writing or reflection, and an organizing ethical framework (e.g., Jinpa, 2010; Ozawa-de Silva et al., 2012; Singer et al., 2016). In addition, individuals may differ widely in their personal motivations for undertaking a particular training or practice. In the absence of studies explicitly controlling for these multiple components, it is impossible to determine their separate, additive, or interacting influences on commonly measured outcomes: any or all of these components may contribute substantively to observed training-related changes. Notably, while most training studies measuring compassion-relevant outcomes include an explicit focus on compassion, it is not clear that this emphasis is an essential element of effective compassion training. Studies that employ training either primarily (e.g., Rosenberg et al., 2015) or exclusively (e.g., mindfulness group in Condon et al., 2013; Lim et al., 2015) centered on attention-training or mindfulness practices have reported changes in responses to suffering as a function of training. However, such focused attention and mindfulness training may include compassion-relevant themes. For instance, while the primary training focus of the Rosenberg et al. (Shamatha Project) study was intensive practice of focused-attention meditation, participants engaged in supportive practice of meditations centered on beneficial aspirations for themselves and others, explicitly including compassion, for approximately 45 minutes each day. This "supportive" practice time is generally comparable to the total time dedicated to contemplative practice in many non-intensive compassion-training programs. In the case of the

Condon et al. (2013) and Lim et al. (2015) studies, which included training programs that exclusively focused on mindfulness practice, both reported improvements in prosocial behavior. These findings suggest the somewhat counter-intuitive possibility that an explicit emphasis on compassion need not be an essential component of programs that nevertheless result in measureable changes in engagement with suffering and prosocial responding. In all of these studies, there are likely to be additional unknown contributions of ethical frameworks (whether provided by teachers, traditional texts, or brought in by participants) that may account in part for observed training-related effects.

What Is the Relationship Between Compassion Training and Compassion?

A core assumption of compassion-training programs is the idea that compassion can, indeed, be trained. Early evidence from studies employing compassion-training programs has provided support for the general efficacy of compassion training in enhancing compassion, but many questions regarding specific outcomes and precise mechanisms of change remain unanswered. As other chapters in this volume provide extensive reviews of specific compassiontraining programs and studies, we offer here a brief survey of the compassion training literature in non-applied, non-clinical settings. We first outline compassion-relevant findings from studies employing compassion-training programs and studies of expert meditators. We next offer a theoretical discussion of potential mechanisms of change involved in such training programs. Finally, we point out several key challenges in interpreting findings from studies of training compassion.

Survey of Compassion Training Outcomes

Compassion has been broadly defined throughout this volume as an affective response to the perception of another's suffering that motivates the desire to relieve that suffering (Goetz,

Keltner, & Simon-Thomas, 2010). The intentional development of this motivation may be supported by inquiry into the nature and causes of suffering—both in one's self and in others the understanding of which can inform a grounded and situationally appropriate response (e.g., Gilbert, 2015; Halifax, 2012). From a cognitive and social psychology perspective, there is a multitude of component processes that underlie compassionate behaviors and motivational states (Batson, Ahmad, & Lishner, 2009; Zaki, 2014; Zaki & Ochsner, 2012), many of which may be influenced and developed by compassion training (e.g., Ashar et al., 2016). In this section, we discuss key findings from the compassion training literature across several compassion-relevant domains, including affect, stress physiology, recognition of emotion and responsiveness to suffering, aversion and related social-evaluative processes, and prosocial behavior.

Affect and Compassion

The relationship between feeling states, their regulation, and compassion training is complex. Although extensive research has been conducted on compassion and related processes outside of the Buddhist-informed perspective offered here (see chapters by Batson and Weisz & Zaki, Chapter 16 in this volume; Singer & Klimecki, 2014), there remain gaps in our understanding. One such gap relates to the precise role of emotion in the generation of a compassionate response to suffering. For example, while emotion regulation is probably critical in the generation of such compassionate responses (e.g., Decety & Jackson, 2006; Eisenberg, 2000), the over-regulation of affect can be prosocially maladaptive, reducing prosocial engagement with witnessed suffering (e.g., Dovidio & Gaertner, 1991). In two studies, Cameron and Payne (2011) found that two groups of participants—those who were naturally skilled at regulating their emotions and those who were instructed to actively down-regulate their emotions—showed reductions in reported compassion as the number of individual suffering

victims increased in salient descriptions of suffering in others. Participants who were unskilled at emotion regulation, or who were instructed to simply "experience" their emotions during the task, did not demonstrate a concomitant decrease in compassion (for more on motivational influences on compassion, see Cameron, C.D., Chapter 20 in this volume). The emotion regulation strategy employed when witnessing suffering also appears to matter: reliance on suppression as an emotion regulation technique has been linked to reduced empathic concern and willingness to engage in helping behaviors, whereas engaging in reappraisal does not seem to carry these same consequences (Lebowitz & Dovidio, 2015).

Within the compassion training literature, CCT has been reported to enhance selfreported feelings of compassion towards one's self and others (Jazaieri et al., 2013), to increase self-reported mindfulness and happiness, and to reduce self-reported worry and emotional suppression in adults (Jazaieri et al., 2014; see Goldin and Jazaieri, Chapter 18 in this volume for a review of studies employing CCT). Despite the improvements in self-reported mindfulness and happiness, and the decreased worry reported in Jazaieri et al. (2014), the training did not result in observed changes in self-reported perceived stress; therefore the authors interpreted this reduction in worry absent changes in perceived stress as indicative of improved *adaptive coping* following CCT. In adolescents, a Buddhist compassion training based on the New Kadampa Tradition (Gyatso, 2003; Lopez, 1998) evidenced similar decreases in self-reported worry, as well as improvements in the environmental mastery and personal growth facets of self-reported well-being (Ryff & Keyes, 1995), but showed no changes in self-reported positive affect (Bach & Guse, 2015). The authors of this study suggest that these reported changes in well-being may reflect a change in personal perspective—that happiness can be achieved through cultivating benevolent states of mind, particularly in situations where external events cannot be easily

controlled. Compassion training may also alter an individual's perspective on what constitutes happiness and what is valuable in life (Ricard, 2008), such that psychological well-being is no longer primarily grounded in hedonic states or pleasant experiences but rather in the ability to live a meaningful life (Ryan & Deci, 2001). This change in perspective may in turn increase individuals' sense of efficacy in regulating their own emotional state. Together, these findings support the view that compassion training may influence how one relates to potentially negative or distressing events, such that events may be framed as less aversive or overwhelming.

Biomarkers of Stress and Inflammation

If compassion training influences how individuals report that they cope with stress and challenging experiences, one might expect to see these changes mirrored in the domain of stress physiology. Across a series of studies, CBCT has been found to reduce markers of stress and inflammation in undergraduate students (Pace et al., 2009; Pace et al., 2010), and inflammation in adolescents in the foster care system (Pace et al., 2013). In the former studies, greater time spent practicing meditation at home over the course of CBCT was associated with a reduction in deleterious biological markers. However, a later study on a larger sample of adults conducted by this same group failed to replicate any of these outcomes and found no effect of CBCT on any relevant behavioral or biological measures (unpublished data; see Mascaro, Negi, and Raison, Chapter 19 in this volume for further discussion). This highlights the potential variability in psychobiological responses to compassion training, and the need for replication studies and the careful consideration of differences in contextual factors between studies (e.g., Van Bavel, Mende-Siedlecki, Brady, & Reinero, 2016).

Recognition of Emotion and Responsiveness to Suffering

Expert meditators—Tibetan Buddhist monks with a range of 10,000–50,000 lifetime hours of meditation experience in a tradition strongly emphasizing compassion (e.g., Jinpa, 2015; Dalai Lama & Ekman, 2008)-demonstrate increased pupil dilation and activation in the insula and cingulate cortex (Lutz et al., 2008), and increased coupling between cardiac rate and BOLD (blood-oxygen-level--dependent) activity in the somatosensory cortex (Lutz et al., 2009) in response to sounds of suffering as compared to novice meditators. These findings suggest increased responsiveness to signals of suffering in others. Consistent with these findings, novices trained in CBCT have demonstrated improved empathic accuracy as measured by the ability to infer what emotion an individual is feeling from a picture of only their eyes (Mascaro, Rilling, Negi, & Raison, 2012). This improvement in empathic accuracy was accompanied by increased activation in the inferior frontal gyrus and dorsomedial prefrontal cortex, brain regions previously associated with theory of mind (for more on this study, see Mascaro et al., Chapter 19 in this volume). In a separate study employing CBCT, training participants demonstrated a trendlevel increase in activation in the amygdala to negative images from the International Affective Picture Set (IAPS; Lang, Bradley, & Cuthbert, 2008), which was significantly correlated with decreases in depression scores (Desbordes et al., 2012). While the amygdala has long been associated with negative affect and fear-relevant processing, it is more broadly implicated in salience detection and general affect processing (Janak & Tye, 2015). Other researchers have also observed increased amygdala activation during the generation of compassion, as compared to cognitive reappraisal in expert meditators viewing film clips of individuals in distress (Engen & Singer, 2015b). Experts in this same study also demonstrated greater activation in the ventral striatum and medial orbitofrontal cortex (part of a network implicated in positive affect and

reward processing), as well as the mid-insula (interpreted as supporting feelings of affiliation), and had greater self-reported positive affect when asked to generate compassion while viewing the films of distress, as compared to when they were asked to view these films in a neutral "watch" condition or to engage in cognitive reappraisal of the films (see also Klimecki and Singer, Chapter 9 in this volume).

Together, these findings suggest that compassion training may enhance perceptual accuracy and alter the salience of social-emotional stimuli, and that these changes may be supported by identifiable differences in associated neural activity following training. Both shorter-term interventions (e.g., CCT, CBCT) and long-term expertise appear to enhance emotional responsiveness to depictions of others' emotional states. One possibility proposed by Engen and Singer (2015) is that enhanced responsiveness related to compassion training may have a protective effect, mitigating empathic distress and burnout by increasing positive affect in the face of emotional challenge. It will be important for researchers to unpack the specific functional or informational qualities of increased positive affect. For example, positive feelings associated with the active deployment of compassion in the face of suffering need to be dissociated from states of self-congratulation for feeling compassion for others or engaging in helping behavior.

It is important to note that physiological responses often demonstrate complex or nonlinear relationships with outcomes of emotional experience and behavior. For example, while higher levels of cardiac vagal activity—an indirect measure of parasympathetic nervous system activity (see Porges, S.W., Chapter 15 in this volume)—are associated with positive affect and have been shown to predict higher levels of self-reported compassion (Stellar, 2013; Stellar, Cohen, Oveis, & Keltner, 2015), cardiac vagal activity has also been demonstrated to show an

inverted U-shaped relationship with prosociality, suggesting that very high levels of vagal activity may be associated with reduced prosocial responding (Kogan et al., 2014). As another example, post-training increases in functional connectivity between the dorsolateral prefrontal cortex and the nucleus accumbens have been linked to increases in altruistic behavior in participants who underwent compassion training, but to decreases in altruistic behavior in participants who underwent reappraisal training (Weng et al., 2013). Thus, interpretation of physiological data absent of accompanying experiential or behavioral measures may be uninformative or even misleading.

Aversive Responding and Social-Evaluative Processes

It is likely that increased responsiveness to the suffering of others is subserved by decreased aversion to those who are suffering (see Weng, Schuyler, and Davidson, Chapter 11 in this volume), and that this is a core capacity trained by compassion interventions. Supporting this possibility, several studies have reported reductions in aversive responses to suffering in others, or to stigmatized groups following training (e.g., Kang, Gray, & Dovidio, 2014; Kemeny et al., 2012; Rosenberg et al., 2015).

As part of the Shamatha Project, participants were asked to watch emotionally evocative film clips of human suffering before and after an intensive meditation retreat (Rosenberg et al., 2015). Participants' facial expressions were unobtrusively recorded and subsequently coded using the Facial Action Coding System (Hager, Ekman, & Friesen, 2002) to identify expressions of emotion, including sadness, as well as aversive emotional expressions (i.e., anger, contempt, and disgust) termed "rejection emotions." Expressions of rejection emotions were conceptualized as indicating aversion or defensiveness towards the graphic depictions of suffering contained in the films. After a three-month focused-attention (*shamatha*; Wallace, 2006) meditation retreat,

training participants were more likely than matched waitlist-controls to show facial expressions of sadness in response to depictions of suffering. Training participants also displayed fewer instances of facial expressions of rejection emotions. Importantly, in the training group, selfreported experiences of sympathy-but not of sadness or distress-in response to the posttraining film were positively related to facial expressions of sadness, and were negatively related to facial displays of rejection emotions. These findings suggest that intensive meditation training that includes both shamatha (concentrated attention) and "four immeasurables" (beneficial aspirations: loving-kindness, compassion, empathetic joy, and equanimity) practices promotes engagement with the suffering of others. It also appears that training reduces defensive responding to suffering, which was operationalized as reduced expression of rejection emotions. It is important to note that while Shamatha Project participants did practice compassion meditation (~45 minutes/day across all four immeasurables practices), the core practice of the retreat was shamatha meditation, which aims to develop stability of attention (MacLean et al., 2010; Sahdra et al., 2011; Zanesco et al., 2013). Overall, these findings highlight the need for continued research into the direct or indirect consequences of attention-based training on the development of compassionate responses to suffering.

In a related finding, when compared to waitlist controls, participants trained in Cultivating Emotional Balance (CEB—a training program that includes compassion-focused and contemplative elements; Kemeny et al., 2012) demonstrated faster implicit access to compassion-related concepts in a lexical decision task after subliminal exposure to images depicting suffering, even when these images included elements designed to elicit feelings of disgust (Kemeny et al., 2012). For suffering images that did not include an element of disgust, participants appeared to take more time to access disgust-related concepts in a lexical decision

task than did controls. This finding once again points to a possible decrease in aversive reactions to suffering following compassion-relevant training.

Sometimes, resistance to feeling or enacting compassion may stem, not from aversion to suffering *itself*, but from an aversion to the *individual* who is suffering. Hence another core aim of compassion training is to broaden the circle of individuals toward whom we may respond compassionately. We tend to feel more compassion for those we perceive as being similar to ourselves, and experimental manipulations of perceptions of similarity have been shown to increase feelings of compassion and prosocial behavior towards others (DeSteno, 2015). On the other hand, individuals frequently feel less concern for, or even celebrate, the suffering of members of a social out-group (e.g., Cikara, Bruneau, & Saxe, 2011). In line with this premise, Kang et al. (2014) reported that training in loving-kindness meditation (a practice that aims to enhance feelings of affective care and well-wishing towards others) was related to decreased implicit bias against stigmatized groups. After training, a group of participants who were randomly assigned to a loving-kindness meditation training demonstrated significant reductions in implicit bias (Greenwald & Banaji, 1995) as measured by the Implicit Association Test (Greenwald, Nosek, & Banaji, 2003) against both blacks and homeless people (two commonly stigmatized groups), as compared to controls. Participants' explicit attitudes (i.e., what they say about their beliefs and feelings), however, did not change. These findings suggest that training in loving-kindness meditation influenced implicit reactions to stigmatized groups, which the authors suggest may result from increased feelings of connectedness towards others.

Taken together, the findings reviewed in this section suggest that compassion-related training may decrease aversive responses to witnessing suffering, as well as widen the scope of individuals towards whom one may experience compassion.

Prosocial Behavior

In the previous section, we considered evidence suggesting that compassion training may adaptively modulate social-evaluative processes that presumably underlie enactment of compassionate responses in the face of suffering. Here we consider a key question in evaluating the training of compassion: Do changes in emotional experience and reactivity to suffering translate into changes in overt helping behavior (see also "behavioral transfer" in Weng et al., Chapter 11 in this volume)? One common method of testing prosocial behavior in a laboratory setting is through the use of economic games. In two independent studies, both (1) long-term meditators (individuals with over 40,000 hours of lifetime practice hours; McCall, Steinbeis, Ricard, & Singer, 2014) and (2) novices trained using a two-week home-based compassion intervention (Weng et al., 2013) offered more money to compensate victims of unfair treatment in an economic game than did controls. In the study by McCall et al. (2014), when expert meditators were themselves the victims of unfair treatment, they punished the player who had treated them unfairly with less severity than did controls. However, when others were the victims of unfair treatment, the expert meditators' punishment of players who had behaved unfairly was equal to that of the controls, suggesting a stronger motivation to enforce fair treatment of others than of themselves. Despite equal ratings of perceived unfairness as compared to controls, experts also reported experiencing less anger at the unfair behavior (McCall et al., 2014). These findings support the idea that both short- and long-term compassion training may encourage altruistic action to relieve witnessed inequity.

In one of the few studies of real-world, ecologically valid helping behavior, Condon and colleagues (2013) found that participants who underwent an eight-week non-intensive training program in either mindfulness or compassion meditation were significantly more likely to offer

their seat to a confederate in apparent suffering (grimacing on crutches), as compared to waitlist controls who received no training (see also Condon and DeSteno, Chapter 22 in this volume). However, the type of meditation training (mindfulness or compassion) had no significant effect on the probability of helping: both groups were equally likely to offer their seat. The findings from this study were recently replicated (though with lower reported effect sizes) using a mobile app-based mindfulness intervention (Headspace) as the training program, when compared to an active control condition based on cognitive skills training (Lim et al., 2015). Thus, the willingness to offer one's seat may not be a compassion training-specific effect, but rather a more generalized effect of contemplative training. One possibility is that skillful, experienced teachers may implicitly communicate and foster ethical views that uphold compassion as an important personal value, even in non-compassion-specific trainings. To this point, while Headspace is presented as a mindfulness training application, the platform's primary teacher, former Buddhist monk Andy Puddicombe, has stated: "I never teach meditation in isolation.... I always teach View, Meditation, and Action. You can't teach the View without altruism" (Widdicombe, 2015, http://www.newyorker.com/magazine/2015/07/06/the-higher-life). This quote emphasizes the inadequacy of referring to classes of training types by using the nonqualified terms "compassion" or "mindfulness," as each class of training will nearly always contain aspects of the other. It should also be noted that, even in the context of the presumably small personal sacrifice of giving up one's seat, these trainings did not result in universal altruism: in the in-person meditation-trained groups, 51% of participants failed to give up their seat (compared to 84% of controls), while in the Headspace study, 63% failed to give up their seat (compared to 86% of active controls). Nonetheless, the demonstration of increased incidence of helping behaviors in real-world situations following training is noteworthy (for more on these

studies, see Condon and DeSteno, Chapter 22 in this volume). Future studies should consider issues of situational factors (such as resource availability or social-evaluative processes) on real-world helping behavior.

Summary

As a whole, the studies surveyed indicate that compassion-based (and in some cases attention- or mindfulness-based) training may sensitize participants to the suffering of others and increase the tendency to experience compassion or sympathy, as opposed to emotions such as disgust or anger, in response to the perceived suffering of others. Furthermore, it appears that training may reduce aversion in the form of automatic bias against stigmatized groups. In terms of prosocial action, findings suggest that both long-term and shorter-term compassion training may increase the tendency to respond altruistically in the context of economic games played in the laboratory and in ecologically valid situations, though data here are sparse.

Mechanisms of Change

So how might directed and deliberate training in compassion change one's behavioral, cognitive, or psychological reactions to suffering in the world? This is a truly open question. As discussed, compassion-training programs comprise a variety of design elements, all of which may influence observed or reported changes in compassionate responding. To date, few studies have attempted to disambiguate these potential mechanisms of change; thus any discussion of such mechanisms is largely theoretical. Nevertheless, we will address several potential pathways through which compassion training may influence real-world compassionate responses, with the goal of motivating future research and encouraging greater delineation of component processes. First, we discuss potential ways in which various types of meditation may influence compassionrelevant processes. We then suggest how broad training elements unrelated to meditation style or

practice may function to support training-related changes. It is important to note that in none of these cases do we suggest a one-to-one or linear relationship of change between any specific outcome measure and element of training. Rather, we point to a range of influences and training factors that, together, may contribute to observed changes in a dynamic, contextually dependent manner.

Meditation

All trainings reviewed in this chapter include elements of guided or silent meditation practice. In many modern psychological accounts, meditation training is often conceptualized as facilitating a process of mental development that can enhance attentional stability and the ability to self-regulate affect and behavior through the application of attention and awareness to various domains of experience (Lutz, Slagter, Dunne, & Davidson, 2008; Lutz et al., 2009; Rosenberg et al., 2015; Sahdra et al., 2011). The process through which meditation may influence real-world responses to suffering is unknown and has largely gone uncharacterized. However, the extent to which meditation practice facilitates trait-like changes in cognition or behavior presumably depends on a confluence of cognitive-affective capacities developed through a given meditation practice. These domains include the cognitive operations and ethical commitments embedded in the meditation instructions; the personal motivations of the practitioner; the relationship between practitioner and teacher (whether in person or via digital media); the sociocultural context in which the training is offered, and resulting alterations in perception, attitudes, or response tendencies; and well-being resulting from continued engagement in the practice. The same meditation techniques delivered by different teachers or in differing contexts may hold divergent effects on a given group of individuals, who are also likely to exhibit considerable interindividual differences in motivation, socio-emotional function, and baseline capacities for

compassionate responses. While recognizing the importance of contextual and individual differences, it is possible that meditation training may generally increase the tendency to respond with compassion, both by influencing the *desire to care* for others, and by improving cognitive-affective capacities that enhance the *ability to enact* these motivational tendencies.

Some meditation practices (e.g., compassion, loving-kindness) focus explicitly on the development of care and concern for oneself and others. These practices often aim to "systematically [alter] the content of thoughts and emotions" (Dahl, Lutz, & Davidson, 2015, p. 518) by cultivating specific affective and motivational states and traits that increase positive feelings and actions towards others. One interesting possibility is that meditation practices of this class may support compassion by fostering a sense of connectedness between oneself and others (Trautwein, Naranjo, & Schmidt, 2014). Indeed, feelings of connectedness and closeness to others appear to increase prosocial behavior. For instance, feeling close to an individual (Beckes, Coan, & Hasselmo, 2013) or having been to the location of a natural disaster before it has occurred (Zagefka, Noor, & Brown, 2013) have both been linked to increased altruistic behavior. It is also possible that compassion-based trainings support a shift in the perceived importance of attuning to suffering in one's life, the connection between suffering and personal happiness, and one's own causal agency in creating or alleviating that suffering (Ozawa-de Silva et al., 2012).

Other meditation practices purport to strengthen the practitioner's ability to regulate, direct, and reorient attention (Dahl et al., 2015; Lutz, Jha, Dunne, & Saron, 2015). Supporting this assertion, our lab has reported that Shamatha Project participants who underwent intensive training in attention-based meditation demonstrated improved perceptual discrimination (MacLean et al., 2010), attentional stability (MacLean et al., 2010), and response inhibition (Sahdra et al., 2011) following a three-month intensive training period. If and how such increases

in attentional stability and cognitive-regulatory capacity support changes in situationallyappropriate affective responding is another open question. In the Shamatha Project, trainingrelated improvements in response inhibition were linked to greater self-reported socio-emotional and psychological functioning (Sahdra et al., 2011). These same participants also demonstrated greater engagement with, and less defensiveness to, film depictions of suffering (Rosenberg et al., 2015).

Overall, these data suggest that training in a variety of contemplative practices may influence socio-emotional outcomes. Interpretation of the effects of specific meditation techniques is complicated by the lack of data on the effects of teachers (independent of the type of meditation taught) in modeling compassionate and altruistic motivations, either directly or indirectly, through their actions, word choice, style of interpersonal interaction, and teaching instructions. Thus, while specific cognitive capacities trained through mindfulness or focusedattention practices probably influence socio-emotional functioning, the role of the teacher in imparting the value of a compassionate attitude toward suffering may constitute an important, and under-studied, element of compassion training.

Other pathways through which meditation practice may influence real-world compassionate responding include the activation of secure attachment primes (Mikulincer & Shaver, 2005; Mikulincer, Shaver, Gillath, & Nitzberg, 2005; Shaver, Lavy, Saron, & Mikulincer, 2007), reducing experiential avoidance of distress (Chiesa, Anselmi, & Serretti, 2014), strengthening meta-awareness (Dahl et al., 2015; Lutz et al., 2015), and increasing the salience of signs of suffering in others (Lutz et al., 2008). Current evidence for these hypothesized pathways is sparse; we believe that future work designed to elucidate specific pathways to change is essential for the field's continued growth.

Non-contemplative Training Elements

Other elements that influence compassion-related training outcomes may operate relatively independent of the specific meditation techniques or practices being taught. These include the grounding of the training in an ethical worldview, personal preferences and motivations for practice, and social factors such as interaction with a respected teacher and identification with a group of like-minded individuals.

Individuals come to meditation practice with different intentions and motivations, which presumably influence the course of an individual's development during training. For example, an individual who engages in meditation practice with the goal of reducing ruminative thought might place a different emphasis on the development of compassion than does an individual who arrives with the goal of feeling more connected to others. Individuals also have personal preferences, which may influence their enjoyment of, responsiveness towards, and commitment to the training program. Indeed, different patterns of neural activity in response to painful stimuli *before* training in CBCT have been found to predict subsequent time spent practicing mindfulness and compassion meditation during training (Mascaro, Rilling, Negi, & Raison, 2013). Thus, it may be important to consider preexisting differences in evaluating the outcomes of meditation interventions, or in tailoring interventions to specific populations.

Compassion-training programs often include teaching and instruction in ethics. Though the lessons and exercises in CCT and CBCT are presented within a primarily secular framework, many of the key concepts and core practices are drawn from Buddhist traditions, and both programs were developed under the guidance of Buddhist teachers and scholars Geshe Thupten Jinpa and Geshe Lobsang Tenzin Negi, respectively. Other interventions may occur within more explicitly religious contexts. The Shamatha Project, for example, was conducted at a Buddhist

retreat center environment under the guidance of Buddhist-trained meditation teacher (B. Alan Wallace). Nevertheless, even within the explicitly Buddhist context of the Shamatha Project, participants varied in their personal religious beliefs and adherence to Buddhist worldviews; the contribution of these individual differences to our reported outcomes, however, is presently unknown. This is but one example of the multiple layers of complexity inherent in many studies of training compassion. Thus, while very little research has been conducted on the influence of intention, motivation, and belief within meditation training, we believe that this is an essential area for future work. In the Shamatha Project, we are examining this issue through qualitative analysis of practitioners' worldviews, goals, and approach to life via thematic coding of interviews collected both during and after training. The goal is to visualize and quantify qualitative shifts in participants' reports using network analytic methods for statistical integration with empirical laboratory findings (Pokorny et al., accepted).

The social interactions with teachers and fellow trainees inherent in many compassionbased trainings may also play an important role in supporting observed training effects. Importantly, studies employing an active control intervention designed to account for some of these social factors have failed to find differences in outcomes between mindfulness training and control interventions on a variety of self-report and physiological variables (MacCoon et al., 2012; Rosenkranz et al., 2013). It will be crucial for future studies to examine whether compassion-relevant outcomes are similarly sensitive to non-specific effects of the training context. In addition to effects of social support, it may also be important to consider the influence of teacher-specific effects on training outcomes. For example, in the earlier reviewed Condon et al. (2013) study—which found no differences in prosocial behavior following training in mindfulness or compassion meditation—both training programs were taught by an experienced

Tibetan Buddhist lama who has extensive compassion meditation experience. It is possible that the experience of interacting with a teacher who embodies compassionate behavior may serve, in itself, as a catalyst for the development of compassion. The influence of teacher-specific factors, independent of delivered content or training materials, is an important consideration for future research.

Summary

Compassion training may influence compassion-related outcomes through a range of hypothesized pathways, including increased motivation and capacity to respond to others in need, development or reorganization of one's ethical priorities, and renewed social support and guidance from others. There are currently few studies that enable researchers to distinguish the effects of these different training elements, and as such, mechanistic explanations of training effects lack clear empirical support. Future study designs that allow for mechanistic hypotheses, that or that derive testable model of predicted results (e.g., Ashar et al., 2016), will be essential for the development of the field. However, we believe it is also healthy to question a core motivating assumption often encountered in the training literature: that researchers should seek to identify primary "active ingredients" that directly correspond to the development of isolatable cognitive or affective capacities. At this stage, the available evidence from mindfulness and compassion-training programs is suggestive of a complex, variable, and contextually dependent developmental process in which acquired skills may generalize to various domains and are supported by multiple interrelated processes. The extant work in this area consists mainly of heuristic outlines and theoretical sketches of how such a dynamic, interactive process may function (e.g., Halifax, 2012), and directed theoretical development is needed.
Issues in the Interpretation of Training Outcomes

There is a range of issues complicating the interpretation of compassion training-related outcomes. Key challenges include the generalization of findings from assessments of expert meditators to non-expert populations, the general lack of rigorous active control interventions (particularly for multi-week, in-person trainings such as CBCT and CCT), the possible dissociation between feelings of compassion and knowledge of appropriate action, and the complexity of drawing inferences from multi-method studies incorporating neuroimaging, selfreported experience, and measured behavior. We will discuss each of these in turn.

Expert Meditators

Many of the key insights in this field—and as cited in this chapter—are based on data collected from expert meditators, often male Tibetan Buddhist monks, who have a day-to-day experience that differs profoundly from that of the novice meditators often used as control comparisons in these studies. Such experts may also have a very different ethical framework and motivation for their meditation practice (Santideva, 1997) than is typically presented in secularized short-term interventions, or that may motivate novices to participate in a study (such as remuneration or academic credit). Beyond these motivational and cultural differences, additional issues include understanding and following delivered instructions, and managing the effort required to engage in specified practices, all of which are likely to change and evolve with acquired expertise. Experts also generally have extensive training in a range of meditation techniques, not just those specifically aimed at cultivating compassion. Thus, observed effects cannot be attributed to training in any specific practice, but are presumably due to a constellation of factors, including specific meditation training, scholastic knowledge, worldview, and life experience.

Active Control Interventions

There is a need for implementation of rigorous, active control interventions within the meditation training literature at large (Davidson & Kaszniak, 2015). Many studies have employed matched waitlist control conditions (e.g., Rosenberg et al., 2015), which are designed to control for general population-level factors such as demographics, the motivation to practice and engage in meditation, and quantification of simple "practice" effects of repeated experimental testing in longitudinal designs. Nevertheless, when such studies report changes in outcomes following an intervention, it is often difficult to attribute these observed changes to specific training elements of interest (e.g., compassion meditation). Rather, such changes may be influenced by a confluence of multiple training elements, or other factors largely unrelated to training, such as demand characteristics. To this end, researchers at the University of Wisconsin– Madison have developed the Health Enhancement Program (HEP), an active control intervention for the evaluation of mindfulness-based stress reduction (MBSR; Kabat-Zinn, 1990). In studies comparing these two programs, no differences were found in self-reported emotional experience in a thermal pain task (MacCoon et al., 2012) or in cortisol rise in response to an acute social stressor (Rosenkranz et al., 2013) between HEP and MBSR. These findings highlight the importance of accounting for aspects of meditation-based interventions that are unrelated to the dissemination of teachings on specific techniques, such as the presence of a compassionate teacher, social support, and relevant didactic information.

Compassion and Appropriate Action

The ability to select an appropriate behavioral response to a given situation may be dissociated from the capacity to generate compassionate feelings or to feel motivated to help

others. In situations where one has the intention to respond compassionately, the successful deployment of an appropriate response requires an understanding of the dynamics of the situational context, knowledge of the potential outcome of different actions, and a felt capacity to cope with the situation (Halifax, 2012). To our knowledge, no studies have examined the effects of compassion training on the ability to determine appropriate action when witnessing others in need of help or aid, or how such behavioral action is moderated by training expertise and individual differences in psychological traits or affective profiles. Further complicating this question, behavioral manifestations of compassionate responses may look quite different, depending on the situational or interpersonal context. For example, skillful and compassionate parenting may at times require gentle nurturance or flexible guidance, and at other times require stern words or the setting of firm limits. Determining what constitutes a compassionate response in which situation is a formidable challenge.

Brain, Experience, and Behavior

Many studies rely on brain imaging data combined with self-report measures to assess training efficacy. While it can be useful to look to neural mechanisms to understand the neurobiological mechanisms of compassion development, this approach can lead to unclear inferences regarding the processes underlying training-related change. For instance, in a study of compassion training versus reappraisal training, Weng et al. (2013) observed similar patterns of neural connectivity between the dorsolateral prefrontal cortex and the nucleus accumbens following training in both intervention groups. However, in the compassion training group, increased connectivity predicted greater altruistic redistribution of funds in an economic game, whereas in the reappraisal group, increased connectivity between these regions predicted less redistribution of funds. The fact that the same pattern of change in measured connectivity was

related to divergent changes in behavior between training groups highlights the complex relationship between training, brain activity, and behavior. Continued efforts to integrate experiential accounts and behavioral measures will strengthen our understanding of the development and experience of compassion, and how these may vary across individuals and contexts.

Summary

In this section, we have reviewed evidence that compassion training may influence participants' attitudes toward difficult emotions, enhance socio-emotional processing, reduce aversion to suffering and to stigmatized others, and support prosocial behaviors. While acknowledging that evidence for specific mechanisms is sparse, we discussed potential pathways for training-related changes, and pointed to key issues in the interpretation of such data, including the joint consideration of experiential and behavioral information in the interpretation of data.

What Is the Trajectory of Compassion Training?

The training of compassion can be conceptualized as a developmental process: changes in compassion-relevant processes occur over time, and they are deepened and strengthened with acquired expertise. The shape of the associated developmental curves likely varies between component processes, and between individuals. For the sake of illustration, consider a hypothetical training trajectory with the following attributes:

 The cognitive effort required to respond compassionately to suffering has a linear, negative slope, with the highest effort demonstrated in novices and the lowest in experts;

- The affective/motivational salience of suffering follows an independent, positive exponential curve, quickly increasing with expertise and then leveling out over time; and
- 3. Personal distress to suffering has an inverted U-shaped curve, in which distress first rapidly increases, peaks with moderate levels of training, and then decreases at higher levels of expertise.

In this imagined scenario, the specification of component developmental curves—and any interactions between them—would aid researchers in generating hypotheses about the experience of compassion and predictions for compassion-relevant outcome measures at different points in training. Despite the potential utility of such curves, there are very few studies that attempt to model developmental trajectories. Importantly, when considering the trajectory of compassion training, this conceptual approach can inform research and theory at several different timescales: the trajectory within a single session (of meditation or of performing a laboratory task), the trajectory across a set training period (such as a course of CCT or CBCT), and the trajectory across a lifetime of practice. Here, we will consider the potential utility of each of these timescales in generating research questions.

Trajectory across a Single Session

There is extremely limited knowledge regarding the time-course of the recruitment of select cognitive and affective processes within a given session of compassion meditation or within a compassion-relevant task (for an example, see Engen & Singer, 2015b). In studies employing brain imaging techniques, neural activity is typically averaged across an entire task block or meditation period, thus information on temporal dynamics is lost. However, time-course analyses of compassion-related processes may offer deeper insights into how these processes

unfold. For example, analysis of the time-course of compassion-based emotion regulation in expert meditators has demonstrated activation in brain regions implicated in reward and social connection *before* the onset of distressing films, suggesting that participants were upregulating their positive affect prior to presentation of the challenging stimuli (Engen & Singer, 2015b). By considering within-session temporal dynamics in this manner, it becomes possible to disambiguate competing hypotheses that hold differing implications for our understanding of compassion—in this case, the hypotheses of *anticipatory* up-regulation versus positive affective *responses* to stimuli designed to elicit distress. This example demonstrates the utility of considering the time course of compassion in elucidating supporting processes and in the interpretation of relevant data. For a more in-depth discussion of the importance of within-session temporal dynamics, and potential methodologies for implementing such analyses, see Weng et al., Chapter 11 in this volume.

Trajectory across Training

In addition to single sessions of practice, one can consider trajectories across the course of multiple sessions of an intervention. Intervention studies typically employ two measurement points: pre-training and post-training. While pre- to post-training change can be informative, it provides little insight into *how* processes develop *during* training. This remains a largely unexplored area of inquiry. Returning to the conceptual illustration of a developmental curve of training presented in the introduction to this section, the length of training and timing of assessment points within a given training program will place training outcome measurements at different points of this hypothetical curve. Where these measurements are placed relative to a given individual's underlying developmental trajectory will, in turn, almost certainly influence the magnitude and direction of reported effects. As discussed in our hypothetical example, a

developmental training trajectory could vary across different elements of training, and these varying curves and their interactions could have differential effects on outcome measures. Exemplifying the utility of this approach, Lumma et al. (2015) examined longitudinal changes in heart rate (HR), high frequency heart rate variability (HF-HRV), participants' reports of how much they liked the training, and perceived effort across different meditation styles within the ReSource Project. This year-long training was divided into three counterbalanced three-month training modules. In each module a different meditation practice was taught: mindfulness of breathing, observing thoughts, and loving-kindness. Analyses revealed that, over the course of the year-long training, ratings of enjoyment of any given practice increased, and perceived effort decreased. Although HR during meditation practice increased over the course of the year-long training, this was only true for the three months of loving-kindness meditation and three months of observing-thoughts meditation; HR did not increase over the three months of breathing meditation. Similarly, HF-HRV significantly decreased over the course of the year-long training; however, when the year-long training period was analyzed according to the specific three-month training modules, this decrease was significant only for the loving-kindness and observingthoughts meditation styles. This pattern of effects supports the notion that trajectories of training may indeed differ across training elements (in this case, per meditation type, but also presumably processes related to attention, emotion regulation, cognitive control, etc.; see Dahl, Lutz, & Davidson, 2016; Engen & Singer, 2015a) and outcome measures.

Trajectory across a Lifetime

The development of compassion does not end at the cessation of formal training individuals continue to integrate and apply the views, motivations, and capacities developed during training into their ongoing life experiences. Despite this, few studies track participants

beyond the conclusion of formal training programs, and therefore little is known about how individuals integrate observed training effects into their daily lives. Much more thought is needed on this issue, as researchers begin to characterize the conceptual dividing line between active training and daily life, and undertake longitudinal studies with measures of compassionate behavior that are optimized for real-world contexts. Measures with clear real-world implications, such as dyadic interactions with close others, second-person reports, or measures of community involvement, may be useful for more fully understanding the development of compassion after formal training and, ultimately, across an individual's lifetime.

A Note on State versus Trait Effects

In contrast to our emphasis on the developmental characteristics of compassion training, even a few minutes of loving-kindness meditation has been shown to induce increased feelings of social connectedness and positivity toward strangers (Hutcherson, Seppala, & Gross, 2008). Likewise, a one-day training in loving-kindness meditation has been shown to increase self-reported positive affect and empathy, as well as associated neural activity in response to distressing videos (Klimecki, Leiberg, Lamm, & Singer, 2012), and to increase helping behavior in a prosocial game (Leiberg, Klimecki, & Singer, 2011). The concept of training as we have framed it suggests that a skill or ability is developed and honed over time; however, these shorter interventions, which lack such an extended developmental trajectory, nevertheless seem to affect compassion-relevant measures. Further contributing to this apparent contrast are issues of measuring and conceptualizing changes in state-like versus trait-like capacities over time. A very short intervention manipulating situational or contextual factors may be sufficient to induce a state-level change, whereas longer-term or intensive trainings may be more likely to influence trait-like tendencies, which in turn influence situational responding. Practices and interventions

at both of these levels of analysis have been shown to influence compassionate responses. Among the situational or contextual factors that can influence compassionate responding are the number of suffering victims (Cameron & Payne, 2011), explanations ascribed to the cause of suffering (Gill, Andreychik, & Getty, 2013), perceptions of agency (Akitsuki & Decety, 2009), and societal factors such as ongoing cultural conflict (Bruneau, Dufour, & Saxe, 2012). Trait-like contributors may include formative early life experiences such as the development of attachment security (Mikulincer & Shaver, 2005; Mikulincer and Shaver, Chapter 7 in this volume). Both trait-level and contextual factors critically contribute to any real-world response to suffering: as one encounters suffering, one's capacity to experience and generate compassion meets situationally specific factors, which dynamically alter the expression of compassion in a given moment (see Condon and DeSteno, Chapter 22 in this volume).

Conclusion: Compassion without Action and Subtle Forms of Suffering

In this chapter, we have offered an overview of current approaches to training compassion and what research on these approaches suggests about the development of compassion and the trajectory of compassion training. In this final section, we address two key issues that present significant research challenges, but are highly relevant to daily life outcomes: the role of compassion when nothing immediate can be done to relieve another's suffering; and manifestations of suffering that are common to the human experience, yet are frequently overlooked in research on compassion.

We are frequently exposed to suffering in others that we cannot immediately act to alleviate, such as media depictions of war, genocide, starvation, and natural disasters. What, in these situations, constitutes an appropriate response? When the scale of suffering exceeds our perception of our own resources to relieve it, we tend to experience "compassion collapse"

(Cameron & Payne, 2011). So how can we respond compassionately when we witness suffering that is far afield and out of our locus of control? In these cases, we would argue that self-care becomes a critical act of compassion. In the moment that we empathize with suffering that we cannot possibly relieve, and feel our own powerlessness in the face of others' pain, our own suffering and distress may increase. Thus, recognizing our own suffering and taking measures to acknowledge, engage with, and care for that pain is itself an act of compassion. In this conceptualization, compassionate regard for oneself becomes can become an important aspect of well-being (see Neff and Germer, Chapter 27 in this volume).

Related to this question, representations of suffering presented in psychological studies of compassion tend to depict obvious physical (mutilation, starvation) or emotional (sadness, distress) pain, or instances of social unfairness (often through economic games). While undeniably salient, these forms of suffering are not fully representative of the range of suffering we often encounter in our daily lives. It is possible that different kinds of suffering and the varying contexts in which they occur may induce heterogeneous affective and motivational states and demand unique or tailored behavioral responses, all of which may still be considered "compassionate" (Ekman, 2014). In other words, suffering does not always present in obvious forms. A range of affective and motivational states can lead to a given compassionate response, with the behavioral manifestation of that response often dependent on the situational context. Thus, the appropriate response to perceived suffering may be quite different, depending on a given situation, and it may be difficult to operationalize these responses in reductionist or simplified terms. The field of contemplative science would benefit from the development of theoretical models that attempt to characterize compassion along multiple experiential and psychological dimensions. A recent work outlining such a phenomenological classification of

mindfulness and related processes (Lutz et al., 2015) could serve as a useful guide in developing a similar framework for organizing compassion-based practices.

From the Buddhist perspective, a central form of suffering is the suffering of change—all life situations and circumstances, no matter how satisfying, are transitory (Patrul, 1998). From this perspective, our basic biological and psychological nature perpetuates a cycle of meeting needs only to then have to meet other needs: "I am hungry, and so I eat"; "I ate, so now I am tired"; "I am tired, so now I must rest"; and so on. Thus, an approach to life that emphasizes only hedonic aspects of well-being (attaining pleasure and avoiding pain; e.g., Ryan & Deci, 2001) may result in a never-ending quest to fulfill these needs. Paradoxically, training in mindful, compassionate self-regard may enable one to savor the pleasurable aspects of these momentary experiences, without attaching one's sense of well-being to the pleasant target or object. With repeated practice, this decoupling of well-being from momentary experiences of pleasure or pain may promote the development of an understanding of one's own agency in creating the conditions for happiness, which is ultimately more consistent with a eudaimonic view of well-being (Bach & Guse, 2015; Ryan & Deci, 2001).

The cultivation of compassion toward suffering resulting from the transitory nature of experience represents an unstudied, but potentially widely applicable, domain of inquiry. This may be particularly relevant for individuals in modern societies with assured access to basic necessities (food, water, shelter, and physical safety). Subtle forms of suffering often go unnoticed, as they are pervasive daily conditions of even the most materially well-off individuals. For example, from the contemplative perspective, meditation-based trainings that foster awareness of this inevitable cascade of small daily losses or changes in hedonic state (e.g., the last bite of a delicious meal, the end of a good book) may provide a gateway towards a

deeper understanding that one's primary external sources of comfort and well-being, such as loved ones, employment, health, or longevity, are also of a transient nature. Building a framework for how to relate to suffering in familiar, seemingly less consequential, life domains may, in turn, provide the experiential basis for compassionate responses to other, more apparent forms of suffering such as physical pain or the loss of a loved one. This may ultimately extend further to more extreme kinds of suffering—such as violence, war, or famine—even if one has no familiarity with such conditions. The understanding that everyone experiences suffering, however subtle, may spark a sense of commonality in which to ground compassion and, bit by bit, extend it to individuals whose lives, experiences, and manifestations of suffering may be quite different from our own. Thus, understanding these more subtle but inescapable types of suffering may be important in working towards global compassion (see Ekman and Ekman, Chapter 4 in this volume), and in moving from idealized to enacted compassion (e.g., Raiche, 2016).

References

- Akitsuki, Y., & Decety, J. (2009). Social context and perceived agency affects empathy for pain: An event-related fMRI investigation. *Neuroimage*, 47, 722–734.
- Albertson, E. R., Neff, K. D., & Dill-Shackleford, K. E. (2015). Self-compassion and body dissatisfaction in women: A randomized controlled trial of a brief meditation intervention. *Mindfulness*, 6, 444–454.
- Ashar, Y. K., Andrews-Hanna, J. R., Yarkoni, T., Sills, J., Halifax, J., Dimidjian, S., & Wager, T. D. (2016, March 28). Effects of compassion meditation on a psychological model of charitable donation. *Emotion*, 16(5), 691. <u>http://dx.doi.org/10.1037/emo0000119</u>
- Bach, J. M., & Guse, T. (2015). The effect of contemplation and meditation on "great compassion" on the psychological well-being of adolescents. *The Journal of Positive Psychology*, 10(4), 359–369.
- Batson, C. D., Ahmad, N., & Lishner, D. A. (2009). Empathy and altruism. In S. J. Lopez & C. R. Snyder (Eds.), *The Oxford Handbook of Positive Psychology* (3rd ed., pp. 417–426). New York: Oxford University Press.
- Becker, L. (2012). Secular Humanism with a Pulse: The New Activists. Free Inquiry, 32(5), 20-21.
- Beckes, L., Coan, J. A., & Hasselmo, K. (2013). Familiarity promotes the blurring of self and other in the neural representation of threat. *Social Cognitive and Affective Neuroscience*, *8*, 670–677.
- Bono, G., & McCullough, M. E. (2006). Positive responses to benefit and harm: Bringing forgiveness and gratitude into cognitive psychotherapy. *Journal of Cognitive Psychotherapy*, 20, 147–158.
- Bruneau, E. G., Dufour, N., & Saxe, R. (2012). Social cognition in members of conflict groups: Behavioural and neural responses in Arabs, Israelis and South Americans to each other's misfortunes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1589), 717–730.
- Cameron, C. D., & Payne, B. K. (2011). Escaping affect: How motivated emotion regulation creates insensitivity to mass suffering. *Journal of Personality and Social Psychology*, *100*, 1–15.
- Chiesa, A., Anselmi, R., & Serretti, A. (2014). Psychological mechanisms of mindfulness-based interventions: What do we know? *Holistic Nursing Practice*, 28, 124–148.
- Cikara, M., Bruneau, E. G., & Saxe, R. R. (2011). Us and them intergroup failures of empathy. *Current Directions in Psychological Science, 20,* 149–153.

- Condon, P., Desbordes, G., Miller, W. B., & DeSteno, D. (2013). Meditation increases compassionate responses to suffering. *Psychological Science*, *24*, 2125–2127.
- Dahl, C. J., Lutz, A., & Davidson, R. J. (2015). Reconstructing and deconstructing the self: Cognitive mechanisms in meditation practice. *Trends in Cognitive Sciences, 19*, 515–523.
- Dahl, C. J., Lutz, A., & Davidson, R. J. (2016). Cognitive processes are central in compassion meditation. *Trends in Cognitive Sciences*, 20, 161–162.
- Dalai Lama, & Ekman, P. (2008). Emotional Awareness: Overcoming the Obstacles to Psychological Balance and Compassion. New York: Macmillan.
- Davidson, R. J., & Kaszniak, A. W. (2015). Conceptual and methodological issues in research on mindfulness and meditation. *American Psychologist*, 70, 581–592. doi:10.1037/a0039512
- Decety, J., & Jackson, P. L. (2006). A social-neuroscience perspective on empathy. *Current Directions in Psychological Science*, 15, 54–58.
- Desbordes, G., Negi, L. T., Pace, T. W., Wallace, B. A., Raison, C. L., & Schwartz, E. L. (2012). Effects of mindful-attention and compassion meditation training on amygdala response to emotional stimuli in an ordinary, non-meditative state. *Frontiers in Human Neuroscience*, 6, 292.
- DeSteno, D. (2015). Compassion and altruism: How our minds determine who is worthy of help. *Current Opinion in Behavioral Sciences, 3,* 80–83.
- Dovidio, J. F., & Gaertner, S. L. (1991). Changes in the expression and assessment of racial prejudice. In H. J. Knopke, R. J. Norrell, & R. W. Rogers (Eds.), *Opening Doors: Perspectives on Race Relations in Contemporary America* (pp. 119–148). Tuscaloosa, AL: The University of Alabama Press.
- Eisenberg, N. (2000). Emotion, regulation, and moral development. *Annual Review of Psychology*, *51*, 665–697.
- Ekman, P. (2014). Moving Toward Global Compassion. San Francisco, CA: Paul Ekman.
- Engen, H. G., & Singer, T. (2015a). Affect and motivation are critical in constructive meditation. *Trends in Cognitive Sciences, 20,* 159–160.
- Engen, H. G., & Singer, T. (2015b). Compassion-based emotion regulation up-regulates experienced positive affect and associated neural networks. *Social Cognitive and Affective Neuroscience, 10,* 1291–1301.
- Gilbert, P. (2015, August 25). Compassion: Universally misunderstood [web log comment]. Retrieved on June 1, 2016 from <u>http://www.huffingtonpost.co.uk/professor-paul-gilbert-obe/compassion-universally-misunderstood_b_8028276.html?utm_content=buffer4dc45&utm_medium=social&utm_source=twitter.com&utm_campaign=buffer</u>

- Gill, M. J., Andreychik, M. R., & Getty, P. D. (2013). More than a lack of control external explanations can evoke compassion for outgroups by increasing perceptions of suffering (independent of perceived control). *Personality and Social Psychology Bulletin, 3*, 73–87.
- Goetz, J. L., Keltner, D., & Simon-Thomas, E. (2010). Compassion: An evolutionary analysis and empirical review. *Psychological Bulletin*, 136, 351.
- Greenwald, A. G., & Banaji, M. R. (1995). Implicit social cognition: Attitudes, self-esteem, and stereotypes. *Psychological Review*, 102, 4.
- Greenwald, A. G., Nosek, B. A., & Banaji, M. R. (2003). Understanding and using the implication association test: I. An improved scoring algorithm. *Attitudes and Social Cognition*, *85*, 197–216.
- Gulliford, L., Morgan, B., & Kristjánsson, K. (2013). Recent work on the concept of gratitude in philosophy and psychology. *Journal of Value Inquiry*, 47, 285.
- Gyatso, G. K. (2003). The New Meditation Handbook (4th ed.). Ulverston, UK: Tharpa.
- Hager, J. C., Ekman, P., & Friesen, W. V. (2002). *Facial Action Coding System*. Salt Lake City, UT: A Human Face.
- Halifax, J. (2012). A heuristic model of enactive compassion. *Current Opinion in Supportive and Palliative Care, 6,* 228–235.
- Hutcherson, C. A., Seppala, E. M., & Gross, J. J. (2008). Loving-kindness meditation increases social connectedness. *Emotion*, *8*, 720.
- Jacobs, T. L., Shaver, P. R., Epel, E. S., Zanesco, A. P., Aichele, S. R., Bridwell, D. A., . . . Sahdra, B. K. (2013). Self-reported mindfulness and cortisol during a Shamatha meditation retreat. *Health Psychology*, 32, 1104.
- Janak, P. H., & Tye, K. M. (2015). From circuits to behaviour in the amygdala. *Nature*, *517*(7534), 284–292.
- Jazaieri, H., Jinpa, G. T., McGonigal, K., Rosenberg, E. L., Finkelstein, J., Simon-Thomas, E., . .
 Goldin, P. R. (2013). Enhancing compassion: A randomized controlled trial of a compassion cultivation training program. *Journal of Happiness Studies*, 14, 1113–1126.
- Jazaieri, H., McGonigal, K., Jinpa, T., Doty, J. R., Gross, J. J., & Goldin, P. R. (2014). A randomized controlled trial of compassion cultivation training: Effects on mindfulness, affect, and emotion regulation. *Motivation and Emotion*, *38*, 23–35.
- Jinpa, T. (2010). "Compassion Cultivation Training (CCT): Instructor's Manual." Unpublished, Stanford, CA.
- Jinpa, T. (2015). A Fearless Heart: How the Courage to Be Compassionate Can Transform Our Lives. New York: Penguin.

- Kabat-Zinn, J. (1990). Full Catastrophe Living: Using the Wisdom of Your Mind and Body to Face Stress, Pain, and Illness. New York: Delacorte.
- Kabat-Zinn, J. (2011). Some reflections on the origins of MBSR, skillful means, and the trouble with maps. *Contemporary Buddhism, 12,* 281–306.
- Kang, Y., Gray, J. R., & Dovidio, J. F. (2014). The nondiscriminating heart: Lovingkindness meditation training decreases implicit intergroup bias. *Journal of Experimental Psychology: General*, 143, 1306.
- Kemeny, M. E., Foltz, C., Cavanagh, J. F., Cullen, M., Giese-Davis, J., Jennings, P., ...Wallace, B. A. (2012). Contemplative/emotion training reduces negative emotional behavior and promotes prosocial responses. *Emotion*, 12, 338.
- Klimecki, O. M., Leiberg, S., Lamm, C., & Singer, T. (2012). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex, 23,* 1552–1561.
- Kogan, A., Oveis, C., Carr, E. W., Gruber, J., Mauss, I. B., Shallcross, A., . . . Cheng, C. (2014). Vagal activity is quadratically related to prosocial traits, prosocial emotions, and observer perceptions of prosociality. *Journal of Personality and Social Psychology*, 107, 1051.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). International Affective Picture System (IAPS): Affective Ratings of Pictures and Instruction Manual. Technical Report A-8. Gainesville, FL: University of Florida.
- Lebowitz, M. S., & Dovidio, J. F. (2015). Implications of emotion regulation strategies for empathic concern, social attitudes, and helping behavior. *Emotion*, 15, 187.
- Leiberg, S., Klimecki, O., & Singer, T. (2011). Short-term compassion training increases prosocial behavior in a newly developed prosocial game. *PloS ONE*, *6*(3), e17798.
- Lim, D., Condon, P., & DeSteno, D. (2015). Mindfulness and compassion: An examination of mechanism and scalability. *PloS ONE*, 10(2), e0118221.
- Lopez, D. S. Jr., (1998). Two sides of the same God. *Tricycle: The Buddhist Review*, 7(3), 67–69.
- Lumma, A. L., Kok, B. E., & Singer, T. (2015). Is meditation always relaxing? Investigating heart rate, heart rate variability, experienced effort and likeability during training of three types of meditation. *International Journal of Psychophysiology*, *97*, 38–45.
- Lutz, A., Brefczynski-Lewis, J., Johnstone, T., & Davidson, R. J. (2008). Regulation of the neural circuitry of emotion by compassion meditation: Effects of meditative expertise. *PloS ONE*, 3(3), e1897.
- Lutz, A., Greischar, L. L., Perlman, D. M., & Davidson, R. J. (2009). BOLD signal in insula is differentially related to cardiac function during compassion meditation in experts vs. novices. *Neuroimage*, 47, 1038–1046.

- Lutz, A., Jha, A. P., Dunne, J. D., & Saron, C. D. (2015). Investigating the phenomenological matrix of mindfulness-related practices from a neurocognitive perspective. *American Psychologist*, 70, 632.
- Lutz, A., Slagter, H. A., Dunne, J. D., & Davidson, R. J. (2008). Attention regulation and monitoring in meditation. *Trends in Cognitive Sciences*, 12, 163–169.
- Lutz, A., Slagter, H. A., Rawlings, N. B., Francis, A. D., Greischar, L. L., & Davidson, R. J. (2009). Mental training enhances attentional stability: Neural and behavioral evidence. *The Journal of Neuroscience*, 29, 13418–13427.
- MacCoon, D. G., Imel, Z. E., Rosenkranz, M. A., Sheftel, J. G., Weng, H. Y., Sullivan, J. C., . . . Davidson, R. J. (2012). The validation of an active control intervention for Mindfulness Based Stress Reduction (MBSR). *Behaviour Research and Therapy*, *50*, 3–12.
- MacLean, K. A., Ferrer, E., Aichele, S. R., Bridwell, D. A., Zanesco, A. P., Jacobs, T. L., . . . Shaver, P. R. (2010). Intensive meditation training improves perceptual discrimination and sustained attention. *Psychological Science*, *21*, 829–839.
- Mascaro, J. S., Rilling, J. K., Negi, L. T., & Raison, C. (2012). Compassion meditation enhances empathic accuracy and related neural activity. *Social Cognitive and Affective Neuroscience*, 8, 48–55.
- Mascaro, J. S., Rilling, J. K., Negi, L. T., & Raison, C. L. (2013). Pre-existing brain function predicts subsequent practice of mindfulness and compassion meditation. *Neuroimage*, 69, 35–42.
- McCall, C., Steinbeis, N., Ricard, M., & Singer, T. (2014). Compassion meditators show less anger, less punishment, and more compensation of victims in response to fairness violations. *Frontiers in Behavioral Neuroscience*, *8*, 424.
- Mikulincer, M., & Shaver, P. R. (2005). Attachment security, compassion, and altruism. *Current Directions in Psychological Science*, 14, 34–38.
- Mikulincer, M., Shaver, P. R., Gillath, O., & Nitzberg, R. A. (2005). Attachment, caregiving, and altruism: Boosting attachment security increases compassion and helping. *Journal of Personality and Social Psychology*, *89*, 817.
- Neff, K. D., & Germer, C. K. (2013). A pilot study and randomized controlled trial of the Mindful Self-Compassion program. *Journal of Clinical Psychology*, *69*, 28–44.
- Ozawa-de Silva, B. R., Dodson-Lavelle, B., Raison, C. L., Negi, L. T., Silva, B., & Phil, D. (2012). Compassion and ethics: Scientific and practical approaches to the cultivation of compassion as a foundation for ethical subjectivity and well-being. *Journal of Healthcare Science and the Humanities, 2*, 145–161.

- Pace, T. W., Negi, L. T., Adame, D. D., Cole, S. P., Sivilli, T. I., Brown, T. D., . . . Raison, C. L. (2009). Effect of compassion meditation on neuroendocrine, innate immune and behavioral responses to psychosocial stress. *Psychoneuroendocrinology*, 34, 87–98.
- Pace, T. W., Negi, L. T., Dodson-Lavelle, B., Ozawa-de Silva, B., Reddy, S. D., Cole, S. P., ... Raison, C. L. (2013). Engagement with cognitively-based compassion training is associated with reduced salivary C-reactive protein from before to after training in foster care program adolescents. *Psychoneuroendocrinology*, 38, 294–299.
- Pace, T. W., Negi, L. T., Sivilli, T. I., Issa, M. J., Cole, S. P., Adame, D. D., & Raison, C. L. (2010). Innate immune, neuroendocrine and behavioral responses to psychosocial stress do not predict subsequent compassion meditation practice time. *Psychoneuroendocrinology*, 35, 310–315.
- Patrul, Rinpoche. (1998). The Words of My Perfect Teacher: A Complete Translation of a Classic Introduction to Tibetan Buddhism. Lanham, MD: Rowman & Littlefield.
- Pokorny, J.J., Norman, A., Zanesco, A.P., Bauer-Wu, S.M., Sahdra, B.K., & Saron, C.D. (accepted). Network analysis for the visualization and analysis of qualitative data. Psychological Methods.
- Raiche, C. (2016). #BlackLivesMatter and living the bodhisattva vow. *Harvard Divinity Bulletin*, *Winter/Spring 2016*. Retrieved on June 1, 2016 from <u>http://bulletin.hds.harvard.edu/articles/winterspring2016/blacklivesmatter-and-living-bodhisattva-vow</u>
- Ricard, M. (2008). *Happiness: A Guide to Developing Life's Most Important Skill*. New York: Little, Brown & Company.
- Rogers, F. J. (2015). Practicing Compassion. Nashville, TN: Fresh Air Books.
- Rosenberg, E. L., Zanesco, A. P., King, B. G., Aichele, S. R., Jacobs, T. L., Bridwell, D. A., . . . Sahdra, B. K. (2015). Intensive meditation training influences emotional responses to suffering. *Emotion*, *15*, 775.
- Rosenkranz, M. A., Davidson, R. J., MacCoon, D. G., Sheridan, J. F., Kalin, N. H., & Lutz, A. (2013). A comparison of mindfulness-based stress reduction and an active control in modulation of neurogenic inflammation. *Brain, Behavior, and Immunity*, 27, 174–184.
- Ryan, R. M., & Deci, E. L. (2001). On happiness and human potentials: A review of research on hedonic and eudaimonic well-being. *Annual Review of Psychology*, *52*, 141–166.
- Ryff, C. D., & Keyes, C. L. M. (1995). The structure of psychological well-being revisited. Journal of Personality and Social Psychology, 69, 719.

- Sahdra, B. K., MacLean, K. A., Ferrer, E., Shaver, P. R., Rosenberg, E. L., Jacobs, T. L., . . . Bridwell, D. A. (2011). Enhanced response inhibition during intensive meditation training predicts improvements in self-reported adaptive socioemotional functioning. *Emotion*, 11, 299.
- Salzberg, S. (2004). *Lovingkindness: The Revolutionary Art of Happiness*. Boston, MA: Shambhala Publications.
- Santideva. (1997). A Guide to the Bodhisattva Way of Life (Bodhicaryavatara). (V. A. Wallace & B. A. Wallace, Trans.). Ithaca, NY: Snow Lion Publications.
- Shaver, P. R., Lavy, S., Saron, C. D., & Mikulincer, M. (2007). Social foundations of the capacity for mindfulness: An attachment perspective. *Psychological Inquiry*, 18, 264– 271.
- Singer, T., & Klimecki, O. M. (2014). Empathy and compassion. *Current Biology, 24*, R875– R878.
- Singer, T., Kok, B. E., Bornemann, B., Zurborg, S., Bolz, M., & Bochow, C. (2016). The ReSource Project: Background, design, samples, and measurements. (2nd ed.). Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.Stellar, J. E. (2013). Vagal Reactivity and Compassionate Responses to the Suffering of Others. Doctoral dissertation, University of California, Berkeley.
- Stellar, J. E., Cohen, A., Oveis, C., & Keltner, D. (2015). Affective and physiological responses to the suffering of others: Compassion and vagal activity. *Journal of Personality and Social Psychology*, 108, 572.
- Trautwein, F.-M., Naranjo, J. R., & Schmidt, S. (2014). Meditation effects in the social domain: Self-other connectedness as a general mechanism? In S. Schmidt & H. Walach (Eds.), *Meditation–Neuroscientific Approaches and Philosophical Implications* (pp. 175–198). Cham, Switzerland: Springer International Publishing.
- Van Bavel, J. J., Mende-Siedlecki, P., Brady, W. J., & Reinero, D. A. (2016). Contextual sensitivity in scientific reproducibility. *Proceedings of the National Academy of Sciences*, 113, 6454–6459.
- Wallace, B. A. (1999). *The Four Immeasurables: Cultivating a Boundless Heart*. Boston, MA: Snow Lion Publications.
- Wallace, B. A. (2006). *The Attention Revolution: Unlocking the Power of the Focused Mind.* Somerville, MA: Wisdom Publications.
- Weng, H. Y., Fox, A. S., Shackman, A. J., Stodola, D. E., Caldwell, J. Z., Olson, M. C., . . . Davidson, R. J. (2013). Compassion training alters altruism and neural responses to suffering. *Psychological Science*, 24, 1171–1180.

- Widdicombe, L. (2015, July 6). The higher life: A mindfulness guru for the tech set. The New Yorker. Retrieved on June 1, 2016 from http://www.newyorker.com/magazine/2015/07/06/the-higher-life
- Zagefka, H., Noor, M., & Brown, R. (2013). Familiarity breeds compassion: Knowledge of disaster areas and willingness to donate money to disaster victims. *Applied Psychology*, 62, 640–654.
- Zaki, J. (2014). Empathy: A motivated account. *Psychological Bulletin*, 140(6), 1608–1647.
- Zaki, J., & Ochsner, K. N. (2012). The neuroscience of empathy: Progress, pitfalls and promise. *Nature Neuroscience*, *15*, 675–680.
- Zanesco, A. P., King, B. G., MacLean, K. A., Jacobs, T. L., Aichele, S. R., Wallace, B. A., . . . Saron, C. D. (2016). Meditation training influences mind wandering and mindless reading. *Psychology of Consciousness: Theory, Research, and Practice, 3*, 12.
- Zanesco, A. P., King, B. G., MacLean, K. A., & Saron, C. D. (2013). Executive control and felt concentrative engagement following intensive meditation training. *Frontiers in Human Neuroscience*, 7, 566.

Chapter 2

Shifting Baselines: Longitudinal Reductions in Beta Oscillatory Power Characterize Resting Brain Activity with Intensive Meditation

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Introduction

A central claim of Buddhist contemplative traditions is that training in meditation can bring about lasting changes in the nature and habits of the mind (e.g., Dalai Lama & Cutler, 2009; Wallace 2006). Consistent with these claims, different forms and regimens of meditation training have been shown to influence capacities as diverse as attentional stability (e.g., Lutz et al., 2009; van Leeuwen et al., 2012; Zanesco et al., 2019), stress buffering (e.g., Creswell & Lindsay, 2014), emotion regulation and reactivity (e.g., Lutz, et al., 2008; Rosenberg et al., 2015), and prosociality (e.g., Ashar et al., 2016; Condon et al., 2013; Weng et al., 2017). Critically, these changes may extend well beyond the bounds of formal meditation sessions, influencing broad domains of daily life (e.g., Donald et al., 2019; Sahdra et al., 2011; Skwara et al., 2017). The manifestation of these effects across domains that are not explicitly trained implies that meditation training might alter domain-general neurocognitive systems. Generalized changes in such systems should theoretically be observed across a variety of situations contexts and, notably, in the spontaneous neural activity of the brain at rest (e.g., Bauer et al., 2019).

In this report, we leverage data from a large-scale, longitudinal study of intensive meditation to ask whether neuroelectric changes observed during formal meditation practice might generalize to an ostensibly non-meditative state. In a previous report, we showed that 3 months of full-time training in *shamatha* meditation (a form of focused attention practice) led to replicable reductions in EEG beta band power during mindfulness of breathing meditation among a group of experienced meditators (Saggar et al., 2012). This cohort of participants also demonstrated improvements across a variety of cognitive and affective domains (see, for example, Rosenberg et al., 2012; Sahdra et al., 2011; Shields et al., 2020, Zanesco et al., 2013, 2018), including the ability to make fine-grained perceptual discriminations in a visual task

(MacLean et al., 2010, Zanesco et al 2019). Our present aim was to investigate whether brain oscillatory changes also occurred during an uninstructed resting state, and whether these changes could predict performance on a separate perceptual discrimination task. By characterizing these domains, we hoped to shed light on neurocognitive factors that might support cross-domain changes in meditation-related processes over a period of intensive practice.

The brain is remarkably responsive to changes in environment and behavior. For instance, immobilizing a person's arm for only 48 hours can lead to neuroplastic changes in functional brain connectivity (Newbold et al., 2020). The capacity of the brain to undergo reorganization has also been observed in the context of contemplative practice. Experienced meditators show persistent shifts in functional (e.g., Davidson and Lutz, 2008; Hasenkamp and Barsalou, 2012) and structural (e.g., Fox et al., 2014; Lumma et al., 2018) brain organization. These changes can be observed during active meditation practice (e.g., Braboszcz et al., 2017; Fucci et al., 2018; Lee et al., 2018; Saggar et al., 2012), during task performance (e.g., Desbordes et al., 2012; Zanesco et al., 2019; van Leeuwen et al., 2012) and in the functional architecture of the resting brain (e.g., Dentico et al., 2018; Hasenkamp & Barsalou, 2012; Zanesco et al., 2021).

Much of the neuroscientific literature on meditation has focused on investigations of brain activity during formal meditation practice (for reviews, Cahn & Polich, 2006; Lomas, Ivtzan, & Fu, 2015; Lee, Kulubya, Goldin, Goodarzi, & Girgis, 2018). During formal meditation practice, practitioners engage with a specified set of mental activities for a given period of time. These formal sessions are typically undertaken in a physical posture, such as sitting or lying down; and are conditioned by social, ethical, and other factors (Lutz et al., 2015). For example, during mindfulness of breathing meditation, a practitioner might sit quietly in an upright posture, focusing on the sensations of breath at the aperture of their nostrils or the rising and falling of

their abdomen. When they notice that their mind has wandered, they are instructed to gently redirect it back to the breath (Gunaratana, 2002). Through repeated practice, practitioners cultivate the ability to regulate attention and to volitionally maintain awareness on a chosen object. Over time, improvements in the ability to direct and sustain attention are thought to extend beyond the meditative context and generalize to other activities (Dalai Lama & Cutler, 2009; Lutz, et al., 2015; Wallace, 2006).

While the boundary conditions of formal meditation sessions are often clearly delineated, the *effects* of meditation training are much less circumscribed (Cahn & Polich, 2006; Skwara et al., 2017). The brain systems and cognitive mechanisms engaged through various meditative practices are implicated in a wide array of psychological processes (Dahl et al., 2015; Lutz et al., 2015). As such, meditation-related changes in these neurocognitive systems may manifest across a range of different contexts and outcomes. Experientially, shifts in perception and awareness experienced during formal practice may, over time, extend into daily life in ways that are both pervasive and persistent (Dalai Lama & Cutler, 2009; Davidson & Kazniak, 2015; Kabat-Zinn 2013; Wallace, 2006), blurring the line between meditative states and everyday experience.

Evidence for meditation-related domain generalization can be gleaned from tasks that engage the specific skills or capacities ostensibly trained by a given meditation practice, as well as from tasks that cut across cognitive and affective domains that were not specifically targeted by that practice. In our own work studying shamatha meditation, we have found that 3 months of intensive training leads to improvements in the capacity to regulate one's attention (MacLean et al., 2010; Sahdra et al., 2011; Shields et al., 2020; Zanesco et al, 2013, 2016, 2018, 2019), but also to alterations in emotional responses to suffering (Rosenberg et al., 2015), and improved socioemotional functioning (Sahdra et al., 2011). It remains unclear, however, what brain

processes support the tendency for cognitive capacities engaged during formal practice to generalize across diverse psychological domains.

To the extent that meditation training leads to generalized changes in cognition and behavior, there should be observable shifts in the activity of underlying brain systems that support these functions. One method for quantifying the functioning of such brain systems is to examine neural oscillations, as indexed by electrical activity at the scalp (e.g., Buzsaki et al., 2012). In a prior study, we examined brain activity—indexed via scalp electroencephalography (EEG)—during a formal session of mindfulness of breathing meditation (Saggar et al., 2012). Experienced meditators were assigned to an initial training or waitlist control group. Participants in the training group entered a 3-month residential retreat, where they practiced formal meditation for 6 to 8 hours a day. Both groups completed testing sessions at the beginning, middle, and end of the intervention period. The waitlist controls were later assessed again during a second 3-month retreat intervention.

For both retreats, participants who received meditation training demonstrated significant reductions in band power in the beta frequency range, as well as reductions in peak individual alpha frequency. These changes were not observed in the waitlist control group. As described above, mindfulness of breathing meditation involves directing and maintaining attention to the tactile sensations of breath. Because prior research has implicated beta band activity in attentional orienting to sensory information (e.g., van Ede et al., 2011; Pfurtscheller and Lopes da Silva, 1999; Schubert et al., 2009), we interpreted our findings as reflecting enhanced attention to, and sensory processing of, the subtle sensations of breath developed through intensive practice (Saggar et al., 2012).

The Present Study

In the present study, we asked whether oscillatory changes concomitant to the Saggar et al. (2012) findings would be observed during an uninstructed resting task. We examined longitudinal changes in EEG spectral power recorded during 2 minutes of eyes closed rest in the same cohort of participants as the prior study. While beta oscillations have long been implicated in sensorimotor and attentional processes, recent work also suggests that beta band activity may be broadly related to the efficiency of communication between core brain networks (Betti et al., 2020). In studies of resting brain activity, beta band activity has been associated with the transient coupling of nodes both within and across resting state networks (de Pasquale et al., 2012; 2018), and with functional connectivity between resting state networks (Wens et al., 2019). These associations appear to be pronounced for nodes of the default mode network. Importantly, moments of high within- and between-network correlation—associated with bandlimited power in the beta frequency—appear to correspond to moments of high network efficiency (Betti et al., 2020).

Experiential (e.g., Dalai Lama & Cutler, 2009; Kabat-Zinn, 2013) as well as empirical (e.g., Desbordes et al., 2012; Fox et al., 2014; Hasenkamp and Barsalou, 2012) accounts suggest that neurocognitive changes instantiated through meditation extend beyond the bounds of formal practice. Thus, it is possible that the changes we previously observed during mindfulness of breathing practice could be indicative of broader changes in patterns of neural activity. These broader changes, in turn, should be observable across multiple contexts including during quiet, uninstructed rest. As support for this idea, an additional study on these same participants revealed retreat-related changes in activity patterns of resting EEG microstates, suggesting broad shifts in the functional architecture of the resting brain over the course of these retreats (Zanesco

et al., 2021). If reductions in beta band activity previously found during mindfulness of breathing practice were also observed during rest, this would suggest more generalized changes in the activity patterns of underlying brain networks, offering a window into the neurocognitive processes supporting domain-general change during meditation training.

The present data comprise part of a multimethod, waitlist-controlled study of intensive residential meditation (e.g., MacLean et al., 2010; Saggar et al., 2012; Sahdra et al., 2011; Zanesco et al., 2019). 88-channel scalp EEG was collected at the beginning, middle, and end of two 3-month meditation retreats while participants rested quietly with their eyes closed. We hypothesized that 3 months of residential training would alter brain oscillatory activity during the uninstructed resting task. We further hypothesized that these changes would mirror those previously observed during mindfulness of breathing meditation: namely, overall reductions in beta band power and individual alpha frequency. We also predicted that any observed reductions in beta band power would be related to concomitant improvements in perceptual discrimination, as measured by a perceptual thresholding task that requires participants to make fine grained visual discriminations. Previously, we reported that retreat participants demonstrated better perceptual discrimination on this task following meditation training (MacLean et al., 2010). Here, we expected that greater reductions in beta power would be related to greater retreat-related improvements in visual discrimination. Linking brain activity during eyes closed rest to behavioral performance on a visual perceptual task would offer further evidence for the relevance of observed neural changes across multiple cognitive and perceptual contexts.

Method

Participants

We recruited experienced meditation practitioners through advertisements in print and online Buddhist publications. Following recruitment, 60 eligible participants (32 females, 28 males; M_{age} = 48 years, range = 22 to 69) were randomly assigned to an initial training group (n = 30) or a waitlist control group (n = 30) using a stratified matching procedure. The groups were matched at baseline on age, sex, ethnicity, and major personality characteristics, as well as several cognitive task variables assessed prior to assignment (for details of recruitment and group matching, see MacLean et al., 2010; Shields et al., 2020). They were also matched on lifetime meditation experience, with an overall mean of 2,610 cumulative hours (initial training: M= 2,549 hours, range = 250 to 9,500; waitlist control: M= 2,668, range = 250 to 15,000). In addition, participants were screened for medical conditions and Axis I psychiatric diagnoses as assessed by the Mini International Neuropsychiatric Interview screen (Sheehan et al., 1998) and a clinical interview administered by a licensed clinical psychologist.

One waitlist participant left the study after completing the control assessments, due to circumstances unrelated to the study. This left a total of 29 participants for the second training intervention. All study procedures were approved by the Institutional Review Board of the University of California, Davis. All participants gave full informed consent and were compensated \$20 per hour of data collection.

Meditation Training and Retreat

The waitlist design included two 3-month-long residential meditation retreats. The two retreats were formally identical in training structure and were held in the same scenic retreat environment. During the first retreat (Retreat 1), active training participants lived and practiced

meditation on-site at Shambhala Mountain Center in Red Feather Lakes, CO. Waitlist control participants continued with their daily lives during this time and were flown to the retreat center to complete on-site assessments at the beginning, middle, and end of the intervention period. At each assessment, waitlist control participants arrived at the retreat center approximately 3 days (range = 65–75 hours) prior to their laboratory session for an initial acclimatization period to adjust to the altitude (~2500 m) and natural environment. Approximately 3 months after Retreat 1, waitlist control participants returned to the retreat center and underwent their own 3-month retreat intervention as active training participants (Retreat 2). Thus, the design comprised three participant statuses: Retreat 1 active training participants, Retreat 1 waitlist controls, and Retreat 2 active training participants. The Retreat 2 training participants were the same participants as Retreat 1 waitlist controls and were initially assessed as active training participants about 3 months after the conclusion of their final wait-list control assessment.

While on retreat, training participants practiced meditation for 6 to 8 hours a day, under the guidance of Dr. B Alan Wallace, an experienced Buddhist teacher and contemplative scholar. Participants gathered twice daily to engage in guided group meditation and instruction and met individually with Dr. Wallace once a week. The meditation instructions were drawn from the Theravada and Mahayana Buddhist traditions and included shamatha and four immeasurables practices (described in Wallace, 2006). Shamatha techniques aim to develop stability of attention, perceptual vividness, and concentration, and were the primary practices taught on retreat. These consisted of: (1) *mindfulness of breathing*, in which attention is focused on the sensations of the breath; (2) *observing mental events*, in which attention is turned to all forms of mental phenomena; and (3) *observing the nature of consciousness*, in which focus is placed on the awareness of being aware. The four immeasurables of *loving-kindness, compassion*,

empathetic joy, and *equanimity* aim to cultivate beneficial aspirations for the self and others, (for a description, see Rosenberg et al., 2015; Wallace, 2010). The four immeasurables were taught as supportive practices, for approximately 45 minutes per day, on average. Overall, training participants reported devoting most of their practice time to mindfulness of breathing (for full practice time details see, Sahdra et al., 2011).

Laboratory Sessions and Measures

On-site laboratory assessments were conducted at the beginning (preassessment), middle (midassessment), and end (postassessment) of each retreat. At each assessment, participants completed approximately 4 hours of testing on each of two consecutive days. The results of these assessments can be found in several other reports (e.g., MacLean et al., 2010; Rosenberg et al, 2015; Saggar et al., 2012; Sahdra et al. 2011; Shields et al, 2020; Zanesco et al., 2019). All testing took place in two field laboratories with darkened, sound-attenuated testing and control rooms built on-site at the retreat center. Retreat 1 training participants completed a total of three on-site assessments, while waitlist controls completed a total of six assessments—three as controls in Retreat 1, and three as active training participants in Retreat 2.

Resting EEG

Resting EEG was collected as the first laboratory task at each assessment. Continuous EEG was recorded across 4 minutes of rest, divided into four 1-minute segments of eyes open and eyes closed rest (open, closed, closed, open). At the beginning of each segment, participants were instructed via an audio recording: "For the next sixty seconds please sit quietly with your eyes closed [open]." Because our goal was to investigate brain activity in the absence of an explicit task, these instructions were intentionally non-directive and avoided any mention of meditation or mind wandering.

In our prior report, participants practiced mindfulness of breathing with their eyes closed. Therefore, for consistency with these data, we included data from the eyes closed resting epochs only. In addition, only participants who had usable EEG data at all assessment points were included in the analyses (four were excluded upon initial inspection; seven were excluded following preprocessing). This resulted in a total of 53 participants (28 female; M_{age} = 48.47 years, SD_{age} = 14.21, range = 22.25 to 69.69) providing a total of 159 observations for Retreat 1. Of these, 26 were training participants (13 female; age: M_{age} = 50.26, SD_{age} = 12.94, range = 23.90 to 69.69), and 27 were waitlist controls (15 female; age: M_{age} = 46.74, SD_{age} = 15.39, range = 22.25 to 65.16). For Retreat 2, 26 training participants (13 female; M_{age} = 46.47 years, SD_{age} = 15.56, range = 22.25 to 65.16) provided 78 observations.

Data acquisition and processing. EEG was recorded with the BioSemi ActiveTwo system (http://www.biosemi.com) at a sampling rate of 2048 Hz. Easycap electrode caps (http://www.easycap.de) were fitted with BioSemi electrode holders in an 88-channel equidistant montage, and individual electrode locations were localized using a Polhemus Patriot digitizer (http://www.polhemus.com). On participant request, some electrodes (primarily at frontopolar locations) were not inserted or were removed to minimize discomfort. The EEG recordings were band-pass filtered offline between 0.1 and 200 Hz (zero-phase; roll-off; 12 dB/octave LP, 24 dB/octave HP) and then referenced to the average of all remaining channels. Data preprocessing was conducted in BESA 5.2 (www.besa.de). Channels with very low signal quality were discarded prior to analysis, and data were manually marked to remove extreme artifacts and intermittent high amplitude EMG contamination.

Separating neural from non-neural signal sources. Following the process outlined in Saggar et al. (2012), second-order blind source identification (SOBI; Belouchrani et al., 1997)

was used to separate signals of putative neural origin from non-neural sources. SOBI is a method similar to ICA that functions to separate signal components. Unlike ICA, which examines only momentary correlations, SOBI uses joint-diagonalization of correlation matrices at multiple temporal delays. This is used to identify maximally independent sources by minimizing the sum of the squared cross-correlations of all pairs of sources across all temporal delays. We used 41 temporal delays, $\tau = [1:1:10, 12:2:20, 25:5:100, 120:20:300]$ ms, as recommended in Tang et al., 2005. The two consecutive 1-minute segments of eyes closed resting EEG were concatenated and submitted to SOBI. A novel SeMi-automatic Artifact Removal Tool (SMART; <u>https://stanford.edu/~saggar/Software.html</u>; Saggar et al., 2012) was used to generate signal source topography, spectra, autocorrelation, and timeseries for inspection. These SMART outputs were used to manually classify signal sources as neural or non-neural (e.g., EMG, ocular artifacts, line noise) in origin (see Saggar et al., 2012, for examples of SMART output and a discussion of the parameters considered in source classification).

Reconstruction and conversion into standardized electrode space. Following application of SOBI, sources identified as non-neural were removed and the remaining putative neural sources were reconstructed into the original 88-channel montage. To ensure that channel locations were standardized across participants, the reconstructed montage was then transformed into a standard 81-channel montage (international 10-10 system) using spherical spline interpolation (smoothing factor of 2e-07) as implemented in BESA 5.2. Eight channels of the standard 81-channel montage (AF9, Fpz, Fp2, Nz, AF10, CB1, CB2) did not have corresponding nearest electrode sites in the original montage and so were removed from the interpolated locations, yielding a final standardized 73-channel montage.

Scalp current density. We used the MATLAB CSD Toolbox

(http://psychophysiology.cpmc.columbia.edu/Software/CSDtoolbox; Kayser & Tenke, 2006), to transform data from the standardized 73-channel montage into a reference-free estimation of scalp current source density (CSD) using spherical spline interpolation (Perrin et al., 1989). Resulting CSD units are given in μ V/m². The surface Laplacian was estimated as the second derivative of the scalp potential and smoothed by a lambda factor of 2e-05. Transformation of scalp voltage to CSD minimizes the effects of volume conduction and improves visualization of scalp topographic differences (Kayser & Tenke, 2012; 2015).

Power spectral estimation. The 2 minutes of reconstructed EEG data were segmented into 2-second (4096 point) segments with 50% overlap. Power spectra estimates, averaged over 2-second windows, were computed in the MATLAB FieldTrip package (Oostenveld et al., 2011) using multi-tapered power spectral density estimation (Mitra & Pesaran, 1999; Oostenveld et al., 2011) and a Hanning window (Welch, 1967) at 0.5 Hz resolution. Frequency bands were defined relative to each individual's peak alpha frequency (IAF). IAF was calculated within a frequency range of 7 Hz (f_1) to 14 Hz (f_2) using the center-of-gravity method of Klimesch (1999):

$$\alpha_{IAF} = \frac{\sum_{i=f_1}^{f_2} (a(f_i) \times f_i)}{\sum_{i=f_1}^{f_2} a(f_i)}$$

where f_i denotes the power-spectral estimate at frequency *i*. For each EEG recording, IAF values were calculated for each channel, separately, and then averaged across all channels to obtain a single mean estimate of IAF per participant per assessment. Frequency bands were then calculated for each participant at each assessment based on their mean IAF. Table 2.1 presents the IAF frequency band definitions and resultant IAF-based frequency band ranges used in the current dataset, alongside the canonical frequency bands. After the IAF-based frequency ranges were defined, power was estimated within each band by averaging over the 2 minutes of eyes closed EEG for each individual's idiosyncratic frequency range. The results presented below are based on a single estimate of power ($\mu V^2/m^2$) per frequency band for each electrode, participant, and assessment. We additionally conducted all analyses using canonical fixed frequency bands. Using fixed bands did not result in major changes to our core findings. These results are presented in the Supplementary Information.

Perceptual Discrimination Task

Participants also completed a perceptual discrimination task, given immediately following the resting task at each assessment. The task was designed to determine each participant's visual perceptual threshold by measuring the minimum difference in line length at which the participant could reliably discriminate between a target and non-target line, with a smaller difference between line types corresponding to a lower threshold. This task has been described in-depth elsewhere (MacLean et al., 2010; Zanesco et al., 2019). Briefly, participants were asked to distinguish between frequent long line non-targets (70% of trials), and infrequent short line targets (30% of trials), which were masked and presented for 150 msec at the center of a dark screen. Participants responded by clicking whenever the target appeared, and were given auditory feedback for their responses.

A PEST (<u>Parameter Estimation through S</u>equential <u>T</u>esting) algorithm (Taylor & Creelman, 1967) was used to converge on a participant's visual threshold by dynamically varying the length of a target line compared to an unchanging longer non-target line. Visual threshold was calculated for all assessments as the visual angle difference in line length at which a participant could perform this task with 75% accuracy, with the exception of the Retreat 1 pre-assessment, where an 85% criterion was used (see MacLean et al., 2010). Because of the

methodological inconsistencies among assessments in Retreat 1 (see also Zanesco et al., 2018, 2019) we limited the current investigation of visual threshold to Retreat 2.

Statistical Analyses

Non-parametric Permutation-based Cluster Identification

We examined changes in electrode-wise band power estimates as a function of assessment (pre-, mid- and post-retreat) using non-parametric cluster-based permutation testing, implemented with the *ft_freqstatistics* function in FieldTrip (Oostenveld et al., 2011). This data-driven approach identifies contiguous clusters of electrodes that demonstrate reliable changes in band power, while also controlling for multiple comparisons (Maris & Oostenveld, 2007). It is important to note that identified clusters provide evidence for differences between conditions—in this case across the three assessment points—but do not provide evidence for changes at any specific electrode site (see Sassenhagen & Draschkow, 2019, for the spatial limitations of cluster-based permutation tests).

A separate non-parametric permutation test was conducted for each participant status (Retreat 1 training, Retreat 1 control, and Retreat 2 training) and IAF-based frequency band (delta, theta, alpha, beta, gamma). In cases where change was identified in the alpha band, we conducted follow up tests for changes in three alpha sub-bands (alpha 1, alpha 2, alpha 3), based on prior evidence for functional differences between lower (alpha 1, alpha 2) and upper (alpha 3) alpha (Klimesch, 1999).

First, for each electrode, change in band power across assessments was evaluated as a multivariate *F*-statistic, and electrodes demonstrating a significance level of $\alpha \le 0.05$ were selected as candidate cluster members. These candidate electrodes were then grouped into clusters based on spatial adjacency. Cluster criteria were set such that each candidate electrode

was required to have two adjacent electrodes that were also cluster candidates, resulting in a minimum cluster size of three electrodes. Cluster-level statistics were then calculated by taking the sum of the *F*-statistics of all electrodes comprising a cluster. The significance of this cluster statistic was assessed non-parametrically through 10,000 permutations of a Monte Carlo approximation. Finally, we subjected the resultant cluster probabilities to the false discovery rate (FDR) procedure of Benjamini and Hochberg (1995) to control for multiple comparisons. Cluster statistics that survive this correction indicate change across assessments that is larger than would be expected by chance.

Parametric Analysis: Mixed Models

Cluster-wise power estimates were subjected to parametric statistical testing to assess the significance and directionality of change across assessments as a function of participant status. First, band power at each electrode included in a significant cluster was log-transformed. Then, these values were averaged within each cluster to create a cluster-wise estimate of band power, or cluster mean, reported in $log(\mu V^2/m^2)$. This was done for each individual at each assessment. Following the approach of Saggar et al, 2012, when a cluster was identified for a given participant status (e.g., Retreat 1 training), cluster mean power estimates based on that cluster were also calculated for the relevant comparison status. For example, if an alpha band cluster of 10 electrodes was identified in Retreat 1 training participants, a cluster mean of these 10 electrodes would also be generated for each Retreat 1 control participant. Likewise, if a cluster was identified for Retreat 2 training participants, this cluster was also applied to the data from these same participants as Retreat 1 waitlist controls. This allowed for direct parametric comparison of power change in corresponding sets of electrodes across experimental conditions.
Changes in cluster mean power were analyzed using linear mixed effects models implemented in SAS PROC MIXED version 9.4. Assessment (pre-, mid-, post-) and participant status were included as fixed effects. In Retreat 1, status functioned as a between-groups effect (Retreat 1 training compared to Retreat 1 controls), while in Retreat 2 it served as a withinsubjects contrast (Retreat 2 training participants compared to their prior status as Retreat 1 controls). A random effect of participant was included to allow for repeated measures within subjects. Parameters were estimated using restricted maximum likelihood, and degrees of freedom were calculated based on the Sattherthwaite approximation.

Of primary interest was the assessment by status interaction, the presence of which would indicate that participants on retreat demonstrated a pattern of change across assessments that differed from participants not currently on retreat. This was followed by a test of the effect of assessment within each status and directed comparisons of model estimated marginal means. The effect of assessment was centered to preassessment and participant status was centered to the control group for all follow-up tests.

Changes in IAF were examined using an identical analytic procedure to that used in the parametric analysis of cluster mean power. Changes in visual perceptual threshold across Retreat 2 assessments were analyzed using the same approach, but without the effect of participant status.

Associations between Cluster Mean Power and Other Measures

Correlations were computed between the cluster mean power and visual threshold measures obtained for Retreat 2 training participants. We examined associations between these measures at the pre- and postassessments, and for mean changes across the retreat intervention. Changes were quantified as difference scores from the pre-retreat to the post-retreat assessment, where

negative scores indicate a reduction over the course of retreat. All values were checked for outliers (defined according to Tukey's rule as 1.5 times the interquartile range below the first quartile, or above the third quartile), and correlations were computed including and excluding outliers. Significance values were adjusted using the Benjamini-Hochberg (1995) procedure.

We also examined correlations between these measures and meditation practice hours while on retreat, as well as cumulative lifetime meditation hours. While on retreat, participants recorded the amount of time, in minutes, that they had dedicated to meditation practice each day (see Sahdra et al., 2011). For each participant, we averaged these daily estimates across days to compute an index of average daily practice time and correlated this with measures of beta band power and visual threshold. Lifetime hours were calculated based on participant self-reports of meditation practice history collected prior to group assignment.

Results

Retreat 1 Spectral Analysis

We first examined changes in IAF over the course of Retreat 1. Table 2.2 presents mean IAF for Retreat 1 training and control participants at each assessment. We observed a main effect of assessment, F(2, 102) = 10.39, p < .001, but no main effect of status F(1, 51) = 0.10, p = .749, or interaction between assessment and status, F(2, 102) = 1.70, p = .188, indicating that the groups did not significantly differ in their change across time.

However, training-related changes in IAF were previously identified among these participants in a prior analysis (Saggar et al., 2012). Therefore, we chose to further explore changes in IAF over assessments in Retreat 1 as a function of group. A test of simple effects indicated that IAF significantly changed over assessments in training participants, F(2, 102) = 9.86, p < .001, but not in waitlist controls, F(2, 102) = 2.08, p = .130. Follow-up comparisons of

model estimated means indicated that IAF did not significantly differ between training and control participants at the pre-retreat assessment (b = 0.01, SE = 0.13, p = .944, 95% CI [-0.24, 0.26]). Additional comparisons indicated that IAF in training participants decreased significantly from pre- to mid-retreat (b = -0.12, SE = 0.03, p < .001, 95% CI [-0.19, -0.05]), and pre- to post-retreat (b = -0.14, SE = 0.03, p < .001, 95% CI [-0.21, -0.07]), but not from mid- to post-retreat (b = -0.02, SE = 0.03, p = .593, 95% CI [-0.08, 0.05]).

Cluster Identification

The nonparametric permutation analysis for Retreat 1 training participants indicated a significant change in alpha band power, *cluster statistic* = 108.97, p = .009, and beta band power, *cluster statistic* = 166.49, p = .004, across assessments (see Figure 2.1). We followed up on the identified alpha cluster in retreat participants by testing for clusters in alpha sub-bands. This analysis indicated significant band power differences between assessments in the upper alpha range only (i.e., alpha 3; IAF – 1.2 x IAF Hz), *cluster statistic* = 172.09, p = .003. No changes were indicated for the remaining bands in training participants. No clusters were identified in any band in waitlist controls.

Table 2.2 presents descriptive statistics for cluster mean power estimates (derived from identified clusters) for frequency bands demonstrating significant change across assessments. Estimates are given for training participants, in whom the clusters were identified, as well as the corresponding values for these clusters in waitlist controls. The findings of the cluster analysis for bands showing significant change (beta, whole band alpha, and the alpha 3 sub-band) in Retreat 1 training participants are shown in the left side of Figure 2.1, Panel A. The electrodes comprising identified clusters are superimposed as stars on the electrode-wise *F*-values. The

leftmost column of Panel B shows the F-values in the beta band for Retreat 1 controls. As no clusters were identified in this group, no electrodes are marked.

Parametric Tests

We next examined condition differences in mean power for the identified alpha and beta band clusters (Figure 2.2). As no clusters of significant change were identified in waitlist controls, their cluster mean power estimates are based on the clusters identified for Retreat 1 training participants, which were applied to both groups (see Methods).

For the alpha band cluster, Type 3 tests of fixed effects indicated a main effect of assessment, F(2, 102) = 4.98, p = .009, a main effect of participant status F(1, 51) = 10.55, p = .002, and a non-significant interaction between assessment and status, F(2, 102) = 2.78, p = .067. Due to the lack of a significant interaction effect, no follow up tests were conducted. For the upper alpha sub-band (alpha 3), there was a main effect of assessment F(2, 102) = 6.68, p = .002, a main effect of status F(1, 51) = 10.74, p = .002, and, again, a non-significant interaction between assessment and status, F(2, 102) = 6.68, p = .002, a main effect of status F(1, 51) = 10.74, p = .002, and, again, a non-significant interaction between assessment and status, F(2, 102) = 2.90, p = .059.

For the beta band, there were significant main effects of assessment, F(2, 102) = 7.15, p = .001, and status F(1, 51) = 11.76, p = .001, and a significant interaction between assessment and status, F(2, 102) = 7.67, p < .001. Tests of simple effects within each group revealed a significant effect of assessment in training participants, F(2, 102) = 14.54, p < .001, but not in controls, F(2, 102) = 0.00, p = .995. Follow-up comparisons of model estimated means indicated that training and control participants did not significantly differ in cluster mean beta power at the pre-retreat assessment (b = -0.31, *SE* = 0.16, p = .055, 95% CI [-0.62, 0.01]). Additional comparisons indicated that training participants decreased significantly in cluster mean beta band power from pre- to mid-retreat (b = -0.26, *SE* = 0.06, p < .001, 95% CI [-0.39, -0.13]), and pre- to post-retreat

(b = -0.33, SE = 0.06, p < .001, 95% CI [-0.46, -0.20]), but not from mid- to post-retreat (b = -0.08, SE = 0.06, p = .248, 95% CI [-0.20, 0.05]).

Retreat 2 Spectral Analysis

For analyses of Retreat 2 data, we compared active training participants to their own prior status as Retreat 1 waitlist controls.

We first checked for change in IAF across assessments. Mean values for IAF in Retreat 2 participants are presented in Table 2.3. For IAF, there was a significant main effect of assessment, F(2, 124) = 16.56, p < .001, a significant main effect of participant status F(1, 125) = 55.77, p < .001, and a significant interaction between assessment and status, F(2, 124) = 6.81, p = .002. Tests of simple effects further indicated a significant effect of assessment when participants were on retreat F(2, 124) = 21.69, p < .001, but not when they served as waitlist controls F(2, 124) = 1.30, p = .277. Follow-up comparisons revealed no difference in preassessment IAF as a function of participant status (b = -0.08, SE = 0.04, p = .082, 95% CI [-0.17, 0.01]). Moreover, during Retreat 2, participants' IAF significantly decreased from pre- to midassessment (b = -0.21, SE = 0.04, p < .001, 95% CI [-0.29, -0.12]), and from pre- to post-retreat (b = -0.28, SE = 0.04, p < .001, 95% CI [-0.36, -0.19]), but not from mid- to post-retreat (b = -0.07, SE = 0.04, p = .120, 95% CI [-0.15, 0.02]).

Cluster Identification

We next conducted nonparametric cluster analyses of Retreat 2 training participants across their 3 assessments while on retreat. Nonparametric tests indicated a significant difference in beta band power, *cluster statistic* = 121.55, p = .008. No clusters were identified in any other band. The identified cluster can be seen in the left side of Figure 2.1, Panel C, and descriptive statistics for cluster mean power estimates can be found in Table 2.3.

Parametric Tests

No clusters were identified in Retreat 2 training participants when they served as waitlist controls (see Retreat 1 Spectral analyses). Consequently, all Retreat 2 cluster mean power estimates are based on the clusters identified in Retreat 2 training participants, applied to their EEG collected during both retreats. Using these estimates, we tested for differences in cluster mean power in Retreat 2 participants in their status as active retreat participants versus waitlist controls (Figure 2.2). Tests of fixed effects for mean beta power indicated no main effect of assessment, F(2, 124) = 2.50, p = .086, a significant main effect of status F(1, 128) = 7.65, p = 1.086.007, and a significant interaction between assessment and status, F(2, 124) = 4.82, p = .010. Tests of simple effects revealed a significant effect of assessment when Retreat 2 participants were actively on retreat, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, but not when they served as controls, F(2, 124) = 6.99, p = .001, p = .001124) = 0.20, p = .820. Follow-up comparisons further indicated that cluster mean beta band power did not differ at the pre-retreat assessment as a function of participant status (b = 0.07, SE = 0.08, p = .421, 95% CI [-0.10, 0.23]). Moreover, during Retreat 2, participants demonstrated a significant decrease in cluster mean beta band power from pre- to mid-retreat (b = -0.27, SE = 0.08, p = .001, 95% CI [-0.44, -0.11]), and pre- to post-retreat (b = -0.25, SE = 0.08, p = .002, 95% CI [-0.41, -0.09]), but not from mid- to post-retreat (b = 0.02, SE = 0.08, p = .780, 95% CI [-0.14, 0.18]).

Associations between Cluster Mean Power and Other Measures

Correlations between Beta Power and Visual Threshold

We next investigated whether patterns of training-related beta band power at rest were associated with changes in visual processing observed in a separate perceptual task. Table 2.4 presents correlations between measures of mean beta band power and visual threshold (see also Supplementary Information) among Retreat 2 participants. Correlations are presented between levels of each measure at pre and postassessment, as well as for difference scores from the pre-to postassessment.

There were no outliers in cluster mean beta band power at either assessment. There were no outliers in visual threshold at the pre-retreat assessment, and one outlier at the post-retreat assessment. Additionally, there was one outlier in change in cluster mean power from pre- to postassessment, and two outliers in change in visual threshold. In no case did removing outliers change the uncorrected statistical significance of a correlation. Both uncorrected p-values and adjusted p-values following FDR correction are presented below.

There was no significant association between mean beta power and visual threshold at the pre-, r(24) = -.37, p = .064. 95% CI [-.66, .02], $p_{adj} = .121$, or post-retreat assessments, r(24) = .03, p = .881, 95% CI [-.36, .41], $p_{adj} = .881$. Moreover, change in visual threshold was not significantly related to mean beta power at the preassessment, r(24) = .20, p = .330, 95% CI[-.20, .54], $p_{adj} = .424$, or the postassessment, r(24) = -.20, p = .339, 95% CI [-.54, .21], $p_{adj} = .424$. Removing outliers did not alter the significance of any of these correlations, all $ps \ge .231$.

Changes in cluster mean beta band power were, however, positively correlated with preassessment visual threshold, r(24) = .71, p < .001, 95% CI [.45, .86], $p_{adj} < .001$, as well as postassessment visual threshold, r(24) = .52, p = .007, 95% CI [.16, .75], $p_{adj} = .017$, such that participants with lower (better) visual thresholds demonstrated greater reductions in beta power across assessments (Figure 2.3). The correlation between visual threshold at pre-retreat and beta cluster mean power change remained significant when outliers were removed, r(23) = .64, p < .001, 95% CI [.32, .82], $p_{adj} = .003$. The correlation between visual threshold at post-retreat and beta deta cluster mean power change was r(22) = .45, p = .026, 95% CI [.06, .73], when outliers were

removed, though the association fell short of significance following FDR correction, $p_{adj} = .067$. Finally, there was a significant negative correlation between change in beta cluster mean power and change in visual threshold, r(24) = -.52, p = .007, 95% CI [-.75, -.16], $p_{adj} = .017$, such that greater improvements in visual angle threshold were related to smaller reductions in beta power across assessments. This relationship remained significant (uncorrected) when outliers were removed, r(22) = -.41, p = .046, 95% CI [-.69, -.01], but fell short of significance with correction, $p_{adj} = .099$.

Correlations with Meditation Practice Time on Retreat

We further examined the relationship between changes in these measures and meditation practice time while on retreat. There was not a significant relationship between beta power change and practice time: there was a modest but not significant negative correlation when outliers were included, r(24) = -.37, p = .060, 95% CI [-.66, .02], which was attenuated when outliers were removed, r(22) = -.20, p = .340, 95% CI [-.56, .22]. Changes in visual threshold showed a positive correlation with meditation time, such that those who meditated the most demonstrated the least improvement in visual threshold. However though this relationship was significant when including all participants, r(24) = .41, p = .037, 95% CI [.03, .69], it was not significant when outliers were removed, r(21) = .27, p = .206, 95% CI [-.16, .62]. Importantly, the partial correlations between beta power change and pre-retreat visual threshold, r(23) = .67, p <.001, post-retreat visual threshold, r(23) = .55, p = .004, and change in visual threshold, r(23)= -.43, p = .031, all remained significant when controlling for practice time. There were no significant correlations between self-reported lifetime meditation hours and beta power or visual threshold at pre- or postassessment, or with change in either measure, all $ps \ge .238$. The same was true for participant age, all $ps \ge .056$.

Associations between Beta Band Reductions at Rest and during Mindfulness of Breathing

Pearson correlations were calculated between significant beta band clusters identified during eyes closed rest and mindfulness of breathing from each of their respective data sets (see Saggar et al., 2012, for a full description of the clusters identified in that analysis). Cluster means from Saggar et al. (2012) were thus based on a different subset of participants and identified electrode clusters than in the present study. For these correlations, we pooled retreat training participants from both retreats to maximize statistical power. Beta band cluster mean power was strongly correlated between rest and mindfulness of breathing in retreat participants at the pre-, r(37) = .65, p < .001, 95% CI [.42, .80], mid-, r(37) = .65, p < .001, 95% CI [.42, .80], and postretreat, r(37) = .65, p < .001, 95% CI [.42, .80], assessments. Pre- to post-retreat change in rest and mindfulness of breathing cluster means were also moderately correlated, r(37) = .44, p =.006, 95% CI [.14, .66]. This association is shown in Figure 2.4.

Intraclass Correlation Coefficients

We also examined the intraclass correlation coefficients (ICCs) for eyes closed rest and mindfulness of breathing across retreat assessments. The ICCs were calculated from null (i.e., unconditional means) models of beta band cluster mean power in retreat participants with complete data for both conditions. The ICC describes the proportion of variance in repeated measures data that is attributable to between- versus within-person differences (Hoffman, 2015), with a larger ICC indicating less variability between assessment points within an individual. This provides an estimate of the overall consistency of individuals' cluster mean power across assessments in each condition.

The ICC for eyes closed rest was 0.813 in Retreat 1, suggesting that 81.3% of the variance in beta band power was attributable to differences between individuals, and 18.7% was

attributable to within-person variation across assessments (including measurement error). The ICC for mindfulness of breathing in Retreat 1 was .920, suggesting that 92% of the variance was attributable to differences between individuals, and only 8% of the variance was attributable to within-person variation across assessments, suggesting high levels of stability between assessments. This pattern of higher ICC during mindfulness of breathing was similar for Retreat 2 active participants, where the ICCs for eyes closed rest and mindfulness of breathing were .691 and .847, respectively.

Discussion

This study was motivated by a central question in contemplative research: can engaging in dedicated periods of meditation practice lead to generalized changes outside of formal practice? To this end, we examined changes in the spontaneous activity of the brain over the course of intensive meditation training. We had participants engage in focused attention (*shamatha*) meditation practice for 6 to 8 hours a day and measured their brain oscillatory activity during a period of uninstructed rest. We found power reductions in the alpha and beta bands during eyes closed rest over the course two 3-month-long retreat interventions. Reductions in beta band activity were replicated across the two independent training periods, mirroring changes we previously observed during active practice of mindfulness of breathing meditation in these same participants (Saggar et al., 2012). Moreover, we found that training-related decreases in resting beta power were related to better baseline visual discrimination in a perceptual task. Our findings demonstrate that intensive meditation training can result in neurophysiological changes that cross cognitive domains and extend beyond the bounds of formal practice.

Our findings, as well those of Saggar et al. (2012), were largely restricted to longitudinal changes in the beta band. The consistency of these effects across meditation and rest points to

beta band activity as a potential indicator of domain-general change in neural processes resulting from meditation training. Beta band activity is broadly implicated in a range of neurocognitive functions and network dynamics, including sensorimotor processing (e.g., van Ede et al., 2011; Pfurtschcheller & Lopes da Silva, 2009), cognitive effort (Kopell et al., 2010), attentional orienting across domains (van Ede et al., 2011), top-down control of visual attention (Bastos et al., 2015; Buschman & Miller, 2007), predictive coding of the sensory environment (e.g, Arnal & Giraud, 2012), and working memory (Axmacher et al., 2008; Miller et al., 2018). Recent work also demonstrates the relevance of beta to cross-domain inhibitory control (e.g., Castiglione et al., 2019, who demonstrated that preventing a thought from coming to mind elicited increases in beta power similar to those elicited when stopping a physical action), offering support for the idea that beta power may reflect the activity of neurocognitive networks that exert effects across domains.

Power in the beta band is inversely related to cortical excitability (Ploner et al., 2006; Tamura et al., 2005), such that lower power is taken to reflect greater activation of local cortical networks. This inverse relationship between power and excitability also appears to be true of the high alpha band (Klimesch, 1999; Samaha, et al., 2017). Although we initially predicted oscillatory changes specific to the beta band only (in line with Saggar et al., 2012), we observed power changes in the high alpha range as well. Suppression in these frequencies may reflect disinhibition of underlying neural assemblies, allowing for greater cortical excitability and thus enhanced stimulus processing. This is consistent with reports of reduced acoustic startle habituation among experienced practitioners of Tibetan nondual traditions (i.e., Dzogchen or Mahamudra; Antonova et al., 2015). This work suggests that the sensory systems of experienced

meditators may maintain their responsiveness in situations that would typically induce habituation.

Alternatively, it is possible that the beta reductions observed in the current study represent alterations in the structure, efficiency, or dynamics of the default mode or other largescale brain networks (e.g., de Pasquale et al, 2012; Wens et al., 2019). Power in the beta range during rest appears to fluctuate with BOLD activity in several canonical resting state networks, notably showing a positive correlation with activity in regions of the default mode network, and a negative correlation with those of the dorsal attention network (Mantini et al., 2007). Beta band activity is also associated with functional connectivity between and within resting state networks (de Pasquale et al., 2012; de Pasquale et al., 2018; Wens et al., 2019), and with band-limited power in the beta frequency corresponding to moments of high network efficiency (Betti et al., 2020). Thus, it appears that beta activity may relate to efficiency of communication between the brain's core networks (Betti et al., 2020).

Other research indicates that long-term meditation training may lead to altered resting functional connectivity and reduced activity within the default mode network (Berkovich-Ohana et al., 2014; Brewer, Worhunsky et al., 2011; Garrison et al., 2015). Moreover, in our own work with these same participants, we found retreat-related changes in dynamic patterns of resting EEG microstates (Zanesco et al., 2021). These lines of research suggest that the observed reductions in beta over retreat could be reflective of altered patterns of functional connectivity, and possibly changes in the predominance of default mode activity during uninstructed rest (e.g., Bauer et al., 2019). This implies that—rather than being specific to meditation states—the observed retreat-related changes in beta band activity could indicate broad shifts in baseline patterns of brain activity and its underlying functional architecture.

Other studies have characterized meditation-related reductions in the beta frequency range *during* meditation practice compared to rest (during shamatha practice: Saggar et al., 2012; during Zen practice: Faber et al., 2015, Hauswald et al., 2015, see also Cahn & Polich, 2006 and Lomas et al., 2015 for reviews). However, to our knowledge the only other study to identify changes in the beta frequency range in the resting brains of experienced meditators found *increases* in power following a day of vipassana or metta practice (Dentico et al., 2018). The inconsistency of these results is indicative of the heterogeneous research findings reported in the meditation literature at large. For example, a study by DeLosAngeles et al. (2016) found that increased alpha band power characterized focused attention meditation when compared to rest, but that decreasing beta band power was associated with self-reported depth of meditation during practice. Similarly, Bauer and colleagues (2019) found a reduction in activity and functional connectivity in the default mode network of experienced meditators at rest compared to novices, but comparative increases in these same metrics during focused attention meditation.

Discrepancies between findings could result from various methodological sources, including 1) differing cognitive-affective processes engaged across distinct styles of practice (e.g., Dahl et al., 2015; Lutz et al., 2015), 2) design and analytic approaches—including the choice of comparison groups (e.g., novice or experienced meditators) and baseline conditions (e.g., instructed mind-wandering, uninstructed rest; see Cahn and Polich, 2006; Kazniak, 2015; Van Dam et al., 2018), and 3) the experience levels of practitioner groups, who may display unique trajectories of training-related change (e.g., King et al., 2018; Skwara et al., 2017). Indeed, the effects of meditation practice and training may manifest differently as a function of these design decisions, pointing to the important, perhaps even deterministic, role that the choice of comparison condition plays in outcomes of meditation studies (cf. Van Dam et al., 2018).

Relating EEG Power and Perceptual Sensitivity

We previously reported improvements in behavioral outcomes of sustained attention and perceptual discrimination in this same cohort of participants (MacLean et al., 2010). Accordingly, we predicted that greater retreat-related reductions in beta power should be associated with improvements in visual threshold. We instead observed that greater reductions in beta power were associated with less improvement in visual threshold across retreat. Moreover, the strongest correlation between visual threshold and beta power was between threshold at the pre-retreat assessment and change in beta power from the pre- to postassessment. Thus, those participants who demonstrated the lowest visual threshold (best acuity) at the beginning of training showed the greatest subsequent reduction in beta power over the course of retreat. It is possible that visual threshold at the onset of training served as a proxy for practitioners' trait-like capacity or motivation to engage with meditation practice over time. This might explain why initial behavioral performance predicted greater meditation-related neurophysiological change (see also the Supplementary Information for an analysis of beta change in a subset of high behavioral performers). Though the relationship did not follow the direction we predicted, the correlation between training-related changes in eyes closed beta band power with performance on a separate visual task demonstrates the functional relevance of the observed changes in resting brain activity across behavioral and sensory domains.

Similarities between Rest and Mindfulness of Breathing

The retreat-related changes in brain activity observed in the current study mirror those previously identified in these same participants during active practice of mindfulness of breathing (Saggar et al., 2012). Both analyses found reductions in frontoparietal EEG power specific to the beta band, as well as IAF slowing. The similarity of these findings raises questions

regarding the meaning of ostensible state versus trait measures in the context of intensive meditation training.

First, might our participants have been meditating when asked to rest quietly? While our instructions discouraged participants from engaging in active, formal meditation practice during the resting period, we were intentionally non-directive as to what mind-state participants *should* maintain. In contrast to more explicit resting instructions given in other studies (e.g., instructed mind wandering; see Braboszcz et al., 2017; Cahn et al., 2010), our instructions allowed us to observe more naturalistic changes in the resting brain, albeit while sacrificing a degree of methodological control and certainty. To address whether participants were engaged in active meditation practice during eyes closed rest, we examined associations between EEG power at rest and during mindfulness of breathing. We found that reductions in beta power during mindfulness of breathing were strongly correlated with reductions in beta during rest at each assessment, while retreat-related changes in the two measures were moderately correlated. This lends support to the idea that a proportion of the observed reductions in beta power reflect patterns of change common to quiet rest and formal practice. However, beta power within an individual was more consistent across assessments during mindfulness of breathing than during rest. This suggests that rest was a more variable brain state from one assessment to another. While inconsistencies between the two datasets could originate from a variety of sources-most notably data length and EEG preprocessing differences-overall these patterns suggest that EEG recorded during rest and mindfulness of breathing is indexing related, but not identical, underlying brain states.

The second question pertains to the fluidity of meditative versus non-meditative states for experienced practitioners, and what it means to "rest" in the context of retreat. While formal

meditation practice is undertaken within relatively circumscribed bounds, the effects of training may be more far-reaching, leading to pervasive shifts in perception, emotion, and cognition that have long been reported in traditional practitioner accounts (e.g., Dalai Lama & Cutler, 2009; Wallace 2006). From this perspective, meditation is not discontinuous with other domains of experience. This may especially be true in the context of a meditation retreat, where participants are encouraged to imbue their daily activities with contemplative awareness. Thus, one's baseline quality of awareness may, over time, come to more closely resemble those states cultivated during sessions of formal meditation. This points to the complexity of separating state and trait effects.

Strengths and Limitations

Our study is limited by having a waitlist, rather than active, control group. Additionally, all of our participants were experienced meditators. As such, our findings speak to patterns that occur during an intensive period of retreat training in already-experienced practitioners. Though participants dedicated many of their waking hours to formal meditation practice during retreat, our findings might also reflect the complex and non-specific influences of retreat experience—including diet, distance from the stressors and commitments of daily life, social and spiritual support, and the idyllic natural setting of the retreat center—rather than the effects of a specific meditative practice in isolation (King et al, 2019).

Our design also conveys several strengths. By studying experienced meditators over a dedicated period of practice, we were able to examine longitudinal changes in similarly-matched participants over time, thus avoiding confounds introduced by comparing across participant groups of differing experience levels. Additionally, our waitlist design included a formal replication with the second retreat that allowed us to conduct between groups comparisons in

Retreat 1 and replicate these effects within individuals in Retreat 2. This allows us to draw conclusions with greater confidence for effects that are consistent across retreats. Taken in the broader context of other findings from this project (e.g., Rosenberg et al., 2012; Sahdra et al., 2011; Shields et al., 2020, Zanesco et al., 2013, 2018), this work speaks to the wide range of domains that were affected by the same retreat experience.

Conclusion

Our results suggest that patterns of neural activity observed during intensive meditation practice translate to eyes closed rest, and that baseline changes in oscillatory activity relate to measures of fine-grained visual discrimination obtained in a separate perceptual task. These findings provide empirical support for the idea that meditation training can exert effects that extend beyond the limits of formal practice to other cognitive and sensory domains. They also clearly demonstrate that rest is not an invariant baseline. Instead, it is influenced in meaningful and behaviorally relevant ways by the effects of meditation training.

Finally, our findings lend support to dimensional, process-oriented models of meditationrelated change (e.g., Dahl et al., 2016; Lutz et al., 2015). The strongest effects of meditation might instantiate in situations where there is active or purposeful engagement of the capacities being trained (such as the volitional focus on the breath during mindfulness of breathing), whereas more subtle effects might manifest in situations where the engagement of these capacities is less central or volitional (such as the processing of ongoing sensory stimuli at rest). Such conceptualizations might allow for greater flexibility in how we investigate and interpret the process and outcomes of contemplative practice, helping to foster a view of the continuity between formal meditation practice and other domains of life.

References

- Antonova, E., Chadwick, P., & Kumari, V. (2015). More meditation, less habituation? The effect of mindfulness practice on the acoustic startle reflex. *PLoS One*, *10*(5), e0123512. https://doi.org/10.1371/journal.pone.0123512
- Arnal, L. H., & Giraud, A. L. (2012). Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences*, 16(7), 390-398. <u>https://doi.org/10.1016/j.tics.2012.05.003</u>
- Ashar, Y. K., Andrews-Hanna, J. R., Yarkoni, T., Sills, J., Halifax, J., Dimidjian, S., & Wager, T. D. (2016). Effects of compassion meditation on a psychological model of charitable donation. *Emotion*, 16(5), 691. <u>https://doi.org/10.1037/emo0000119</u>
- Axmacher, N., Schmitz, D. P., Wagner, T., Elger, C. E., & Fell, J. (2008). Interactions between medial temporal lobe, prefrontal cortex, and inferior temporal regions during visual working memory: a combined intracranial EEG and functional magnetic resonance imaging study. *Journal of Neuroscience*, 28(29), 7304-7312. https://doi.org/10.1523/JNEUROSCI.1778-08.2008
- Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J. M., Oostenveld, R., Dowdall, J. R., De Weerd, P., Kennedy, H., & Fries, P. (2015). Visual areas exert feedforward and feedback influences through distinct frequency channels. *Neuron*, 85(2), 390-401. <u>https://doi.org/10.1016/j.neuron.2014.12.018</u>
- Bauer, C. C. C., Whitfield-Gabrieli, S., Díaz, J. L., Pasaye, E. H., & Barrios, F. A. (2019). From state-to-trait meditation: Reconfiguration of central executive and default mode networks. *eNeuro*, 6(6). https://doi.org/10.1523/ENEURO.0335-19.2019
- Belouchrani, A., Abed-Meraim, K., Cardoso, J. F., & Moulines, E. (1997). A blind source separation technique using second-order statistics. *IEEE Transactions on Signal Processing*, 45(2), 434-444. <u>https://doi.org/10.1109/78.554307</u>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57(1), 289-300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x
- Berkovich-Ohana, A., Glicksohn, J., & Goldstein, A. (2014). Studying the default mode and its mindfulness-induced changes using EEG functional connectivity. *Social Cognitive and Affective Neuroscience*, 9(10), 1616-1624. <u>https://doi.org/10.1093/scan/nst153</u>
- Betti, V., Della Penna, S., de Pasquale, F., & Corbetta, M. (2020). Spontaneous beta band rhythms in the predictive coding of natural stimuli. *The Neuroscientist*. <u>https://doi.org/10.1177/1073858420928988</u>

- Braboszcz, C., Cahn, B. R., Levy, J., Fernandez, M., & Delorme, A. (2017). Increased gamma brainwave amplitude compared to control in three different meditation traditions. *PLoS One*, *12*(1): e0170647. <u>https://doi.org/10.13711/journal.pone.0170647</u>
- Brewer, J. A., Worhunsky, P. D., Gray, J. R., Tang, Y. Y., Weber, J., & Kober, H. (2011). Meditation experience is associated with differences in default mode network activity and connectivity. *Proceedings of the National Academy of Sciences*, 108(50), 20254-20259. https://doi.org/10.1073/pnas.1112029108
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, *315*(5820), 1860-1862. <u>https://doi.org/10.1126/science.1138071</u>
- Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents—EEG, ECoG, LFP and spikes. *Nature Reviews Neuroscience*, 13(6), 407-420. https://doi.org/10.1038/nrn3241
- Cahn, B. R., Delorme, A., & Polich, J. (2010). Occipital gamma activation during Vipassana meditation. *Cognitive Processing*, *11*(1), 39-56. https://doi.org/10.1007/sl0339-009-0352-1
- Cahn, B. R., & Polich, J. (2006). Meditation states and traits: EEG, ERP, and neuroimaging studies. *Psychological Bulletin*, *132*(2), 180-211. https://doi.org/10.1037/00332909.132.2.180
- Castiglione, A., Wagner, J., Anderson, M., & Aron, A. R. (2019). Preventing a thought from coming to mind elicits increased right frontal beta just as stopping action does. *Cerebral Cortex*, 29(5), 2160-2172. <u>https://doi.org/10.1093/cercor/bhz017</u>
- Cohen, M. X. (2014). Analyzing neural time series data: Theory and practice. MIT Press.
- Condon, P., Desbordes, G., Miller, W. B., & DeSteno, D. (2013). Meditation increases compassionate responses to suffering. *Psychological Science*, *24*(10), 2125-2127. https://doi.org/10.1177/0956797613485603
- Creswell, J. D., & Lindsay, E. K. (2014). How does mindfulness training affect health? A mindfulness stress buffering account. *Current Directions in Psychological Science*, 23(6), 401-407. <u>https://doi.org/10.1177/0963721414547415</u>
- Dahl, C. J., Lutz, A., & Davidson, R. J. (2015). Reconstructing and deconstructing the self: cognitive mechanisms in meditation practice. *Trends in Cognitive Sciences*, 19(9), 515-523. <u>https://doi.org/10.1016/j.tics.2015.07.001</u>

Dalai Lama & Cutler, H.C. (2009). The art of happiness: A handbook for living. Penguin Group.

- Davidson, R. J., & Kaszniak, A. W. (2015). Conceptual and methodological issues in research on mindfulness and meditation. *American Psychologist*, 70(7), 581-592. <u>https://doi.org/10.1037/a0039512</u>
- Davidson, R. J., & Lutz, A. (2008). Buddha's brain: Neuroplasticity and meditation [in the spotlight]. *IEEE Signal Processing Magazine*, 25(1), 176-174. https://doi.org/10.1109/MSP.2008.4431873
- DeLosAngeles, D., Williams, G., Burston, J., Fitzgibbon, S. P., Lewis, T. W., Grummett, T. S., Clark, C. R., Pope, K. J., & Willoughby, J. O. (2016). Electroencephalographic correlates of states of concentrative meditation. *International Journal of Psychophysiology*, 110, 27-39. <u>https://doi.org/10.1016/j.ijpsycho.2016.09.020</u>
- de Pasquale, F., Della Penna, S., Snyder, A. Z., Marzetti, L., Pizzella, V., Romani, G. L., & Corbetta, M. (2012). A cortical core for dynamic integration of functional networks in the resting human brain. *Neuron*, 74(4), 753-764. <u>https://doi.org/10.1016/j.neuron.2012.03.031</u>
- de Pasquale, F., Corbetta, M., Betti, V., & Della Penna, S. (2018). Cortical cores in network dynamics. *Neuroimage*, *180*, 370-382. <u>https://doi.org/10.1016/j.neuroimage.2017.09.063</u>
- Dentico, D., Bachhuber, D., Riedner, B. A., Ferrarelli, F., Tononi, G., Davidson, R. J., & Lutz, A. (2018). Acute effects of meditation training on the waking and sleeping brain: Is it all about homeostasis?. *European Journal of Neuroscience*, 48(6), 2310-2321. <u>https://doi.org/10.1111/ejn.14131</u>
- Desbordes, G., Negi, L. T., Pace, T. W., Wallace, B. A., Raison, C. L., & Schwartz, E. L. (2012). Effects of mindful-attention and compassion meditation training on amygdala response to emotional stimuli in an ordinary, non-meditative state. *Frontiers in Human Neuroscience*, 6, 292. <u>https://doi.org/10.3389/fnhum.2012.00292</u>
- Donald, J. N., Sahdra, B. K., Van Zanden, B., Duineveld, J. J., Atkins, P. W., Marshall, S. L., & Ciarrochi, J. (2019). Does your mindfulness benefit others? A systematic review and meta-analysis of the link between mindfulness and prosocial behaviour. *British Journal* of Psychology, 110(1), 101-125. <u>https://doi.org/10.111/bjop.12338</u>
- Faber, P. L., Lehmann, D., Gianotti, L. R., Milz, P., Pascual-Marqui, R. D., Held, M., & Kochi, K. (2015). Zazen meditation and no-task resting EEG compared with LORETA intracortical source localization. *Cognitive Processing*, 16(1), 87-96. <u>https://doi.org/10.1007/s10339-014-0637-x</u>
- Fox, K. C., Nijeboer, S., Dixon, M. L., Floman, J. L., Ellamil, M., Rumak, S. P., Sedlmeier, P., & Christoff, K. (2014). Is meditation associated with altered brain structure? A systematic review and meta-analysis of morphometric neuroimaging in meditation practitioners. *Neuroscience & Biobehavioral Reviews*, 43, 48-73. <u>https://doi.org/10.1016/j.neubiorev.2014.03.016</u>

- Fucci, E., Abdoun, O., Caclin, A., Francis, A., Dunne, J. D., Ricard, M., Davidson, R. J., & Lutz, A. (2018). Differential effects of non-dual and focused attention meditations on the formation of automatic perceptual habits in expert practitioners. *Neuropsychologia*, 119, 92-100. <u>https://doi.org/10.1016/j.neuropsychologia.2018.07.025</u>
- Garrison, K. A., Zeffiro, T. A., Scheinost, D., Constable, R. T., and Brewer, J. A. (2015). Meditation leads to reduced default mode network activity beyond an active task. *Cognitive, Affective, & Behavioral Neuroscience, 15*(3), 712-720. <u>https://doi.org/10.3758/s13415-015-0358-3</u>
- Gunaratana, H. (2002). *Mindfulness in plain English (revised and expanded ed)*. Wisdom Publications.
- Hasenkamp, W., and Barsalou, L. W. (2012). Effects of meditation experience on functional connectivity of distributed brain networks. *Frontiers in Human Neuroscience*, *6*, 38. <u>https://doi.org/10.3389/fnhum.2012.0038</u>
- Hauswald, A., Übelacker, T., Leske, S., & Weisz, N. (2015). What it means to be Zen: Marked modulations of local and interareal synchronization during open monitoring meditation. *NeuroImage*, 108, 265-273. <u>https://doi.org/10.1016/j.neuroimage.2014.12.065</u>
- Hedden, T., & Gabrieli, J. D. (2004). Insights into the ageing mind: A view from cognitive neuroscience. *Nature Reviews Neuroscience*, 5(2), 87-96. <u>https://doi.org/10.1038/nrn1323</u>
- Kabat-Zinn, J. (2013). Full catastrophe living, revised edition: How to cope with stress, pain and illness using mindfulness meditation. Hachette UK.
- Kayser, J., & Tenke, C. E. (2006). Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: I. Evaluation with auditory oddball tasks. *Clinical Neurophysiology*, 117(2), 348-368. <u>https://doi.org/10.1016/j.clinph.2005.08.034</u>
- Kayser, J., & Tenke, C. E. (2012). Generator localization by current source density. *Clinical Neurophysiology*, 123(12), 2328-2345. <u>https://doi.org/10.1016/j.clinph.2012.06.005</u>
- Kayser, J., & Tenke, C. E. (2015). Issues and considerations for using the scalp surface Laplacian in EEG/ERP research: A tutorial review. *International Journal of Psychophysiology*, 97(3), 189-209. <u>https://doi.org/10.1016/j.ijpsycho.2015.04.012</u>
- King, B. G., Conklin, Q. A., Zanesco, A. P., & Saron, C. D. (2019). Residential meditation retreats: Their role in contemplative practice and significance for psychological research. *Current Opinion in Psychology*, 28, 238-244. <u>https://doi.org/10.1016/j.copsyc.2018.12.021</u>

- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, 29(2-3), 169-195. https://doi.org/10.1016/S0165-0173(98)00056-3
- Kopell, N., Kramer, M. A., Malerba, P., & Whittington, M. A. (2010). Are different rhythms good for different functions?. *Frontiers in Human Neuroscience*, 4, 187. https://doi.org/10.3389/fnhum.2010.00187
- Lee, D. J., Kulubya, E., Goldin, P., Goodarzi, A., & Girgis, F. (2018). Review of the neural oscillations underlying meditation. *Frontiers in Neuroscience*, 12, 178. <u>https://doi.org/10.3389/fnins.2018.00178</u>
- Lomas, T., Ivtzan, I., & Fu, C. H. (2015). A systematic review of the neurophysiology of mindfulness on EEG oscillations. *Neuroscience & Biobehavioral Reviews*, 57, 401-410. <u>https://doi.org/10.1016/j.neubiorev.2015.09.018</u>
- Lopes da Silva, F. (2013). EEG and MEG: Relevance to neuroscience. *Neuron*, 80(5), 1112-1128. https://doi.org/10.1016/j.neuron.2013.10.017
- Lumma, A. L., Valk, S. L., Böckler, A., Vrtička, P., & Singer, T. (2018). Change in emotional self-concept following socio-cognitive training relates to structural plasticity of the prefrontal cortex. *Brain and Behavior*, 8(4): e00940. <u>https://doi.org/10.1002/brb3.940</u>
- Lutz, A., Brefczynski-Lewis, J. A., Johnstone, T., & Davidson, R. J. (2008). Regulation of the neural circuitry of emotion by compassion meditation: Effects of meditative expertise. *PloS one*, 3(3). <u>https://doi.org/10.1371/journal.pone.0001897</u>
- Lutz, A., Jha, A. P., Dunne, J. D., & Saron, C. D. (2015). Investigating the phenomenological matrix of mindfulness-related practices from a neurocognitive perspective. *American Psychologist*, 70(7), 632-658. <u>https://doi.org/10.1037/a0039585</u>
- Lutz, A., Slagter, H. A., Rawlings, N. B., Francis, A. D., Greischar, L. L., & Davidson, R. J. (2009). Mental training enhances attentional stability: neural and behavioral evidence. *Journal of Neuroscience*, 29(42), 13418-13427. <u>https://doi.org/10.1523/JNEUROSCI</u>
- MacLean, K. A., Ferrer, E., Aichele, S. R., Bridwell, D. A., Zanesco, A. P., Jacobs, T. L., King, B. G., Rosenberg, E. L., Sahdra, B. K., Shaver, P. R., Wallace, B. A., Mangun, G. R., & Saron, C. D. (2010). Intensive meditation training improves perceptual discrimination and sustained attention. *Psychological Science*, 21(6), 829-839. <u>https://doi.org/10.1177/0956797610371339</u>
- Mantini, D., Perrucci, M. G., Del Gratta, C., Romani, G. L., & Corbetta, M. (2007). Electrophysiological signatures of resting state networks in the human brain. *Proceedings* of the National Academy of Sciences, 104(32), 13170-13175. <u>https://doi.org/10.1073/pnas.0700668104</u>

- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEGdata. *Journal of Neuroscience Methods*, *164*(1), 177-190. <u>https://doi.org/10.1016/j.jneumeth.2007.03.024</u>
- Miller, E. K., Lundqvist, M., & Bastos, A. M. (2018). Working Memory 2.0. *Neuron*, 100(2), 463-475. <u>https://doi.org/10.1016/j.neuron.2018.09.023</u>
- Mitra, P. P., & Pesaran, B. (1999). Analysis of dynamic brain imaging data. *Biophysical Journal*, *76*(2), 691-708. <u>https://doi.org/10.1016/S0006-3495(99)77236-X</u>
- Newbold, D. J., Laumann, T. O., Hoyt, C. R., Hampton, J. M., Montez, D. F., Raut, R. V., Ortega, M., Mitra, A., Nielsen, A. N., Miller, D. B., Adeyemo, B., Nguyen, A. L., Scheidter, K. M., Tanenbaum, A. B., Van, A. N., Marek, S., Schlaggar, B. L., Carter, A. R., Greene, D. J.,... Dosenbach, N. U. F. (2020). Plasticity and spontaneous activity pulses in disused human brain circuits. *Neuron*, *107*(3), 580-589. <u>https://doi.org/10.1016/j.neuron.2020.05.007</u>
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011; 2011:156869. <u>https://doi.org/10.1155/2011/156869</u>
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, 72(2), 184-187. <u>https://doi.org/10.1016/0013-4694(89)90180-6</u>
- Pfurtscheller, G., & Lopes da Silva, F. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*(11), 1842-1857. https://doi.org/10.1016/S1388-2457(99)00141-8
- Ploner, M., Gross, J., Timmermann, L., Pollok, B., & Schnitzler, A. (2006). Oscillatory activity reflects the excitability of the human somatosensory system. *Neuroimage*, 32(3), 1231-1236. <u>https://doi.org/10.1016/j.neuroimage.2006.06.004</u>
- Rosenberg, E. L., Zanesco, A. P., King, B. G., Aichele, S. R., Jacobs, T. L., Bridwell, D. A., MacLean, K. A., Shaver, P. R., Ferrer, E., Sahdra, B. K., Lavy, S., Wallace, B. A., & Saron, C. D. (2015). Intensive meditation training influences emotional responses to suffering. *Emotion*, 15(6), 775. <u>https://doi.org/10.1037/emo0000080</u>
- Saggar, M., King, B. G., Zanesco, A. P., MacLean, K. A., Aichele, S. R., Jacobs, T. L., Bridwell, D. A., Shaver, P. R., Rosenberg, E. L., Sahdra, B. J., Ferrer, E., Tang, A. C., Mangun, G. R., Wallace, B. A., Miikkulainen, R., & Saron, C. D. (2012). Intensive training induces longitudinal changes in meditation state-related EEG oscillatory activity. *Frontiers in Human Neuroscience*, *6*, 256. <u>https://doi.org/10.3389/fnhum.2012.00256</u>

- Sahdra, B. K., MacLean, K. A., Ferrer, E., Shaver, P. R., Rosenberg, E. L., Jacobs, T. L.,
 Zanesco, A. P., King, B. G., Aichele, S. R., Bridwell, D. A., Mangun, G. R., Lavy, S.,
 Wallace, B. A., & Saron, C. D. (2011). Enhanced response inhibition during intensive
 meditation training predicts improvements in self-reported adaptive socioemotional
 functioning. *Emotion*, 11(2), 299-312. <u>https://doi.org/10.1037/a0022764</u>
- Samaha, J., Gosseries, O., & Postle, B. R. (2017). Distinct oscillatory frequencies underlie excitability of human occipital and parietal cortex. *Journal of Neuroscience*, 37(11), 2824-2833. <u>https://doi.org/10.1523/JNEUROSCI.3413-16.2017</u>
- Sassenhagen, J., & Draschkow, D. (2019). Cluster-based permutation tests of MEG/EEG data do not establish significance of effect latency or location. *Psychophysiology*, *56*(6), e13335. <u>https://doi.org/10.1111/psyp.13335</u>
- Schubert, R., Haufe, S., Blankenburg, F., Villringer, A., & Curio, G. (2009). Now you'll feel it, now you won't: EEG rhythms predict the effectiveness of perceptual masking. *Journal of Cognitive Neuroscience*, 21(12), 2407-2419. <u>https://doi.org/10.1162/jocn.2008.21174</u>
- Sheehan, D. V., Lecrubier, Y., Sheehan, K. H., Amorim, P., Janavs, J., Weiller, E., Hergueta, T., Baker, R., & Dunbar, G. C. (1998). The Mini-International Neuropsychiatric Interview (M.I.N.I): The development and validation of a structured diagnostic psychiatric interview for DSM-IV and ICD-10. *The Journal of Clinical Psychiatry*, 59(Suppl 20), 22–33.
- Shields, G. S., Skwara, A. C., King, B. G., Zanesco, A. P., Dhabhar, F. S., & Saron, C. D. (2020). Deconstructing the effects of concentration meditation practice on interference control: The roles of controlled attention and inflammatory activity. *Brain, Behavior, and Immunity*. <u>https://doi.org/10.1016/j.bbi.2020.06.034</u>
- Skwara, A. C., King, B. G., & Saron, C. D. (2017). Studies of training compassion: What have we learned; what remains unknown. In E. M. Seppälä, E. Simon-Thomas, S. L. Brown, M. C. Worline, C. D. Cameron, & J. R. Doty (Eds.), *The Oxford Handbook of Compassion Science* (pp. 219-236). Oxford University Press.
- Tamura, Y., Hoshiyama, M., Nakata, H., Hiroe, N., Inui, K., Kaneoke, Y., Inoue, K., & Kakigi, R. (2005). Functional relationship between human rolandic oscillations and motor cortical excitability: an MEG study. *European Journal of Neuroscience*, 21(9), 2555-2562. <u>https://doi.org/10.1111/j.1460-9568.2005.04096.x</u>
- Tang, A. C., Sutherland, M. T., & McKinney, C. J. (2005). Validation of SOBI components from high-density EEG. *NeuroImage*, 25(2), 539-553. <u>https://doi.org/10.1016/j.neuroimage.2004.11.027</u>
- Taylor, M., & Creelman, C. D. (1967). PEST: Efficient estimates on probability functions. *The Journal of the Acoustical Society of America*, 41(4A), 782-787. <u>https://doi.org/10.1121/1.1910407</u>

- Van Dam, N. T., van Vugt, M. K., Vago, D. R., Schmalzl, L., Saron, C. D., Olendzki, A., Meissner, T., Lazar, S. W., Kerr, C. E., Gorchov, J., Fox, K. C. R., Field, B. A., Britton, W. B., Brefczynski-Lewis, J. A., & Meyer, D. E. (2018). Mind the hype: A critical evaluation and prescriptive agenda for research on mindfulness and meditation. *Perspectives on Psychological Science*, *13*(1), 36-61. https://doi.org/10.1177/1745691617709589
- van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha-and beta-band oscillations. *Journal of Neuroscience*, 31(6), 2016-2024. <u>https://doi.org/10.1523/JNEUROSCI.5630-10.2011</u>
- van Leeuwen, S., Singer, W., & Melloni, L. (2012). Meditation increases the depth of information processing and improves the allocation of attention in space. *Frontiers in Human Neuroscience*, 6, 133. <u>https://doi.org/10.3389/fnhum.2012.00133</u>
- Wallace, B. A. (2006). *The attention revolution: Unlocking the power of the focused mind*. Simon and Schuster.
- Wallace, B. A. (1999). *The four immeasurables: Practices to open the heart*. Snow Lion Publications.
- Weng, H. Y., Schuyler, B., & Davidson, R. J. (2017). The impact of compassion meditation training on the brain and prosocial behavior. In E. M. Seppälä, E. Simon-Thomas, S. L. Brown, M. C. Worline, C. D. Cameron, & J. R. Doty (Eds.), *The Oxford Handbook of Compassion Science* (pp. 133-146). Oxford University Press.
- Welch, P. (1967). The use of fast Fourier transform for the estimation of power spectra: A method based on time averaging over short, modified periodograms. *IEEE Transactions* on Audio and Electroacoustics, 15(2), 70-73. <u>https://doi.org/10.1109/TAU.1967.1161901</u>
- Wens, V., Bourguignon, M., Vander Ghinst, M., Mary, A., Marty, B., Coquelet, N., Naeije, G., Peigneux, P., Goldman, S., & De Tiège, X. (2019). Synchrony, metastability, dynamic integration, and competition in the spontaneous functional connectivity of the human brain. *NeuroImage*, 199, 313-324. <u>https://doi.org/10.1016/j.neuroimage.2019.05.081</u>
- Zanesco, A. P., King, B. G., MacLean, K. A., Jacobs, T. L., Aichele, S. R., Wallace, B. A., Smallwood, J., Schooler, J. W., & Saron, C. D. (2016). Meditation training influences mind wandering and mindless reading. *Psychology of Consciousness: Theory, Research, and Practice*, 3(1), 12-33. <u>https://doi.org/10.1037/cns0000082</u>
- Zanesco, A. P., King, B., MacLean, K., & Saron, C. D. (2013). Executive control and felt concentrative engagement following intensive meditation training. *Frontiers in Human Neuroscience*, 7, 566. <u>https://doi.org/10.3389/fnhum.2013.00566</u>

- Zanesco, A. P., King, B. G., MacLean, K. A., & Saron, C. D. (2018). Cognitive aging and longterm maintenance of attentional improvements following meditation training. *Journal of Cognitive Enhancement*, 2(3), 259-275. <u>https://doi.org/10.1007/s41465-018-0068-1</u>
- Zanesco, A. P., King, B. G., Powers, C., De Meo, R., Wineberg, K., MacLean, K. A., & Saron, C. D. (2019). Modulation of event-related potentials of visual discrimination by meditation training and sustained attention. *Journal of Cognitive Neuroscience*, 31(8), 1184-1204. <u>https://doi.org/10.1162/jocn_a_01419</u>
- Zanesco, A. P., Skwara, A. C., King, B. G., Powers, C., Wineberg, K., & Saron, C. D. (2021). Meditation training modulates brain electric microstates and felt states of awareness. *Human Brain Mapping 42*(10), 3228-3252. https://doi.org/10.1002/hbm.25430

Tables and Figures

Frequency band	Range based on IAF	Range in current data set	Fixed band range
Delta	2.0 - 0.4 x IAF Hz	2.0 – 3.93 (0.19) Hz	$0.1-4 \ Hz$
Theta	$0.4 \mathrm{x} \mathrm{IAF} - 0.6 \mathrm{x} \mathrm{IAF} \mathrm{Hz}$	3.93 (0.19) – 5.90 (0.29) Hz	$4-8 \ Hz$
Alpha	0.6 x IAF – 1.2 x IAF Hz	5.90 (0.29) – 11.80 (0.58) Hz	8 – 13 Hz
Alpha 1	0.6 x IAF – 0.8 x IAF Hz	5.90 (0.29) – 7.87 (0.39) Hz	
Alpha 2	0.8 x IAF – IAF Hz	7.87 (0.39) – 9.83 (0.48) Hz	
Alpha 3	IAF – 1.2 x IAF Hz	9.83 (0.48) – 11.80 (0.58) Hz	
Beta	1.2 x IAF – 30 Hz	11.80 (0.58) – 30 Hz	13 – 30 Hz
Gamma	30 – 50 Hz	30 – 50 Hz	$30-50 \ \mathrm{Hz}$
IAF		$8.69-11.28~\mathrm{Hz}^\dagger$	

Table 2.1. IAF-based frequency band values and ranges

Note. Ranges for the current data set are presented as the mean (SD) of the lower and upper limits of each IAF-based frequency band across all participants and assessments. Canonical band definitions are as described in Cohen (2014), with the exception of alpha sub-bands, for which there are no established canonical ranges independent of IAF. †Range for IAF is the absolute minimum and maximum observed in the current dataset.

		Band power			
	IAF	Alpha cluster	Alpha 3 cluster	Beta cluster	
Training participants					
Pre	9.94 (0.36)	3.05 (0.96)	2.71 (0.91)	1.42 (0.63)	
Mid	9.82 (0.44)	2.90 (0.85)	2.48 (0.77)	1.17 (0.59)	
Post	9.80 (0.43)	2.72 (0.88)	2.35 (0.82)	1.09 (0.64)	
Waitlist controls					
Pre	9.93 (0.47)	3.70 (1.00)	3.30 (0.98)	1.73 (0.57)	
Mid	9.87 (0.48)	3.63 (0.90)	3.21 (0.84)	1.73 (0.55)	
Post	9.88 (0.54)	3.65 (0.81)	3.23 (0.78)	1.74 (0.42)	

Table 2.2. Descriptive statistics for Retreat 1 dependent measures

Note. Values are presented as mean (SD). Band power units are $log(\mu V^2/m^2)$. Cluster means for waitlist controls (n = 27) are based on the clusters identified in Retreat 1 training participants (n = 26).

	IAF	Band power in beta cluster	Visual threshold
In training			
Pre	9.84 (0.50)	1.49 (0.59)	0.73 (0.29)
Mid	9.63 (0.50)	1.21 (0.57)	0.59 (0.16)
Post	9.56 (0.49)	1.24 (0.53)	0.59 (0.18)
As controls			
Pre	9.93 (0.47)	1.41 (0.53)	-
Mid	9.87 (0.48)	1.46 (0.54)	-
Post	9.88 (0.54)	1.44 (0.42)	-

Table 2.3. Descriptive statistics for Retreat 2 dependent measures

Note. Values are presented as means (SD). Band power units are $log(\mu V^2/m^2)$. Cluster means for participants as controls (n = 27) are based on the clusters identified in these participants during Retreat 2 training (n = 26).

Table 2.4. Correlations between cluster mean beta power and visual threshold in Retreat 2 Training Participants

	Beta power		Visual threshold		hold	
Measure	Pre	Post	Δ	Pre	Post	Δ
Beta power						
Pre-retreat						
Post-retreat	.71**†					
Δ Post-Pre	49*†	.26				
Visual angle threshold						
Pre-retreat	37 [×]	.16	.71**†			
Post-retreat	35	.03	.52** ^{†◊}	.69**†	—	
Δ Post-Pre	.20	20	52** ^{†◊}	77** [†]	06	

Note. Correlations are with outliers included. Δ indicates change from pre to post retreat (post-pre). The uncorrected significance of all correlations remains unaltered when outliers are removed, though two correlations^{\diamond} fall short of significance with FDR correction when outliers are removed. df = 24. p = 0.06. p < 0.05. p < 0.01. Correlation survives FDR correction.



Figure 2.1. Identified clusters of current source density (CSD) power change across retreat in (A) Retreat 1 training participants, n = 26; (B) Retreat 1 waitlist controls, n = 27; and (C) Retreat 2 training participants (previously waitlist controls), n = 26. The asterisk (*) indicates electrodes that comprise a significant cluster. All cluster *ps* < 0.01. For each panel, the leftmost maps depict cluster statistic F-values; the right upper maps depict CSD Beta power at pre-, mid-, and post-retreat; and the right lower maps depict raw subtracted differences in CSD power between assessments (e.g., "Pre to Post" = post – pre)



Figure 2.2. Beta cluster mean power at each assessment point in clusters identified for each retreat training group (Retreat 1, Retreat 2). Significant clusters were identified in the training groups only, and were then applied to the waitlist control group, for whom no significant clusters were identified. Black dots are individual data points, yellow circles are group means, and yellow lines are the standard error of the mean. Retreat 1, n = 26, Waitlist Control, n = 27. Retreat 2, n = 26. Note that the Waitlist Control and Retreat 2 Training groups represent the same participants before attending, and while attending retreat, respectively.



Figure 2.3. Correlation between change in mean beta cluster power during eyes closed rest and pre-retreat visual threshold in Retreat 2, r(24) = .71, p < .001. The density distribution of each variable is represented on the respective axis.



Figure 2.4. Correlation between change in beta band cluster mean power during eyes closed rest and during mindfulness of breathing practice in active retreat participants, r(37) = .435, p = .006. The density distribution of each variable is represented on the respective axis.

Supplementary Information

Verification of Spectral Findings Using Canonical Frequency Bands

We conducted an additional set of analysis to verify that the observed changes in spectral power were not merely a feature of changes in IAF-based band definitions over the course of retreat. If the results were not unduly influenced by the IAF-based frequency bands, then we should find that—even in the presence of IAF change—the results of the cluster analysis should be similar regardless of whether IAF-based or canonical frequency bands are used. This should be true both for the bands in which clusters are identified, and the change in these clusters over retreat.

We repeated all primary analyses using canonical fixed frequency bands, following identical data processing and analysis procedures as outlined in the Methods, with the exception that canonical frequency bands rather than IAF-based frequency bands were used for power spectral estimation (see Table 2.1 of the manuscript for canonical band definitions). Cluster based permutation tests were run on the five frequency bands (delta, theta, alpha, beta, gamma) to identify clusters of change, and mixed models were used to assess group differences in change over time in clusters demonstrating significant change.

Using canonical frequency bands, we identified three significant clusters in Retreat 1 training participants: one in alpha, *cluster statistic* = 130.11, p = .006; and two in beta, *cluster statistic* = 75.25, p = .024, and *cluster statistic* = 57.77, p = .041, respectively. In Retreat 2 training participants we identified one significant cluster of change in beta power, *cluster statistic* = 265.87, p < .001. No significant clusters of change were identified in Retreat 1 waitlist controls. Supplementary Figure 2.1 depicts the identified clusters of change using canonical frequency bands.



Supplementary Figure 2.1. Identified clusters of CSD power change using canonical fixed frequency bands in Retreat 1 (n = 26) and Retreat 2 (n = 26) training participants. No clusters were identified in waitlist controls. *p < .01; *p = .024; *p = .041.

Mixed models were then used to compare changes in identified clusters between groups. As with the IAF-based clusters, clusters identified in Retreat 1 and Retreat 2 active training participants were applied to Retreat 1 waitlist controls to provide a basis for between group comparisons. Model specification was identical to those used in the primary analysis.

For the Retreat 1 alpha cluster, there were significant main effects of assessment, F(2, 102) = 6.00, p = .003, and status F(1, 51) = 11.21, p = .002, but the interaction between assessment and status fell short of significance, F(2, 102) = 2.61, p = .079.

In the first beta band cluster, the effect of assessment was not significant, F(2, 102) = 2.76, p = .068. However, status, F(1, 51) = 9.15, p = .004, and the interaction between assessment and status, F(2, 102) = 8.07, p < .001, both revealed significant effects. Tests of simple effects within each group demonstrated a significant effect of assessment in training participants, F(2, 102) = 9.88, p < .001, but not in controls, F(2, 102) = 0.78, p = .461. Follow-up comparisons of model estimated means indicated that training and control participants did not

significantly differ at the pre-retreat assessment (b = -0.21, SE = 0.16, p = .179, 95% CI [-0.53, 0.10]). Further comparisons indicated that training participants decreased significantly in cluster mean beta band power from pre- to mid-retreat (b = -0.25, SE = 0.07, p < .001, 95% CI [-0.39, -0.11]), and pre- to post-retreat (b = -0.30, SE = 0.07, p < .001, 95% CI [-0.44, -0.15]), but not from mid- to post-retreat (b = -0.05, SE = 0.07, p = .529, 95% CI [-0.19, 0.10]).

For the second beta cluster, there were significant main effects of assessment, F(2, 102) = 10.17, p < .001, and status F(1, 51) = 11.41, p = .002, as well as a significant interaction between the two F(2, 102) = 3.90, p = .023. Tests of simple effects demonstrated a significant effect of assessment in training participants, F(2, 102) = 12.85, p < .001, but not in controls, F(2, 102) = 0.99, p = .374. Follow-up comparisons indicated that active training participants had slightly lower cluster mean beta band power at the pre-retreat assessment than did waitlist controls (b = -0.44, SE = 0.18, p = .017, 95% CI [-0.81, -0.08]). Additional comparisons indicated that training participants decreased significantly from pre- to mid-retreat (b = -0.23, SE = 0.07, p = .001, 95% CI [-0.47, -0.20]), but not from mid- to post-retreat (b = -0.11, SE = 0.07, p = .113, 95% CI [-0.24, 0.03]).

In Retreat 2, the mixed model comparing active training participants to themselves as controls showed significant main effects of assessment, F(2, 124) = 4.52, p = .013, and status, F(1, 127) = 16.87, p < .001, in the identified beta cluster, as well as a significant interaction between the two, F(2, 124) = 5.55, p < .001. Tests of simple effects revealed that Retreat 2 participants significantly changed in beta power over assessments when they were active retreat participants, F(2, 124) = 9.85, p < .001, but not while they were waitlist controls, F(2, 124) =0.04, p = .964. Follow-up comparisons indicated that these participants showed no difference in power in the identified beta cluster at the beginning of Retreat 1 versus the beginning of Retreat 2 (b = 0.01, SE = 0.07, p = .870, 95% CI [-0.12, 0.15]). Further comparisons indicated that, during Retreat 2 training, these participants decreased significantly in cluster mean beta band power from pre- to mid-retreat (b = -0.24, SE = 0.07, p < .001, 95% CI [-0.38, -0.11]), and preto post-retreat (b = -0.27, SE = 0.07, p < .001, 95% CI [-0.41, -0.14]), but not from mid- to postretreat (b = -0.03, SE = 0.07, p = .637, 95% CI [-0.17, 0.10]).

Overall, the analysis using canonical frequency bands show a similar pattern of change as when IAF-based frequency bands are employed. This suggests that our findings are not an artifact of shifts in IAF-based band definitions resulting from changes in IAF.

Change in Visual Threshold

In previously published analyses, we demonstrated improvements in visual angle threshold among active training participants from the larger retreat study (MacLean et al., 2010; Retreat 1: n = 59; Retreat 2: n = 27). We confirmed that these changes held in the current subset of Retreat 2 participants that provided usable EEG data (n = 26). Means and standard deviations for visual angle threshold are reported in Table 2.3 of the main manuscript. As expected, Type 3 tests of fixed effects revealed a significant effect of assessment F(2, 50) = 7.33, p = .002, and follow-up comparisons indicated that visual threshold improved from pre- to mid-retreat (b = -0.14, SE = 0.04, p = .001, 95% CI [-0.22, -0.06]), and from pre- to post-retreat (b = -0.13, SE = 0.04, p = .002, 95% CI [-0.21, -0.05]), but not from mid- to post-retreat (b = 0.00, SE = 0.04, p = .911, 95% CI [-0.08, 0.09]).

Clarifying the Relationship between Visual Threshold and Beta Power in a Subset of High-Performing Participants

To better understand the relationship between visual threshold and beta power, we examined a subset of participants who demonstrated very low (good) visual thresholds at the beginning of retreat—a group that we have termed the "high-performers." We defined highperformers as participants who, at the beginning Retreat 2, demonstrated a visual angle threshold of at least .5 standard deviations below the mean. We hoped that investigating this subset of participants would help clarify the pattern of observed correlations between beta power and visual threshold. Specifically, we suspected that the observed negative correlation between change in visual threshold and change in beta power across retreat could be driven, in part, by a ceiling effect in visual angle threshold: participants who began retreat with a very low (good) threshold might already be performing near the physical limits of their perceptual system, and thus have little room to improve.

Because analyses of the relationship between visual threshold and beta power were limited to Retreat 2 (see Method in the main manuscript), we also limited our analysis of highperformers to Retreat 2. We used Welch's Test for Unequal Variances, as the subset of highperformers (N = 8) comprised a smaller group than the remainder of Retreat 2 participants (N =18) against which we compared them. In cases where we had a directional hypothesis about the high-performers, we used a one-tailed test, which we noted in the reporting of statistics. The high-performers did not significantly differ from the remaining participants in age t(13.75) = -0.19, p = .86, 95% CI [-15.63, 13.14], or previous lifetime meditation hours, t(15.90) = 0.13, p =.89, 95% CI [-2680.07, 3023.95]. The gender breakdown of the high-performing group was also consistent with Retreat 2 as a whole (~50% female).

Among the high-performing participants, change in visual angle threshold (M = 0.01, SD = 0.11) from pre- (M = 0.43, SD = 0.06) to post-retreat (M = 0.45, SD = 0.10) did not significantly differ from zero, t(7) = 0.38, p = .71, 95% CI [-.08, .12]. This is not true of the remaining Retreat 2 participants (those not defined as high performers), in whom change in
visual threshold (M = -0.20, SD = 0.21) significantly differed from zero, t(17) = -3.97, p < .001, 95% CI [-.30, -.09]. Confirming this difference, a direct comparison of the high-performing subset to the remaining Retreat 2 participants demonstrated that the high-performers (M = 0.01, SD = 0.11) showed significantly less subsequent reduction in visual threshold than the other participants (M = -0.20, SD = 0.21), *tone-tailed*(23.18) = 3.37, p = .001, 95% CI [.10, Inf].

The high-performing subset also appears to have differed from the remaining participants on two other key measures. Consistent with the sample-wide positive correlation between preretreat visual threshold and beta power reductions (i.e., lower starting thresholds correlate with greater beta power reductions), the high-performers demonstrated greater retreat-related reduction in beta power (M = -0.57, SD = 0.40) than did the remaining Retreat 2 participants (M= -0.11, SD = 0.37), tone-tailed (12.56) = -2.80, p = .007, 95% CI [-Inf, -.17]. We further found that the high-performing subset meditated significantly more minutes per day on average during retreat (M = 437.65, SD = 111.27) than did the remaining Retreat 2 participants (M = 348.15, SD= 69.24), tone-tailed (9.50) = 2.10, p = .032, 95% CI [11.88, Inf].

Overall, these patterns suggest that visual threshold at the onset of training might represent a complex indicator of traits relating to mental effort, motivational drive, or the ability for cognitive engagement over time. Thus, participants who perform well on these baseline measures may tend to engage in more meditation practice while on retreat, and subsequently manifest stronger psycho-physiological changes. Performance in the thresholding task depends on the ability to discriminate between subtle differences in line length, but also on visual working memory, and the ability to maintain focus throughout the task period. Participants who begin retreat with a stronger ability to engage with the task over long periods could feasibly demonstrate better performance during this task at baseline. This same capacity could allow participants to dedicate more time to formal meditation practice over retreat, resulting in greater neurophysiological change. In this case, the observed correlations between visual threshold and beta power could be explained by such a mediating effect. Unfortunately, the current data set is not sufficiently powered to directly address this possibility. Investigations of the influence of baseline individual differences on subsequent meditation-related effects may be a fruitful avenue for future research.

Chapter 3

Microstate Correlates of Compassion Meditation: The Representation of Close and Difficult Others

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Introduction

At the heart of many world religions and ethical traditions, we find the instruction to love others as you love yourself (Blackburn, 2003; Wattles, 1996). While the precise formulation varies across traditions and has generated philosophical debate (e.g., Singer, 1963; Wattles, 1996), the core principle is so universal that we refer to the imperative to "do unto other as you would have them do unto you" as the Golden Rule (Flew, 1979).

Though the principle may be intuitive (Wattles, 1996) and near universally referenced, the reality is far from that. One salient issue is how we draw boundaries between those others who we see as deserving of our care and kind treatment, and those who we do not. In situations of intergroup conflict, the dehumanization of "others" is often used as justification for violence (e.g., Harris & Fiske, 2011; Kteily et al., 2015; Kteily et al., 2016; Struch & Schwarz, 1989; Viki et al., 2013). Though recent work has called into question whether the moral justification of such violence rests on the dehumanized perception of victims, or on a moral reframing of the act of violence itself (Lang, 2020), the pattern remains that these cycles of violence are both enforced by—and in turn reinforce—a perceived divide between those who would harm the ones I love, and those whom I must protect from this harm (see, for example, essays on breaking intergenerational cycles of violence in Gobodo-Madikizela, 2016).

While we may see the most extreme manifestations of this divide in situations of intergroup conflict and violence, the tendency to draw lines between varying classes of others is not limited to these contexts. Rather, social psychologists have long observed that, across many situations, humans distinguish between people we perceive as belonging to our in-group versus those we perceive as belonging to an out-group (e.g., Allport, 1954; Brewer, 1999; Brown, 2011; Hastorf & Cantril, 1954; Sherif et al., 1961). These perceptions in turn influence the degree to

which we feel empathy, compassion, and the motivation to help (e.g., Cikara et al., 2011). Human ethnocentrism—the perception that one's own group is more important or better than others—can facilitate cooperation and trust within the perceived in-group, but can also contribute to prejudice and violence against other groups (e.g., De Drue et al., 2011; Fiske, 2002; Hammond & Axelrod, 2006). In fact, there is some evidence that the same neurochemicals that can facilitate intergroup cooperation can also increase hostility toward outgroups (e.g., De Drue et al., 2011). At the neurocognitive level, group divides can influence multiple aspects of perception and appear to be a cornerstone of human social cognition (for a review, see Molenberghs, 2013). At the same time, there is evidence that the boundaries between groups are flexible and context-dependent (e.g., Turner et al., 1994). This highlights the point that these groups are not set or unchangeable and opens the possibility that—given the right motivation and context—a person's existing boundaries could be redrawn to encompass a wider group of others.

Buddhism, Compassion, and the Extension of the Circle of Care

Buddhist tradition explicitly takes the broadest view of who should be included in the circle of care: all sentient beings. In the Theravada school, this value is expressed through the four brahmaviharas (also known as the four immeasurables): karuna (compassion), metta (loving kindness), mudita (sympathetic joy), and upekkha (equanimity), which the practitioner is instructed to cultivate in their mind and send out in all directions.¹ In Mahayana Buddhism, the value of compassion is one of the two core qualities of mind—alongside enlightened wisdom (prajña)—which the practitioner must cultivate on the bodhisattva (enlightenment seeker) path (Dalai Lama & Kamalashila, 2001). Though Buddhist schools diverge on the motivation² for

¹ These instructions are found in the Kālāmas Sutta (AN 365), trans. Thanissaro Bhikkhu, 1994. https://www.accesstoinsight.org/tipitaka/an/an03/an03.065.than.html

² In the Theravada school, the practitioner works to achieve their own enlightenment, thus the purpose of these practices is to purify their mind of obstacles such as envy, greed, and hatred. In the Mahayana and Vajrayana

engaging in these practices, the cultivation of compassion remains a shared and fundamental aspect.

Reflecting this shared commitment, practices to cultivate compassion can be found throughout Buddhism. Some practices—found primarily in the Vajrayana and Dzogchen traditions—aim to awaken the compassionate mind through the practice of non-referential compassion, visualization of the self as one with a deity of compassion, or the direct realization of the nondual nature of reality.³ Others, such as tonglen (trans. "taking and giving), provide the practitioner the opportunity to practice taking personal responsibility for the alleviation of suffering by engaging in a visualization of breathing in others' suffering and breathing out compassion and love (e.g., Chödrön, 2001). Yet other practices instruct the practitioner to reflect on their interconnectedness with⁴ or fundamental similarity to⁵ all beings.

In the Western context, a compassion practice commonly taught in secularized settings builds on the care and concern we naturally feel for loved ones and works to extend the motivation to alleviate suffering to a wider and wider circle of others. In this practice—which draws from the Theravada brahmaviharas and Tibetan four immeasurables (e.g., Salzberg, 2002; Wallace, 1999)—the practitioner begins by imagining a loved one (such as a dear friend or even

schools, the practitioner vows to liberate all sentient beings from the suffering of samsara (the cycle of birth, death, and rebirth), and to continue to be reborn themselves until this work is complete. Thus the practitioner's individual liberation is fundamentally tied to the liberation of all beings (Dalai Lama & Chodron, 2017). This motivation, called bodhicitta or "awakening mind" is closely linked to the Tibetan concept of interdependence and is at the core of Tibetan compassion practices (Makransky, 2012).

³ These traditions understand the true nature of mind as pristine, compassionate awareness, and thus all the practitioner must do to awaken is realize the fundamental nature of their own mind (Lingpa, 2016; Patrul Rinpoche, 1998).

⁴ See, for example, from *Path of the Bodhisattva*: "Since all beings have at one time been your very own mother, you should think like this: 'If all my mothers that have loved me since beginningless time continue to suffer, what is the use of my own happiness?'" (Gyatrul Rinpoche, 2008, p. 57).

⁵ From *The Bodhisattva's Way*: "Strive at first to meditate upon the sameness of yourself and others. In joy and sorrow all are equal; Thus be guardian of all, as of yourself. The hand and other limbs are many and distinct, But all are one--the body to be kept and guarded. Likewise, different beings, in their joys and sorrows, are, like me, all one in wanting happiness." (Shāntideva, 2006, p. 122).

pet) who is suffering. They try to imagine what this suffering is like for that person, and, moved by their love and concern, generate the genuine wish that their loved one be free of suffering. The practitioner then repeats this process, taking as the target of their meditation progressively more distant or difficult individuals, until, in the final visualization, all beings are encompassed. This same general format is also used to generate and extend the boundaries of loving kindness, empathetic joy, and equanimity. These practices often rely on a combination of visualizations and mental repetition of phrases (e.g., "may you be free of suffering") to generate these beneficial aspirations toward the chosen target (e.g., Salzberg, 2002).

It is important to note that, while we have described here a small subset of practices used to explicitly generate compassion, in a traditional Buddhist context all practices are undertaken with the core motivation of achieving liberation from suffering (e.g., Dalai Lama & Chodron, 2017). As such, even practices that do not have an explicit focus on compassion are conditioned by this intention and worldview.

Other-oriented Effects of Compassion Meditation

Though mindfulness practices have received more research attention, compassion-based teachings and practices have begun to draw scientific interest in recent years (for reviews, see Quaglia et al., 2021; Skwara et al., 2017; see Kirby et al., 2017 for a meta-analysis). As a recent review points out, these studies have disproportionately focused on the benefits of compassion practice to the self (Quaglia et al., 2021). Indeed, a recent meta-analysis (Kirby et al., 2017) found only four studies of compassion-based interventions over the previous 12 years that included a self-report measure of other-oriented compassion (13 included self-compassion). Across these four studies, they reported an overall effect size of d = .55, which represented a significant increase in self-report compassion.

Consistent with this reported increase, there is evidence that compassion-based interventions and meditative expertise may modulate brain systems involved in salience detection, appraisal, social cognition, and affective processing in response to suffering. A number of neuroimaging studies examining compassion training interventions report posttraining increases in positive affect and activation in brain regions associated with affect, reward, and social cognition in response to witnessing suffering (e.g., Ashar et al., 2021; Klimecki et al., 2013, 2014; Weng et al., 2013). Others report reductions in negative affect (Desbordes et al., 2012; Weng et al., 2018; Klimecki et al., 2013), and increases in markers of attention to suffering (Weng et al., 2018). Studies in experts with extensive meditation training have found similar compassion meditation-related upregulation of positive affect and associated brain activity (Engen & Singer, 2015), as well as enhanced central and peripheral nervous system responses to sounds of suffering (Lutz et al., 2008, 2009). Taken as a whole, these findings suggest that compassion training may increase sensitivity to and the salience of others' suffering. At the same time, experience with compassion meditation may also help reduce negative affect in response to suffering, and increase feelings of care and affiliation. Together, one might expect such changes to increase the likelihood of helping behavior and prosocial responding. Supporting this possibility, several studies have indeed found evidence of increased prosocial and altruistic helping behavior following compassion training (Ashar et al., 2016; Böckler et al., 2018; Condon et al., 2013; Weng et al., 2013, 2015).

However, compassion-based interventions and practices are not the only form of contemplative training that has been shown to increase other-oriented compassion. For example, a study by Condon and colleagues (2013) demonstrated that a meditation training intervention increased the likelihood that participants would offer their chairs to an injured stranger, but these

effects were of the same magnitude regardless of whether participants had received compassionbased or mindfulness training. In our own work, we've found that an intensive meditation retreat primarily focused on shamatha (calm-abiding) meditation—with the four immeasurables taught as ancillary practices—led to increased expressions of sympathy and reduced expressions of rejection emotions (e.g, anger, disgust, contempt) in response to witnessed suffering (Rosenberg et al., 2015). These participants also showed greater physiological orienting to, and increased depth of processing of, others' suffering (King et al., *in prep*). Lending further support to these observations, a recent meta-analysis found a positive association between mindfulness based contemplative trainings and prosocial behavior (Donald et al., 2019). Thus there is evidence that contemplative training can enhance other-oriented concern, but that these effects may not be specific to compassion-based trainings or compassion meditation practices.

There is less research exploring whether the boundaries of others for whom this concern is experienced can be extended with training. While a number of studies have explored the effects of mindfulness (for a recent review, see Oyler et al., 2021) or loving kindness (Kang et al., 2014) training on intergroup bias, to our knowledge no studies to have explicitly looked at the effects of compassion training on responses to the suffering of different classes of others. Furthermore, no neuroimaging studies have systematically investigated whether there is a modulating effect of target during compassion meditation practices. Indeed, the need for a more systematic approach to understanding the potential impact that different targets of compassion have on training effects was noted by Kirby and colleagues (2017) in their recent review of the compassion training literature. This is a key gap that the current study aims to address.

Theories of How Compassion Meditation Influences Compassionate Action

Theoretical approaches have tried to account for how contemplative training might lead to changes in real-world compassionate responses. One recent account proposes that visualization-based compassion meditation may act as a mental simulation, priming neurocognitive systems for compassionate responses in daily life (Wilson-Mendenhall et al., 2021). Building on research on voluntary imagination (e.g., Pearson et al., 2019), grounded cognition (e.g., Barsalou, 2008, 2009), sensorimotor (e.g., Hardwick et al., 2018) and interoceptive (Wilson-Mendenhall, Henriques, et al., 2019) simulation, and the prosocial outcomes of imagined helping (e.g., Gaesser, 2013; Gaesser & Fowler, 2020), the authors propose that visualization-based compassion meditation may precipitate real-world compassionate action by engaging the same brain systems responsible for compassionate responses in daily life. This account focuses primarily on the vivid compassion visualization practices found in Tibetan Buddhism. While these exact practices were not employed in the current study, the four immeasurables practices taught were informed by and share a number of features with Tibetan compassion practices, including visualizations and the volitional extension of the circle of care.

While the theory laid out by Wilson-Mendenhall and colleagues (2021) offers a plausible neurocognitive pathway by which visualization-based compassion practices may prime the practitioner for real-world compassionate action, it cannot account for the compassion-relevant effects observed following meditation training that does not include explicit compassion practices (see Skwara et al., 2017 for a discussion). Another theoretical framework suggests that compassion is contextual and emergent and therefore cannot itself be directly trained (Halifax, 2012). Instead, this model posits that compassionate responses can be strengthened by training

underlying component processes, which in turn support the emergence of contextuallyappropriate compassionate responses. While this model draws on contemplative theory and experiential accounts rather than empirical research findings, the idea that compassionate responses are emergent and contextually-grounded and depend, at least in part, on noncompassion processes offers a useful frame for considering the non-specific effects of contemplative training.

EEG Microstates as a Window into Network Dynamics

Regardless of the exact mechanisms of training-related change, the mental representations of various suffering others imagined during compassion meditation should be reflected in the continuous activity of the brain. While a number of neuroimaging studies, reviewed above, have used fMRI to localize regional brain activity during compassion practice, far fewer studies have investigated time-varying brain dynamics during compassion meditation (e.g., Lutz et al., 2004; Schoenberg et al., 2018). A large body of research has explored the functional significance of localized brain areas, but other work suggests that brain functions are supported by parallel processing distributed across large-scale networks (see: Bressler & Menon, 2010; Fries, 2005; Meehan & Bressler, 2012; Michel & Koenig, 2018). The ongoing neural activity of these networks can in part be recorded at the scalp via electroencephalography (EEG), and the spatial and temporal features of this activity can be described by segmenting the EEG time series into brain electric microstates (Lehmann, 1971; Michel & Koenig, 2018).

The voltage topographic distribution of the EEG time series has been shown to vary in a dynamic but organized manner, characterized by periods of relative stability followed by rapid transitions to another state (Lehmann et al., 1987). These moments of stability—typically lasting 60-150 ms—correspond to peaks in the global field power, ostensibly reflecting moments of high

synchrony in underlying neural generators (Michel & Koenig, 2018; Zanesco et al., 2020). Microstate analysis takes advantage of this feature by describing the continuous EEG time series as a series of categorical topographical states, derived from these global field power peaks. Changes in the topographic pattern of EEG scalp voltage require changes in the spatial distribution of activity in underlying neural generators (Murray et al., 2008, Vaughn, 1982), and thus different microstate configurations are thought to reflect shifts in the predominance of activity in different contributing brain networks (Zanesco et al., 2021).

Studies have consistently found that a handful of these topographic configurations can account for a large proportion of the observed topographic variance in the EEG time series (for a review, see Michel & Koenig, 2018; for large sample studies in normative populations, see Koenig et al., 2002; Zanesco et al. 2020). Thus microstate analysis provides an approach for describing patterns of underlying network dynamics using an "alphabet" of relatively few categorical states. These patterns can be described in terms of the features of the representative topographies (strength, duration, frequency, and the amount of variance explained), or in terms of the temporal sequencing of microstates. Such sequences have been found to demonstrate scale-free mono-fractal dynamics (van de Ville et al., 2010), meaning that they are organized in lawful, but unpredictable ways (Michel & Koenig, 2018). By employing a series of techniques that allow for the characterization and comparison of multivariate symbolic data (sequence analysis; Abbott & Tsay, 2000), these sequences can be examined for the overall similarity of their temporal patterning. This allows for the holistic comparison of the dynamics of the EEG time series without relying on any single parameter or indicator, making it an ideal approach to assess the overlap in brain activity generated during different mental tasks.

In a previous analysis, we demonstrated that an intensive meditation retreat intervention resulted in global reductions in microstate strength and duration during eyes closed rest (Zanesco et al., 2021). These changes were observed across all microstate configurations, suggesting global changes in the brain systems organizing neuronal communication and excitability (Michel & Koenig, 2018). We also observed retreat-related changes in the temporal sequencing of microstates, which were related to increases in felt attentiveness and serenity. This study serves as evidence that microstate analysis can provide a meaningful window into meditation-related changes in brain dynamics and subjective experience. While a limited number of other studies have examined meditation-related modulation of microstate dynamics (e.g., Brechet et al., 2021; Faber et al., 2017; Panda et al., 2016; Zarka et al., 2021), to our knowledge none have looked at compassion or other emotion-generative practices (Dahl et al., 2015). Further, no known study has attempted to investigate the potential effect of the target of compassion on these dynamics.

The Current Study

In the current study, we examined the effects of a residential meditation retreat intervention on the electrophysiological functioning of brain networks during a guided compassion meditation. Experienced meditators engaged in three months of full-time meditation training in a residential retreat setting, or were assigned to an initial waitlist control group. These waitlist controls completed all measurements in the first retreat, and later returned to complete their own retreat intervention. While on retreat, participants engaged in full-time meditation training in shamatha practices, as well as the four immeasurables. They completed a battery of assessments at the beginning, middle, and end of retreat. As part of these assessments, they engaged in a guided compassion meditation, and EEG was recorded throughout. In this meditation, they imagined the suffering of—and then took as the target of their compassion—

three different categories of others: a loved one (close other), someone with whom they have experienced difficulty (difficult other), and the various forms of suffering experienced by beings throughout the world (all others).

We were interested in longitudinal changes in microstate dynamics, as well as variations in the temporal sequencing of microstates as a function of the target of compassion. All core analyses and hypotheses were preregistered on the Open Science Framework. We hypothesized that retreat training should result in global alterations to brain electric microstates during compassion meditation, reflected in changes to the parameters (e.g., strength, duration) describing them. We did not, however, have specific predictions regarding which parameters should show change or the direction of this change. We further hypothesized that retreat training should alter the temporal dynamics of the microstate time series, and that this should be reflected in greater sequence dissimilarities between assessment points than within them. Our main hypotheses pertained to differences in the temporal sequences of microstates as a function of the target of compassion. We hypothesized that microstate sequences generated during compassion for a close versus for a difficult other should significantly differ, reflecting differences in the brain systems engaged (and experiences evoked) by these different tasks. However, we expected these differences to attenuate over the course of retreat, reflecting a reduction in the differentiation between loved and challenging others, and providing evidence for the extension of the circle of care.

Method

Participants and Retreats

These data comprise part of a large, multi-method study of residential retreat meditation training - The Shamatha Project. Experienced meditation practitioners were recruited through advertisements in print and online Buddhist publications and assigned via a stratified matching procedure to an initial training group (n = 30) or waitlist control group (n = 30) for Retreat 1. Waitlist control participants later returned to complete their own training in Retreat 2. One waitlist participant left the study after Retreat 1 for reasons unrelated to the study, leaving a total of n = 29 in Retreat 2. The groups were matched at a baseline assessment on age, sex, ethnicity, personality, and cognitive task performance (for details on recruitment and matching, see MacLean et al., 2010, Shields et al., 2020). Additionally, participants were matched on lifetime meditation experience, having an overall mean of 2,610 lifetime practice hours (initial training group: M = 2,549 hours, range = 250 to 9,500 hours; waitlist control group: M = 2,668 hours, range = 250 to 15,000 hours). All participants were screened for medical conditions and Axis I psychiatric disorders as assessed by a clinical psychologist through a clinical interview the Mini International Neuropsychiatric screen (Sheehan et al., 1998). All study procedures were approved by the University of California, Davis Institutional Review Board, and participants provided informed consent and were compensated \$20 per hour for data collection.

The waitlist-controlled design of the study consisted of two formally identical 3-month long residential meditation retreats. Retreats were held at Shambhala Mountain Center (SMC) in Red Feather Lakes, Colorado. In Retreat 1, training participants lived and practiced onsite for the 3-month duration, completing assessments at the beginning (pre-), middle (mid-), and end (post-) of the retreat. Waitlist control participants continued about their daily lives, but were flown to the retreat center to complete the pre-, mid-, and post-retreat assessments on-site. At each assessment, waitlist participants arrived at SMC approximately 3 days (range: 65 to 75 hours) prior to laboratory assessments to allow for an initial acclimatization period to the altitude (~2,500 meters) and retreat environment. Approximately 3 months after the end of Retreat 1,

waitlist control participants returned to SMC to complete their own 3-month residential retreat (Retreat 2).

Meditation Training

During their 3 months in retreat training, participants practiced meditation for 6 to 8 hours per day under the guidance of B. Alan Wallace, an experienced Buddhist contemplative scholar and meditation teacher. While on retreat, participants gathered for group meditation practice guided by Mr. Wallace twice per day, and met individually with Mr. Wallace once per week for one-on-one instruction. Meditation practices and contemplative instruction were based in the Theravada and Mahayana Buddhist traditions. The retreats emphasized a family of concentrative practices, collectively called shamatha meditation. These practices are thought to develop stability of attention, perceptual vividness, and strength of concentration. The primary techniques taught on retreat were: (1) *mindfulness of breathing*, in which the attention is focused on the sensations of the breath; (2) *observing mental events*, in which attention is directed to all forms of mental phenomena as they arise; and (3) *observing the nature of consciousness*, in which attention is placed on the awareness of being aware (for an in-depth description of various shamatha techniques, see Wallace, 2006; for a discussion of different classes of meditation practice, see Dahl et al., 2015).

In addition to these primary shamatha meditation practices, teacher B. Alan Wallace instructed participants in the four immeasurables of loving-kindness, compassion, empathetic joy, and equanimity. These emotion-generative practices aim to foster a sense of common humanity with—and care for—others and provide the ethical and motivational framing to contextualize shamatha practices (Wallace, 1999). In *loving kindness meditation*—aimed to foster aspirations of benevolence toward others—practitioners use imagery and silent phrases of

kindness (e.g., "May you find happiness and the causes of happiness") to generate the wish for others' happiness. In *compassion meditation*—aimed to develop concern for the suffering of others—practitioners imagine another's suffering and, moved by the understanding that no being wishes to suffer, generate the wish that this person be free of their suffering. In *empathetic joy meditation*—aimed to enhance the capacity to experience joy at other's happiness—practitioners bring to mind another's good fortune and practice delighting in it. In *equanimity meditation* aimed to cultivate a sense connectedness and interdependence with others—practitioners practice seeing all others (loved ones, strangers, enemies) as fundamentally similar to themselves, sharing the wish for happiness and freedom from suffering (Rosenberg, 2015; Wallace, 1999). Together, these practices are thought to support the development of genuine care and concern for an everwidening circle of others, and to combat feelings of envy, indifference, and spite.

Participants reported spending most of their daily meditation time (6 to 8 hours per day) practicing the primary shamatha techniques. On average, training participants reported engaging in approximately 40 minutes of four immeasurables practice per day (M = .68 hours, SD = .30 hours). For a full breakdown of time committed to various practices, see Sahdra et al., 2011).

Procedure

Assessments were completed at the beginning, middle, and end of each retreat in two field laboratories constructed on site at SMC. These laboratories consisted of darkened and sound-attenuated testing and control rooms to allow for the capture of research laboratory-quality measurements. Retreat 1 training participants completed three assessments in total (pre-, midand postassessment in Retreat 1); Retreat 2 training participants completed a total of six assessments (pre-, mid-, and postassessment as Retreat 1 waitlist controls, and pre-, mid-, and postassessment as Retreat 2 training participants). At each assessment point, laboratory

assessments were conducted over two consecutive days, each of which included approximately 4 hours of laboratory testing.

EEG Data Collection and Processing

Compassion Meditation. The compassion meditation was completed as the final measure on the first day of each assessment. During the compassion meditation, participants sat in a darkened, sound-attenuated testing room and engaged in a guided meditation pre-recorded by Mr. Wallace. The recording began with an introduction that provided general instructions for the meditation (~1 min 22 sec), then guided participants through a Tibetan Buddhist-derived compassion meditation (~11 min 23 sec), and closed with gongs to signal the end of the meditation (~32 sec). The recording was preceded and followed by two 1-minute resting periods, first with eyes open, then with eyes closed. Thus the full order of each compassion meditation, gongs, eyes open rest, eyes closed rest.

The compassion meditation comprised three epochs, each focusing on a different target for compassion:

- A close other: "someone you know and care about who is suffering from physical or psychological distress."
- (2) A difficult other: "a person who, despite wishing to be of suffering him or herself, causes you a great deal of difficulty."
- (3) All others: "let the scope of your awareness rove through the world, attending to those who suffer, whether from hunger and thirst, from poverty or the miseries of war, from social injustice, or the imbalances and afflictions of their own minds."

Each epoch followed the same general structure: first participants were instructed to bring the target to their mind, then to imagine the target's suffering and the causes of that suffering, next to take the target's perspective and imagine what that suffering is like for them, and finally to generate the wish that the target be free from suffering. A full transcript of the recording can be found in Appendix 3A.

EEG Recording and Preprocessing. Continuous EEG was recorded at a sampling rate of 2048 Hz with the BioSemi ActiveTwo system (http://www.biosemi.com) for the duration of the session, including the pre- and post-meditation resting periods. Easycap electrode caps (http://easycap.de) fitted with BioSemi electrode holders were arranged in an 88-channel equidistant montage, and individual electrode locations were localized using a Polhemus Patriot digitizer (http://www.polhemus.com). On participant request, electrodes were removed or not inserted to minimize discomfort (primarily at frontopolar locations). Following recording, the EEG was band-pass filtered between 0.1 and 200 Hz (zero-phase; roll-off of 12 dB/octave LP, 24 dB/octave HP). Channels with very low signal quality were discarded, and the reference was set to the average of all remaining channels. Data were then manually artifact marked to remove extreme artifacts. These preprocessing steps were conducted in BESA 5.3.

Following artifact marking, the EEG files were spliced to remove the following epochs: eyes open resting periods, the introduction, and the gongs, and any interstitial periods between recording epochs. Thus the structure of the final files was as follows: eyes closed rest (~1 min), compassion meditation (~11 min 23 sec), eyes closed rest (~1 min). These spliced files were then submitted to second-order blind source identification (SOBI; Belouchrani et al., 1997), which was used to separate out signals stemming from putative noise versus neural sources. SOBI is similar to ICA in that it functions to separate out maximally independent signal sources. Unlike

ICA, SOBI uses joint-diagonalization of correlation matrices at multiple temporal delays to determine independence. SOBI functions by minimizing the sum of the squared cross-correlations of all pairs of sources across all temporal delays. As recommended in Tang et al. (2005), we employed 41 temporal delays, $\tau = [1:1:10, 12:2:20, 24:5:100, 120:20:300]$ ms. A SeMi-automatic Artifact Removal Tool (SMART; <u>https://stanford.edu</u>/~saggar/Software.html; Saggar et al., 2012) was used to generate outputs depicting signal source topography, spectra, autocorrelation, and signal time series for visual inspection (see Saggar et al., 2012 for examples of SMART output and a discussion of parameters considered in source classification). These outputs were manually classified as neural or noise (e.g., EMG, ocular artifact, line noise), and the ostensible neural signals were then reconstructed into the original 88-channel montage. The reconstructed data were then transformed into a standardized 81-channel montage (international 10-10 system) using spherical spline interpolation with a smoothing factor of 2e-06 as implemented in BESA 5.3.

Standardized 81-channel montage EEG files were then imported into Cartool and converted to native format for topographic segmentation. Once in Cartool, EEG were downsampled to 102.4 Hz, DC-removed, band-pass filtered between 0.1 and 40 Hz, average-referenced, and spatially smoothed to minimize the influence of signal outliers in the montage (Michel & Brunet, 2019). These steps were all conducted using the Cartool software toolbox version 3.91 (Brunet et al., 2011).

Topographic Segmentation and Microstate Parameter Estimation

Topographic segmentation of the 267 individual EEG recordings was conducted using an adapted k-means clustering method, as implemented in Cartool 3.91. This approach determines the optimal number of clusters (k) that can account for the greatest global explained variance

(GEV) in the spatial time series using the fewest representative topographic maps (Michel et al., 2009; Murray et al., 2008). First, peaks in global field power (GFP) are identified in the continuous EEG time series. Then, maps of the scalp topographic voltage at each GFP peak are generated. The GFP—equivalent to the spatial standard deviation of amplitude across the entire average-referenced electrode montage (Skrandies, 1990)—is a reference-independent measure of scalp voltage potential (μ V) that quantifies the strength of the electric field at a given sample of the EEG recording. GFP peaks are thought to reflect moments of high global neuronal synchrony within the continuous time series. Thus the maps of scalp voltage at these peaks provide optimal representations of moments of quasi-stable voltage topography (Koenig and Brandeis, 2016; Zanesco et al., 2020). These maps were then submitted 100 iterations of recording-level *k*-means clustering as described below.

Clustering of voltage maps. For each recording, *k*-means clustering proceeded as follows. First, a subset of 1 to 12 maps (k = [1:12]) was randomly selected from the total set of GFP peak voltage maps. This subset of maps served as the initial centroids for clustering. Then, the spatial correlation between the *k* centroid maps and the remaining voltage maps was computed. Correlations were computed from the relative topographic configuration of the maps, ignoring polarity by correcting the sign of the spatial correlation coefficients (Michel et al., 2009). Based on these correlations, voltage maps were assigned to the centroid with which they had the strongest spatial correlation, creating *k* clusters of maps. Maps were only assigned to a cluster if their spatial correlation with the cluster centroid exceeded .5; maps that did not have a correlation of at least .5 with any of the *k* cluster centroids were left unassigned. After all correlations were calculated and each GFP peak voltage map was assigned to a cluster, *k* new centroid maps were created by averaging across all the constituent maps assigned to each of the *k*

clusters. This process continued iteratively until the global explained variance (GEV) between the average centroids and the voltage maps converged to a limit.

This procedure was repeated 100 times for each value of k = [1:12], with each of these 100 iterations beginning with a new subset of randomly selected *k* centroids. After 100 iterations, the set of *k* centroids with the highest GEV was identified and selected. Finally, the optimal number of *k* clusters was selected from these maximal GEV centroids across all levels of *k* using a metacriterion defined by 7 independent optimization criteria (see Brechet et al., 2019; Custo et al., 2017 for a discussion of the metacriterion). Across all 267 files, the optimal number of average centroid maps determined by the recording-level *k*-means clustering procedure ranged from 4 to 7 topographic maps (M = 5.01, SD = 0.85) that explained an average of 75.86% (SD =4.45%, range = 64.91% to 88.72%) of the variance in the GFP peak voltage maps.

Clustering of recording-level centroids. The final sets of recording-level optimal centroids identified in the previous step were then submitted to a second round of *k*-means clustering. In this second step, we conducted *k*-means clustering on these centroids to identify the global clusters that best explain the recording-level representative centroids across all 267 recordings. To do this, a set of k = [1:15] maps were randomly selected from across all sets of recording-level centroid maps, then used as global centroids for clustering, with each recording-level centroid map assigned to the global centroid map with which it had the highest spatial correlation. Recording-level centroid was .5 or higher. For each level of *k*, this was repeated over 200 iterations and the *k* centroids with the highest GEV were selected. After all iterations across all levels of *k* were complete, the optimal number of global clusters was determined by using the

optimization metacriterion. This resulted in a set of k global centroids that best represent the topographic configurations across all EEG recordings.

This second round of clustering identified five global centroids that best satisfied the metacriterion and together explained 82.43% of the variance in the 1337 recording-level topographic maps. Four recording-level maps had a correlation of less than .5 with all global centroids and therefore went unassigned to a cluster. Figure 3.1 depicts the five global centroids, each with the subset of recording-level centroids that were assigned to that cluster.

Parameterization of the Microstate Time Series. Following the clustering procedure and identification of global centroids, the downsampled continuous EEG files were then spliced into conditions: pre-meditation rest, compassion meditation, and post-meditation rest.

The five global centroids were then fit back to the epoched EEG files to derive a time series of microstate sequences for each condition. All samples of each downsampled EEG file were categorized by assigning them to the global cluster centroid (microstate configuration) with which they demonstrated the highest spatial correlation, ignoring polarity. EEG samples that had low spatial correlations (<.5) with all global centroids were left unassigned. Microstate sequence time series were then temporally smoothed by ignoring assigned microstates that were present for less than 3 consecutive samples (~30 msec), and reassigning those samples by splitting them between the preceding and following microstates in the series. In addition to fitting the continuous EEG, we also fit the five global centroids to the voltage maps at the global field power peaks to create a GFP peak microstate time series for each recording.

We then derived four microstate parameters from each epoch of each recording-level microstate time series. *Global explained variance* (GEV) is the percentage of observed variance in the EEG time series that is explained by a given microstate configuration (global centroid).

Mean microstate duration is the average total duration (in msec) of contiguous samples assigned to a given microstate configuration when that microstate appears in the time series. *Occurrence per second* is the average number of times per second a given microstate occurs in the continuous time series. Lastly, *mean global field power* is the average of the fitted GFP peaks assigned to a given microstate configuration, indicating the maximal field strength and degree of synchronization among the neural generators contributing to the voltage topography of each global centroid. The first three parameters (*GEV*, *mean microstate duration, and occurrence per second*) were derived from the microstate time series of the continuous EEG recordings. The last (*mean global field power*) was derived from the GFP peaks of each recording.

In the compassion meditation condition, on average 90.21% (SD = 5.99%) of time samples from a given file of continuous EEG were successfully assigned to a global centroid, while 98.06% (SD = 2.42%) of GFP peaks were successfully assigned. Of the 267 recordings, one was excluded from further analysis because a large proportion of samples (53.54% in continuous EEG; 32.40% of GFP peaks) were unable to be assigned to a global cluster (had less than a .5 spatial correlation with all global centroids). In the retained recordings, the five global centroids explained on average a total of 57.09% GEV (SD = 4.75%) of the continuous EEG time series and 71.31% (SD = 4.48%) of the GFP peaks. Descriptive statistics for microstate parameters during compassion meditation are reported in Table 3.1 for Retreat 1 and Table 3.2 for Retreat 2.

In the pre-meditation resting condition (pre rest), an average of 90.81% (SD = 5.99%) of time samples in the continuous EEG were successfully assigned to a global centroid, and 98.26% (SD = 2.32%) of the GFP peaks were successfully assigned. Of the 267 recordings, one recording had a large proportion of samples that could not be assigned (48.85% continuous EEG time

samples; 28.70% of GFP peaks) and was excluded from further analysis. This was the same file that was excluded in the compassion meditation condition. In the remaining recordings, the five global centroids explained an average total of 57.42% GEV (SD = 5.16%) of the continuous EEG time series, and an average total of 71.94% GEV (SD = 4.47%) in the GFP peaks. Descriptive statistics for microstate parameters during pre-meditation rest for Retreats 1 and 2 can be found in Tables 3.3 and 3.4, respectively.

In the post-meditation resting condition (post rest), an average of 90.61% (SD = 6.06%) of time samples in the continuous EEG were successfully assigned to a global centroid, and 98.17% (SD = 2.36%) of the GFP peaks were successfully assigned. Of the 267 recordings, one recording had a large proportion of samples that could not be assigned (51.76% continuous EEG time samples; 29.20% of GFP peaks) and was excluded from further analysis. This was the same file that was excluded in the compassion meditation and pre rest conditions. In the remaining recordings, the five global centroids explained an average total of 57.19% GEV (SD = 5.23%) of the continuous EEG time series, and an average total of 71.44% GEV (SD = 4.80%) in the GFP peaks. Descriptive statistics for microstate parameters during post-meditation rest are reported in Table 3.5 for Retreat 1 and Table 3.6 for Retreat 2.

Microstate Sequence Analysis

We next employed sequence analysis (Abbott & Tsay, 2000) to examine the time series of microstates (see Zanesco et al., 2020 and Zanesco et al., 2021 for previous applications of this approach to microstate time series data). Sequence analysis is a way of characterizing and comparing multivariate symbolic data - in this case, the time series of symbolic states represented by the sequence of microstate configurations. We employed the optimal matching (OM) of spells algorithm (Studer & Ritschard, 2016) to determine dissimilarities between

sequences and multivariate distance matrix regression (MDMR; McArdle & Anderson, 2001; McArtor et al., 2017; Zapala & Schork, 2012) to compare these dissimilarities between groups, assessments, and epochs of the compassion meditation.

For the analysis of microstate sequences, the compassion meditation condition was divided into three sub-epochs based on the target of compassion participants were instructed to visualize: close other, difficult other, and all others. The sequence analysis examines the microstate series in the continuous EEG (and not the series of GFP peaks), therefore fit information for the continuous data only is reported here for each epoch. Across all files, an average 90.54% (SD = 6.01%) of time samples were successfully assigned to a global centroid in the close other epoch, 90.20% (SD = 5.95%) in the difficult other epoch, and 89.83% (SD = 6.24%) in the all others epoch. One file was excluded from further analysis in all epochs because a large proportion of samples (53.96% in the close other epoch; 52.57% in the difficult other epoch; 54.26% in the all others epoch) were unable to be assigned to a global centroid.

In the retained recordings, the close other epoch had an average length of 3 min 27.06 sec (SD = 20.38 sec, min = 1 min 0.27 sec, max = 3 min 39.69 sec), the difficult other epoch had an average length of 3 min 47.84 sec (SD = 20.46 sec, min = 1 min 53.08 sec, max = 4 min 2.35 sec), and the all others epoch had an average length of 3 min 25.15 sec (SD = 19.41 sec, min = 1 min 41.68 sec, max = 3 min 41.49 sec). On average in these retained recordings, the five global centroids explained a total of 57.24% (SD = 4.92%) GEV in the close other epoch, 57.06% (SD = 4.68%) GEV in the difficult other epoch, and 56.83% (SD = 4.91%) in the all others epoch.

Optimal Matching and Analysis of Sequence Dissimilarities. Sequence analysis was conducted in *R* using the *seqHMM* (Helske & Helske, 2019) and *TraMineR* (Gabadinho et al., 2011) packages. We first converted each file of downsampled, fitted continuous EEG into a

sequence of microstate configurations, such that each subject/assessment/epoch was expressed as a series of the five identified configurations with each time sample represented by a single microstate label (e.g., AADBCCCEC). Time samples that went unassigned during the fitting process (i.e., had lower than .5 correlation with all global centroids) were marked as missing, but were retained as part of the sequence (e.g., for example, if the D configuration of the previous sequence were instead unassigned, the sequence would be: AA"missing"BCCCEC). Figure 3.2 depicts the full microstate sequence for each participant at each assessment, in each epoch of compassion meditation.

These sequences served as the input for the OM of spells algorithm. OM of spells uses the order and duration of categorical states to calculate the dissimilarity between pairs of sequences. Sequences are defined as a series of categorical states or "spells" (microstate configuration) each with a duration (the number of contiguous time samples of the same configuration). For example, the series AADBCCCEC has 6 spells (A, D, B, C, E, C), each of which has a corresponding duration (2, 1, 1, 3, 1, 1). Thus the series would be represented as A2, D1, B1, C3, E1, C1. Dissimilarity between pairs of sequences is operationalized as the edit distance: the minimum number of substitutions, insertions, and deletions necessary to transform one sequence of spells into another (Abbot & Tsay, 2000; Studer et al., 2011). Each operation (substitution, insertion, deletion) has a corresponding edit "cost." The cost to perform an operation on a given categorical state is weighted based on the frequency of that state across all sequences, with more common states having lower associated edit costs than rarer states. Additionally, the OM of spells algorithm incorporates expansion and contraction operations to account for the duration of each spell. The cost of expansion and contraction operations are

subject to a reduced edit cost compared to other operations (insertion, deletion), thus the ordering of spells is weighted more heavily than their durations.

Edit costs were calculated separately for Retreat 1 and Retreat 2. Insertion/deletion (indel) costs for each microstate configuration were first derived from the log-transform of the inverse frequency (log[2/(1 + fi)]) of that state across all sequences (Gabadinho et al., 2011). Unassigned samples were included in the list of states to be matched. Pairwise substitution costs (e.g., the cost to substitute configuration A for configuration B) were then calculated by summing the indel costs of each pair (e.g., substitutionA,B = indelA + indelB). The indel edit cost (the cost of inserting or deleting rather than substituting a state) to be used in OM was set to the maximum indel of all states. The expansion cost (δ) was set to one third of this maximum indel edit cost. Thus the cost to substitute a state was always less than the cost to delete it and insert another, and the cost to expand the duration of a spell was equal to approximately one quarter the cost of inserting an entirely new microstate, biasing the OM algorithm to use substitutions and contractions/expansions whenever possible.

Indel costs calculated for each retreat were as follows. Retreat 1: A = 0.597, B = 0.590, C = 0.476, D = 0.532, E = 0.543, Unassigned = 0.609; Retreat 2: A = 0.606, B = 0.591, C = 0.455, D = 0.533, E = 0.541, Unassigned = 0.614. Additionally, we calculated indel costs separately within each group of participants for use in MDMR follow up tests. These were as follows. Retreat 1 training: A = 0.590, B = 0.587, C = 0.495, D = 0.528, E = 0.547, Unassigned = 0.607; Retreat 1 waitlist control: A = 0.604, B = 0.592, C = 0.457, D = 0.536, E = 0.539, Unassigned = 0.611; Retreat 2 training: A = 0.607, B = 0.591, C = 0.453, D = 0.530, E = 0.543, Unassigned = 0.617.

Finally, we also conducted a sensitivity analysis to verify that any observed effects were not due to differences in data length between the compassion meditation epochs. To do this, we shortened all sequences to the length of the longest sequence of the shortest epoch. We then recalculated indel costs on this shortened data, which were as follows. Retreat 1: A = 0.590, B = 0.582, C = 0.460, D = 0.520, E = 0.532, Unassigned = 0.602; Retreat 2: A = 0.599, B = 0.584, C = 0.438, D = 0.522, E = 0.530, Unassigned = 0.608.

Statistical Analysis

Mixed Effects Models of Microstate Parameters

We modeled changes in microstate parameters (GEV, duration, occurrence, and GFP) using mixed effects models implemented with the LME4 package in R (Bates et al., 2015). Model parameters were estimated using restricted maximum likelihood with degrees of freedom calculated using Satterthwaite approximation. All participants who provided any data at any assessment were included. Retreat 1 models for change in microstate parameters during compassion meditation included the between-subjects fixed effect of group (control versus training), and the within-subjects effects of assessment (pre-, mid, and post-retreat) and microstate configuration (A, B, C, D, and E). Retreat 2 models included the within-subject effects of status (waitlist control versus in training), assessment, and microstate configuration. Random subject intercepts were included to allow for between-person variability in baseline level, and effects were referenced to the control group at the pre-retreat assessment. Microstate configuration was referenced to configuration C. For all parameters, we first tested a full model including all potential main effects and interactions, and followed up with simplified model retaining only significant terms. We report type III tests of fixed effects from the full model, and parameter estimates for significant fixed effects in the simplified models. To correct for multiple

comparisons, we used a blanket cut-off of p = .01 to assess the significance of type III tests and parameter estimates.

To elucidate whether observed effects were specific to compassion meditation, we built an additional set of mixed effects models comparing compassion meditation to pre- and postmeditation eyes closed rest. These expanded models were identical to the models described above, adding the within-subjects effect of condition (pre-meditation rest, compassion meditation, post-meditation rest), referenced to compassion meditation. These models were targeted to test for effects of condition, therefore we only followed up with simplified models in cases where the omnibus test indicated a main or interaction effect of condition. As with the compassion-only models, we used a blanket cut-off of p = .01 for considering an effect statistically significant.

Multivariate Distance Matrix Regression of Sequence Dissimilarities

We modeled changes in sequence dissimilarities using multivariate distance matrix regression (MDMR; McArdle & Anderson, 2001; McArtor et al., 2017; Zapala & Schork, 2012), implemented in *R* using the *MDMR* package (McArtor, 2018). MDMR is a person-centered regression method that regresses a distance matrix onto a set of predictors. This makes it possible to test the significance of associations between the dissimilarities of individual response profiles and the chosen predictors (McArtor, 2017). Like mixed effects models, mixed effects MDMR can account for hierarchies and dependencies in the data structure. When partitioning sums of squares of dissimilarities in MDMR, dissimilarities were not squared as this the preferred approach when the dissimilarities are edit distances (Studer et al., 2011; Zanesco et al., 2021).

We used MDMR to test for differences in sequence dissimilarities calculated by OM of spells. For each retreat, we built a series of mixed effects MDMR models to test the effects of

group (in Retreat 1) or status (in Retreat 2), assessment (pre, mid, post), and epoch (close other, difficult other, all other) on sequence dissimilarities. For each retreat, the analysis proceeded as follows: we first built a main-effects only model, which we used to interpret the main effects of group/status, assessment, and epoch; we next expanded the model by adding in all two-way interactions, which we used to assess interactions between any two predictors; we finally built a model that included three-way interactions between group/status, assessment, and epoch. We followed up interaction terms using directed MDMR comparisons on dissimilarities calculated within each group separately because 1) differences in edit costs between groups could affect estimation of within-group dissimilarities; and 2) the partitions of sums of squares of dissimilarities are affected by the overall dissimilarity of all sequences in a given analysis, thus dissimilarities in one group will influence the calculation of dissimilarities in the other (Zanesco et al., 2021). In all models, effects were referenced to the control group at the pre-retreat assessment during the close other epoch. As MDMR only calculates the differences between between dissimilarities and does not provide parameter estimates, centroid distances are provided where relevant in place of parameter estimates. Centroid distances are the dissimilarity between multivariate distance centers for each grouping of data. We also provide estimates of discrepancy—or dispersion around the distance center of a group—which serves as an indicator of between-person variability.

Results

Mixed Effects Models of Microstate Parameters

Global Explained Variance

We first checked for any differences in GEV—the proportion of observed variance explained by a given microstate configuration—in Retreat 1 continuous EEG. We found no significant effect of group, F(1, 865) = 0.60, p = .441, or assessment, F(2, 865) = 0.01, p = .992, and a significant effect of microstate configuration, F(4, 865) = 250.49, p < .001. There was no interaction between group and assessment, F(2, 865) = 0.02, p < .984, assessment and configuration, F(8, 865) = .50, p = 0.854, or three-way interaction between group, assessment, and configuration, F(8, 865) = .25, p = .981. There was a significant interaction between group and configuration, F(4, 865) = 10.43, p < .001. A simplified model was then created by removing the non-significant terms. The parameter estimates from this simplified model are reported in Table 3.7. Briefly, parameter estimates from this simplified model indicated that configuration C accounted for a greater proportion of the GEV than any other microstate configuration in the control group (all ps < .0001) and in the retreat group (all ps < .001). However, it explained a significantly greater proportion of GEV in the control group than in the training group both in terms of absolute GEV explained (p < .001), and relative to other configurations (all ps < .001).

We next examined GEV in Retreat 2 by comparing Retreat 2 participants to themselves as waitlist controls. Type III tests of fixed effects indicated that there was no effect of status, F(1, 855) = 0.04, p = .847, or of assessment, F(2, 855) = 0.06, p = .941, and no interaction between status and assessment, F(2, 855) = 0.05, p = .947. There was a significant effect of microstate configuration, F(4, 855) = 343.15, p < .001, but no interaction of configuration with status, F(4, 855) = 0.23, p = .921, or assessment, F(8, 855) = 0.67, p = .718, and no three-way interaction between status, assessment, and configuration, F(8, 855) = 0.23, p = .985. We therefore created a simplified model containing only the effect of configuration. Parameter estimates from this simplified model are reported in Table 3.7. As in Retreat 1, configuration C explained a greater proportion of GEV than any other microstate (all ps < .001).

We also examined GEV in each retreat using expanded models comparing compassion meditation to pre- and post-meditation rest. These models were designed to test for differences in microstate parameters between meditation and rest. Type III tests of fixed effects in these models indicated no main effect of condition in Retreat 1, F(2, 2595) = .02, p = 0.978, or in Retreat 2, F(2, 2536.4) = 0.03, p = .970, and no interaction between condition and any other factor in either retreat. All other effects were similar to those observed in the models testing compassion meditation alone. See Table 3.11 for the type III tests of fixed effects in these expanded models.

Overall, these results indicate that there were differences in GEV between different microstate configurations—with microstate C explaining the preponderance of variance—as well as baseline group differences in the proportion of GEV explained by different microstate configurations. However, there were no group differences in the total GEV, and no effects of retreat training on total GEV or the proportion of GEV explained by a particular microstate configuration. They also indicate that GEV does not seem to differ between compassion meditation and quiet rest.

Mean Microstate Duration

We next examined Retreat 1 parameters for changes in microstate duration—the average amount of time a given microstate configuration remains dominant when it appears in the microstate timeseries. Type III tests of fixed effects indicated that there was not a significant effect of group, F(1, 57.99) = 1.76, p = .190, assessment, F(2, 807.72) = 2.17, p = .115, or interaction between group and assessment, F(2, 807.72) = 2.14, p = .118. There was a significant main effect of configuration, F(4, 807.72) = 168.27, p < .001, and interaction between group and configuration, F(4, 807) = 6.91, p < .001, but no interaction between assessment and configuration, F(8, 807) = 0.21, p = .989, or three-way interaction between group, assessment, and configuration, F(8, 807) = 0.15, p = .996. A simplified model was then created removing non-significant terms. The model parameters from this simplified model are reported in Table 3.8. Briefly, in both groups, configuration C showed a longer average duration than any other microstate configuration (controls: all *ps* < .001, training: all *ps* < .001), had a longer absolute duration in the control group than in the retreat group (p < .001) and was longer relative to other microstates in the control group than in the retreat group (all *ps* < .01).

In Retreat 2, type III tests of fixed effects indicated a significant main effect of status, F(1, 828.90) = 16.78, p < .001, assessment, F(2, 826.06) = 9.53, p < .001, and configuration, F(4, 826.06) = 212.82, p < .001, as well as a significant interaction between status and assessment, F(2, 826.06) = 6.78, p = .001. There was no interaction between status and configuration, F(4, 826.06) = 0.13, p = .971, or assessment and configuration, F(8, 826.06) = 0.130.49, p = .864, nor was there a three-way interaction between status, assessment, and configuration, F(8, 826.06) = 0.25, p = .980. A simplified model including only significant terms was created. Parameters from this simplified model are reported in Table 3.8, and marginal estimated means of key effects are described here, referenced to configuration C. At the preretreat assessments, the estimated marginal means of duration for Retreat 2 participants in training, *EMMtraining*, pre = 90.19, 95% CI [87.79, 92.60], versus as Retreat 1 waitlist controls, *EMMcontrol, pre* = 89.83, 95% CI [87.44, 92.21], did not significantly differ, b = 0.37, SE = 0.82, t(847.04) = 0.45, p = .655. Participants did not demonstrate change in mean duration as waitlist controls: estimated marginal means at the mid-retreat assessment, EMM = 88.68, 95% CI [86.30, 91.07], did not significantly differ from at the pre-retreat assessment, b = -1.14, SE = 0.80, t(846.07) = -1.41, p = .158; nor did estimated marginal means at the post-retreat assessment, EMM = 90.43, 95% CI [88.04, 92.81], b = 0.60, SE = 0.80, t(846.07) = 0.74, p = 0.74

.457. However, when in training in Retreat 2, participants demonstrated significantly reduced duration at the mid-retreat, *EMM* =86.30, 95% CI [83.89, 88.69], *b* = -3.90, *SE* = 0.82, *t*(846.06)= -4.74, *p* < .001, and post-retreat, *EMM* = 86.58, 95% CI [84.18, 88.98], *b* = -3.61, *SE* = 0.82, t(846.06) = -4.39, *p* < .001, than at pre-retreat.

Additional models comparing compassion meditation to rest did not indicate any effect of condition, F(2, 2536.10) = 0.37, p = .692, or interaction between condition and any other effect. However, when including this extra data, a significant group by assessment interaction did emerge in Retreat 1, F(2, 2537.20) = 4.75, p = .009, and was maintained in Retreat 2, F(2, 2535) = 13.97, p < .001, replicating the pattern observed in the Retreat 2 compassion meditation only model. Type III tests fixed effects from these models are reported in Table 3.12.

Overall, these results demonstrate a baseline between groups difference in the average duration of configuration C, as well as the duration of configuration C relative to other configurations, with configuration C demonstrated longer average and relative durations in the waitlist control group compared to the Retreat 1 training group. Additionally, they suggest that duration might be sensitive to retreat training as mean duration decreased over the course of Retreat 2. However, these findings did not reliably replicate across retreats. Finally, models comparing compassion meditation to pre- and post-meditation rest indicated no effect of condition, indicating that duration, and retreat-related change in duration, did not vary by task.

Occurrence per Second

We next tested the average occurrence per second of each microstate configuration. In Retreat 1, type III tests of fixed effects indicated no main effect of group, F(1, 58.11) = 3.96, p =.051, or assessment, F(2, 809.78) = .43, p = .652, or interaction between group and assessment, F(2, 809.78) = 0.13, p = .118, or three-way interaction between group, assessment, and

configuration, F(8, 807) = 0.15, p = .882. There was a significant effect of configuration, F(4, 807.23) = 138.68, p < .001, as well as a significant interaction between group and configuration, F(4, 807.23) = 5.14, p < .001, but no interaction between assessment and configuration, F(8, 807.23) = 0.75, p = .646. A simplified model was created removing non-significant effects. Model parameters from this simplified model are reported in Table 3.9. Briefly, microstate configuration C occurred more times per second on average than any other configuration in both the control (all ps < .001) and training (all ps < .008) groups. Compared to the control group, the training group had more occurrences per second of microstate configurations A (p < .001), B (p = .002), and D (p < .001) relative to the occurrence of microstate C.

Consistent with this, in Retreat 2, the main model indicated a significant effect of configuration, F(4, 826.33) = 204.72, p < .001, but no main effect of status, F(1, 835.08) = 2.84, p = .092, or assessment, F(2, 826.33) = 1.25, p = .287, or interaction between status and assessment, F(2, 826.33) = 0.39, p = .678, status and configuration, F(4, 826.33) = 0.30, p = .879, assessment and configuration, F(8, 826.33) = 1.10, p = .359 or status, assessment, and configuration, F(8, 826.33) = 0.37, p = .937. Model parameters from the simplified model retaining only the effect of configuration are reported in Table 3.9. These parameters indicated that configuration C occurred more times per second on average than did any other configuration (all ps < .001).

Models incorporating data from pre- and post-meditation rest for each retreat did not indicate any effect of condition, or interaction with condition with any other factor. Solutions for type III tests of fixed effects for these models can be found in Table 3.13.

Overall, these results indicate that microstate configuration C occurred more times per second on average than any other microstate, and that this difference relative to other microstates
was greater in the waitlist controls than in the Retreat 1 training group. They also suggest that condition (rest versus meditation) did not influence occurrence per second.

Global Field Power

Finally, we assessed mean global field power at the fitted GFP peaks. In Retreat 1, Type III tests of fixed effects indicated significant main effects of group, F(1, 58) = 7.80, p = .007, assessment, F(2, 807.06) = 12.58, p < .001, and configuration, F(4, 807) = 112.17, p < .001, as well as a significant interaction between group and configuration, F(4, 807) = 6.87, p < .001. There was not a significant interaction between group and assessment, F(2, 807.06) = 1.76, p =.173, assessment and configuration, F(8, 807) = 0.28, p = .974, or group, assessment, and configuration, F(8, 807) = 0.04, p = .999. Parameter estimates from a simplified model removing non-significant interactions are presented in Table 3.10 and marginal estimated means of key effects are described here, with all effects centered to configuration C. Across all assessments, the training group had significantly lower GFP than did the waitlist control group, b = -1.65, SE = 0.46, t(62.18) = -3.61, p < .001. However, both groups demonstrated the same pattern of change, with all participants showing reductions in GFP from the pre-retreat, *EMMtraining* = 6.30, 95% CI [5.65, 6.95], EMMcontrol = 7.95, 95% CI [7.30, 8.60], to mid-, EMMcontrol = 7.75, 95% CI [7.10, 8.40], EMMtraining = 6.10, 95% CI [5.45, 6.75], retreat assessment, b = -0.20, SE = 0.05, t(825) = -3.91, p < .001, and from the pre- to post-, EMM control = 7.70, 95%CI [7.05, 8.35], *EMMtraining* = 6.05, 95% CI [5.41, 6.70], retreat assessment, b = -0.25, SE = -0.25, S0.05, t(825) = -4.73, p < .001.

In Retreat 2, type III tests of fixed effects showed main effects of status, F(1, 826.22) =7.17, p = .008, assessment, F(2, 825.99) = 5.39, p = .005, and configuration, F(4, 825.99) =126.66, p < .001. There were no significant interactions between status and assessment, F(2, 825.99) = 825.99) = 0.91, p = .404, status and configuration, F(4, 825.99) = 0.02, p = .999, assessment and configuration, F(8, 825.99) = 0.24, p = .984, or status, assessment, and configuration, F(8, 825.99) = 0.05, p = 1. A simplified model consisting of only main effects was created. Parameter estimates from this model are reported in Table 3.10, and estimated marginal means are reported here, referenced to configuration C. Compared to themselves as waitlist controls, Retreat 2 participants showed significantly lower GFP when in training, b = -0.13, t(848.22) = -2.71, p =.007. However they demonstrated the same pattern of GFP reductions as waitlist controls and in retreat training. This reduction fell short of our p = .01 significance cut-off from the pre-, *EMMcontrol* = 7.76, 95% CI [6.97, 8.55], *EMMtraining* = 7.62, 95% CI [6.99, 8.56], to mid-, *EMMcontrol* = 7.76, 95% CI [6.97, 8.55], *EMMtraining* = 7.62, 95% CI [6.83, 8.41] retreat assessments, b = -0.15, SE = 0.06, t(847.99) = -2.54, p = .011, but was significant when comparing the pre-, and post-, *EMMcontrol* = 7.72, 95% CI [6.93, 8.51], *EMMtraining* = 7.58, 95% CI [6.80, 8.38] retreat assessments, b = -0.19, SE = 0.06, t(847.99) = -3.13, p = .002.

We then tested models comparing compassion meditation to the pre- and post-meditation resting periods. As these were targeted models created to examine the effect of condition, we report only effects that directly pertain to condition here. A full report of type III tests of fixed effects for these models can be found in Table 3.14, and all parameter estimates from subsequent simplified models are presented in Table 3.15.

In Retreat 1, there was a significant main effect of condition, F(2, 2537) = 63.13, p < .001, and a significant interaction between assessment and condition, F(4, 2537) = 4.58, p = .001. Additionally, there was a significant main effect of group, F(1, 58) = 7.84, p = .007, and a significant interaction between group and assessment, F(2, 2537) = 5.12, p = .006, replicating the pattern in the compassion only model. Parameter estimates from a simplified model retaining

only significant effects indicated that at the Retreat 1 pre-assessment, GFP during compassion meditation in both the control *EMMcontrol* = 7.95, 95% *CI* [7.29, 8.61], and training *EMMtraining* = 6.36, 95% *CI* [5.70, 7.02] groups was significantly lower than during premeditation, *EMMcontrol* = 8.41, 95% *CI* [7.75, 9.07], *EMMtraining* = 6.82, 95% *CI* [6.16, 7.48], b = 0.46, SE = 0.06, t(2607) = 7.67, p < .001, or post-meditation rest, *EMMcontrol* = 8.26, 95% *CI* [7.60, 8.92], *EMMtraining* = 6.67, 95% *CI* [6.01, 7.33], b = 0.31, SE = 0.06, t(2607) = 5.16, p < .001. This pattern was maintained at subsequent assessments, though GFP in premeditation rest declined significantly more than in compassion meditation from pre- to midretreat, b = -0.26, SE = 0.08, t(2607) = -3.10, p = 0.002.

Retreat 2 analyses replicated these patterns. In Retreat 2, the omnibus model again indicated a main effect of condition, F(2, 2536) = 41.21, p < .001, and an interaction between assessment and condition, F(4, 2536) = 3.74, p = .004. However the status by assessment interaction originally observed in the compassion only model fell just short of our significance cut-off, F(2, 2536) = 4.52, p = .011. A simplified model retaining only significant effects indicated that participants demonstrated significantly lower GFP at the pre-retreat assessment during compassion meditation, *EMMcontrol* = 7.99, *95% CI* [7.20, 8.78], *EMMtraining* = 7.76, *95% CI* [6.96, 9.25] than in pre-meditation rest, *EMMcontrol* = 8.46, *95% CI* [7.67, 8.92], *EMMtraining* = 8.23, *95% CI* [7.43, 9.02], b = 0.47, SE = 0.07, t(2612) = 6.89, p < .001, and post-meditation rest, *EMMcontrol* = 8.33, *95% CI* [7.53, 9.12], *EMMtraining* = 8.10, *95% CI* [7.30, 8.89], b = 0.34, SE = 0.07, t(2612) = 4.94, p < .001. As in Retreat 1, this pattern was maintained across assessments, though GFP declined significantly more from the pre- to midretreat assessment during pre-meditation rest than during compassion meditation, b = -0.28, SE = 0.01, t(2612) = -2.87, p = 0.004.

In summary, these results demonstrate that GFP consistently decreased across assessments. This decrease occurred in both waitlist control and training participants, suggesting that it was not specific to retreat training. However training participants did demonstrate overall lower GFP than did waitlist controls both when comparing groups in Retreat 1, and when comparing controls to themselves in training in Retreat 2. GFP decreased over assessments regardless of whether participants were engaging in compassion meditation or quiet rest. However, GFP was lower overall during compassion meditation than during pre- or postmeditation rest. Finally, GFP appeared to decrease more from pre- to mid-retreat during premeditation rest than during compassion meditation.

Multivariate Distance Regression of Sequence Dissimilarities

Retreat 1

We first modeled the main effects of group (waitlist control, training), assessment (pre, mid, post), and epoch (close other, difficult other, all other) on sequence dissimilarities in Retreat 1. This model indicated that sequences were not significantly different between groups, *stat* = 0.95, p = .740. Across all groups and epochs, sequences were significantly different between the pre- to mid-retreat assessments, *stat* = 1.48, p < .001. However, differences in sequences between the pre- and post-retreat assessments were not significantly differed from both in the difficult other, *stat* = 2.76, p < .001, and all others, *stat* = 1.42, p < .001 epochs. We next expanded this model to examine pairwise interactions between predictors. This model included all two-way interactions. This second-level model indicated that the groups had significantly different stat = 1.15, p = .033) but not from the pre- to post-retreat assessments (*stat* = 1.10, p = .094). None of

the two-way interactions between group and epoch or assessment and epoch were significant (all ps > .387). Finally, a model including the three-way interactions between group, assessment, and epoch was tested. This model indicated that there were no significant three-way interactions (all ps > .288).

We followed up on significant effects from these models with directed comparisons of dissimilarities calculated within each group, and examined centroid distances—a measure of dissimilarity between multivariate distance centers—and discrepancies—a measure of between-person variability within a given condition—to aid interpretation (Zanesco et al., 2021). For a map of pairwise dissimilarities in Retreat 1, see Figure 3.3; for matrix of centroid distances, see Figure 3.4, panel A.

In the waitlist control group, the effect of assessment collapsing across epochs indicated that sequences differed significantly between the pre- and mid-retreat assessments, *stat* = 1.27, *p* = .007, but not between the pre- and post-retreat assessments, *stat* = 1.09, *p* = .168. Consistent with this, the centroid distance between the pre- and mid-retreat assessments, *centroid distance* = 642.85, was greater than the centroid distance between the pre- and post-retreat assessments, *centroid distance* = 598.85. Discrepancies were very similar between the pre-, *discrepancy* = 2,957.49, and mid-retreat, *discrepancy* = 2,927.53, assessments, and slightly lower at the post-retreat assessment, discrepancy = 2,887.07, indicating similar levels of between-subject variability at pre- and mid-retreat, with slightly lower between-person variability by post-retreat. Collapsing across assessments, sequences during the close other epoch were significantly differ from sequences during the all others epoch, *stat* = 1.11, *p* = .121. Consistent with this, centroid distances between the close other and difficult other epochs, *centroid distance*

= 627.63, were greater than between the close other and all others epochs, *centroid distance* = 586.59. Discrepancies were similar between the close other, discrepancy = 2,835.88, and all others, discrepancy = 2,816.24, epochs, but were higher in the difficult other epoch, discrepancy = 3117.32. This indicates that sequences during the difficult other epoch had greater between-subject variability.

In the training group, sequences at the pre-retreat assessment were significantly different from sequences at the mid-retreat assessment, stat = 1.32, p = .002, but not from sequences at the post-retreat assessment, stat = 1.16, p = .052. Consistent with this, the centroid distance between sequences at pre- and sequences at mid-retreat, *centroid distance* = 610.38 was slightly larger than the centroid distance from pre- to post-retreat, *centroid distance* = 606.85. Discrepancies were similar at the pre-, discrepancy = 2,856.39, mid-, discrepancy = 2,845.35, and post-retreat, discrepancy = 2,878.57 assessments, indicating similar levels of between-subjects variability in microstate sequences. Comparing meditation epochs, sequences during the close other epoch were significantly different from sequences during the difficult other, stat = 2.47, p < .001, and all others, stat = 1.33, p = .002, epochs. An examination of centroid distances showed a greater distance between the close other and difficult other epochs, *centroid distance* = 663.97, than between the close and all others epochs, *centroid distance* = 599.08. Discrepancies once again indicated higher levels of between-subjects variability in the difficult other epoch, *discrepancy* = 3,063.37, than in the close other, discrepancy = 2,759.50, or all others, discrepancy = 2,738.65, epochs.

Retreat 2

We next tested for sequence dissimilarities as a function of our predictors in Retreat 2. These analyses compared Retreat 1 waitlist controls to themselves in training during Retreat 2. The initial main effects model indicated a significant difference in microstate sequences as a function of participants' status as waitlist controls versus as training participants, *stat* = 1.39, p < .001. Sequences also differed as a function of assessment, with significant differences between the pre- and mid-retreat assessments, *stat* = 1.83, p < .001, and the pre- and post-retreat assessments, *stat* = 1.25, p = .003. Finally, sequences differed as a function of epoch: the close other epoch significantly differed from both the difficult other, *stat* = 2.11, p < .001, and all others, *stat* = 1.32, p < .001, epochs. The second model incorporating all two-way interactions indicated that participants showed different patterns of dissimilarities from the pre- to mid-retreat assessments, *stat* = 1.32, p < .001, and the pre- to post-retreat assessments, *stat* = 1.69, p < .001, when they were training participants versus when they were waitlist controls. There were no significant two-way interactions between status and epoch, or assessment, and epoch, all ps > .399. Finally, we tested for three-way interactions between status, assessment, and epoch. This third model found no significant three-way interactions, all ps > .268.

We then conducted directed comparisons within the Retreat 2 training group. For a map of pairwise dissimilarities in Retreat 2, see Figure 3.3; for matrix of centroid distances, see Figure 3.4, panel A. For directed comparisons in these participants as waitlist controls, see Retreat 1 analyses above. Comparisons collapsing the effect of assessment across epochs indicated that Retreat 2, participants' microstate sequences significantly differed between the pre- and mid-retreat, *stat* = 2.36, p < .001, and the pre- and post-retreat, *stat* = 2.27, p < .001, assessments. The centroid distance between the pre- and mid-retreat assessments, *centroid distance* = 731.28, was slightly larger than between the pre- and post-retreat assessments, *centroid distance* = 712.67, while discrepancies were similar at the pre-, *discrepancy* = 2,900.90, mid-, *discrepancy* = 2,955.37, and post-retreat, *discrepancy* = 2,926.40 assessments, indicating similar levels of between-subjects variability. Across assessments, the close other epoch was significantly different from both the difficult other, stat = 2.07, p < .001, and all others, stat = 1.26, p = .008, epochs. The centroid distance between the close other and difficult other epochs, *centroid distance* = 661.50, was greater than between the close other and all others epochs, *centroid distance* = 613.13. Consistent with Retreat 1 findings, discrepancy in the difficult other epoch, *discrepancy* = 3,105.82, was larger than in the close other, discrepancy = 2842.66 or all others, *discrepancy* = 2835.41, epochs, indicating that sequences in this epoch demonstrated greater between-subjects variability.

Sensitivity Analysis

Finally, we conducted a sensitivity analysis to confirm that observed dissimilarities were not a function of different sequence lengths across the different epochs. To do this, all files were truncated to the length of the longest file in the shortest epoch (e.g., the length of a close other file with no artifacts removed, 3 min 39.69 seconds), and then all analysis steps were repeated on these shortened files. In Retreat 1, results from all models were consistent with the findings from models of the full length data. Sequences were not significantly different between groups, *stat* = .961, p = .693, but across groups were significantly different from pre- to mid-retreat, *stat* = 1.48, p < .001, though not from mid- to post-retreat, *stat* = 1.12, p = .056. Importantly, the differences between epochs was maintained, with sequences in the close other epoch significantly differing from sequences in the difficult other, *stat* = 1.56, p < .001, and all others, *stat* = 1.46, p < .001, epochs. The model incorporating two-way interactions indicated a significant interaction between group and assessment at the mid-retreat assessment, *stat* = 1.15, p = 0.029. No other interactions reached significance, all ps > .085. Finally, the model incorporating interactions between group, assessment, and epoch indicated that there were no significant three-way interactions, all ps > .340.

In Retreat 2, results were once again consistent with findings from the models of the full length data. The main effects model indicated significant differences between microstate sequences when participants were waitlist controls versus training participants, *stat* = 1.42, *p* < .001. Across statuses, sequences differed as a function of assessment: sequences at the pre-retreat assessment were significantly different from sequences at the mid-, *stat* = 1.84, *p* < .001, and post-retreat, *stat* = 1.27, *p* = .002, assessments. Importantly, these standardized-length sequences also differed between epochs: the close other epoch significantly differed from both the difficult other, *stat* = 1.24, *p* = .004, and all others, *stat* = 1.36, *p* < .001, epochs. The model incorporating two-way interactions indicated a significant interaction between status and assessment at the mid-, *stat* = 1.30, *p* = .001, and post-retreat, *stat* = 1.67, *p* < .001, assessments. No other two-way interactions were significant, all *ps* > .431. The final model incorporating three-way interactions found no significant interactions between status, assessment, and epoch, all *ps* > .344.

As a whole, these models suggest that observed effects reported in the main analysis are not due to differences in sequence lengths between meditation epochs.

Discussion

Overview

In a waitlist-controlled study, we found shifts in the duration, strength, and temporal patterning of EEG microstates while experienced meditators engaged in a guided compassion meditation. We also found consistent differences in the temporal sequencing of microstates as a function of who participants were generating compassion for (a close other, a difficult other, all others). Microstates were derived by segmenting continuous EEG into sequences of quasi-stable categorical configurations reflecting moments of phase-synchronized network activity, and were examined for changes over the course of two 3-month long retreats. Our findings corroborate evidence from previous studies suggesting that a central effect of intensive retreat-based meditation training is a global shift toward increased neural flexibility and excitability (Saggar et al., 2012; Skwara et al., *in revision*; Zanesco et al., 2021). Additionally, to our knowledge they provide the first neural evidence that the mental operations evoked when generating compassion may vary based on who the compassion is directed toward.

Discussion of Core Findings

Data-driven clustering identified five global centroids that best accounted for the variance in topographic voltage patterns across our 267 EEG recordings. The topographic configurations of these centroids matched up well with canonical microstate configurations A through E that have been identified in prior research (see Michel & Koenig, 2018 for a review). While these five global centroids together accounted for the majority of observed topographic variance in the recording-level centroids in clustering (~83%), and in both the global field power peaks (~71%) and the continuous time series (~57%) in fitting, an appreciable proportion of the variance went unexplained. Thus, while the set of global centroids chosen met the criterion of explaining the most variance with the minimum number of configurations at the group level, it is possible that other microstate configurations not included in this set—or selection criteria favoring specificity over generalizability (e.g., Koenig et al., 2014)—would have better explained variance in individual files or demonstrated relevance to meditation-related processes.

Of these five global configurations, microstate C explained the greatest proportion of observed variance, had the longest duration, occurred most frequently, and had the strongest global field power. This was true across waitlist control and training participants in both retreats,

and is consistent with patterns observed in large-scale studies of normative populations (e.g., Koenig et al., 2002; Zanesco et al., 2020) as well as for a previous analysis of these same participants during eyes closed rest (Zanesco et al., 2021). Although there were group differences in the predominance of configuration C in Retreat 1—with the waitlist control group showing greater differences between microstate C and other configurations—these differences were present at the pre-retreat assessment and did not change with training, suggesting that they were likely due to baseline individual differences between groups. Supporting this assertion, these group differences were not identified when comparing waitlist controls to themselves in Retreat 2 training.

We did not find any configuration-specific training effects, suggesting that the retreatrelated changes observed in the current study did not differentially affect specific microstate configurations and their underlying generators. This implies that changes captured by the current analysis are likely related to global shifts in brain dynamics regulating arousal or excitability (Michel & Koenig, 2018; Zanesco et al., 2021).

Across configurations, we observed longitudinal reductions in microstate duration and strength during compassion meditation. Decreases in duration appeared to be specific to training participants, but this effect was not consistent across the two retreat interventions. This finding indicates that microstate duration may be sensitive to retreat training, but lacks the robust evidence offered by replication across retreats. Global field power—or the strength of a given microstate—showed consistent reductions over the course of the retreats. These reductions were not specific to participants in retreat training—they were also present in the waitlist control group. Training participants did, however, display lower microstate strength overall comparing between subjects in Retreat 1, as well as within subjects in Retreat 2. Thus while the pattern of

longitudinal change did not appear to differ by groups, the average level was lower in training participants. It is possible that there was, in fact, a training-related difference the trajectories of microstate strength, but we lacked the statistical power to detect it. Supporting this possibility, we found that retreat participants had greater overall reductions in global field power in models incorporating pre- and post-meditation rest. It is also possible that observed reductions in the strength of microstates were related to repeated practice of the guided compassion meditation rather than to the retreat intervention, and would therefore be expected to be present in both groups. Alternatively, the observed reductions could be due to factors unrelated to training or compassion meditation, such as increasing comfort with the testing paradigm or familiarity with the retreat center.

Irrespective of the source of the change, reductions in microstate durations suggest less momentary stability in underlying neural generators (Khanna et al., 2015), while reductions in the peaks of global field power can be interpreted as a reflection of fewer phase-synchronized neurons contributing to the overall strength of a given topographic configuration (Zanesco et al., 2021). Together, these patterns are indicative of more labile microstate dynamics. This lability may reflect greater present-centered awareness (Zanesco et al., 2021) and greater flexibility of dynamical neural systems that must balance the integration and segregation of information (e.g., Deco et al., 2011; Bressler & Kelso, 2016).

Notably, these patterns of change appear similar to those found in a recent analysis of resting EEG in these same participants (Zanesco et al., 2021). In that study, EEG collected during 2 minutes of eyes-closed rest showed training-related reductions in microstate duration and strength. Consistent with this, in the present data we found no discernable differences between compassion meditation and quiet rest in the proportion of topographic variance

explained by the global centroids, nor in microstate duration or frequency of occurrence. One parameter did distinguish compassion meditation from rest: microstate strength. Participants across both retreats demonstrated lower overall global field power during compassion meditation than during rest, regardless of whether they were in training or acting as waitlist controls. While global field power was lower during meditation, microstate strength demonstrated larger decreases from the beginning to the middle of the retreats during pre-meditation rest than it did during compassion meditation.

Global field power is thought to reflect the degree of neural synchronization within underlying generators, while microstate topography is primarily driven by activity in the alpha envelope (Milz et al., 2017). Compassion meditation is presumably a more directed mental activity than uninstructed rest. As such, the current observation of lower global field power during compassion meditation compared to rest would be broadly consistent with the wellestablished pattern of task-related increases in alpha desynchronization (e.g., Klimesch et al., 1998; Klimesch, 1999; Pfurtscheller et al., 1996). It is, however, inconsistent with the offreported observation of increased alpha power during meditation compared to rest (for a review, see Cahn and Polich, 2006). One possible interpretation is that the patterns observed in microstate parameters in the current study are more related to changes in general neurocognitive systems than to any compassion meditation-specific effects or neural generators. Indeed, this would be unsurprising given that microstate analysis 1) assumes the presence of global (nontask-specific) brainstates and 2) is concerned with capturing the broad dynamics of these global brainstates rather than variations within them (Michel & Koenig, 2018).

Consistent with this interpretation, when we employed multivariate sequence analysis an approach better-suited to capturing shifts in the temporal dynamics of microstates—we were

able to identify more nuanced changes in the microstate syntax. This analysis revealed trainingrelated differences in microstate sequences, and was able to distinguish sequences as a function of the target of compassion. Sequence dissimilarities tended to be more pronounced from the beginning to the middle of retreat than from the beginning to the end. We have observed this in previous analyses of EEG data in these same participants (Saggar et al., 2012; Skwara et al., *in revision*), though not consistently so. Additionally, while the training and control groups displayed different patterns of change, the direction of these differences was not consistent between retreats. In Retreat 1, the waitlist controls demonstrated more dissimilar sequences from pre- to mid-retreat than did the training group. However when these participants completed the training intervention in Retreat 2, they displayed greater dissimilarities from the pre- to midretreat assessments, as well as significant changes from the pre- to post-assessments. This suggests that at least some of the sequence differences we observed are due to practice effects of repeated engagement with the guided compassion meditation.

The strongest effect emerged when comparing microstate sequences generated during epochs of the meditation that instructed participants to focus on different targets of compassion. In line with our prediction that mental operations—and thus microstate patterns—should vary with the target of compassion, we found that sequences differed as a function of compassion meditation epoch (close other, difficult other, all others). This was true across retreats and groups – training status did not modulate this effect. However, despite our prediction that mental representations of close and difficult others should become less differentiated over retreat, we found no evidence that the similarities of these epochs reliably changed with training. Across all assessments and groups, sequences during the difficult other epoch demonstrated the highest dissimilarity from other epochs (Figure 3.3; Figure 3.4). This remained the case when controlling

for differences in sequence lengths between epochs. As the epochs were always presented in the same order, one possibility is that differences between epochs could reflect deepening states of absorption (e.g., Faber et al., 2017; Schoenberg et al., 2019). While we cannot rule out this possibility, it seems unlikely as difficult other, which consistently had the highest dissimilarity with the other two epochs, was the middle epoch of the meditation.

Sequences during the difficult other epoch also demonstrated the greatest discrepancies, meaning that the sequences within this epoch showed the most dispersion around their multivariate distance center. This suggests this epoch evoked the most variable mental activity between subjects. This could potentially reflect variation from a number of sources. For instance, it is possible that participants took more varied approaches to the generation of compassion for a difficult person, given the ostensible greater difficulty of this task. Indeed, practitioners are often instructed to engage in more elaborative storytelling, such as imagining the difficult other as a baby, to assist in overcoming feelings of resistance to compassion (e.g., Wallace, 1999). Though the guided meditation did not include these details, all of the participants in this study were experienced meditators and likely had practice with these more elaborative techniques. Another possibility is that imagining the suffering of difficult others elicited more varied emotional or cognitive reactions, including feelings of schadenfreude, indifference, or resistance, that are less likely to be triggered in the close or all others epochs. However, while these are tempting explanatory theories, without detailed phenomenological reporting it is impossible to truly know if participants undertook a greater range of mental activities in this epoch, or if this could account for the observed variability.

A recent theoretical account has proposed that compassion-based contemplative practices may influence real-world compassionate behaviors by simulating the experience of encountering

suffering and responding with compassion as if it were actually happening (Wilson-Mendenhall, 2021). By using vividly-imagined scenarios of suffering and compassionate action to engage the neurocognitive networks involved in compassionate responding, these practices may prime the practitioner to act compassionately when they encounter these scenarios in daily life. Following on this, if we consider each microstate to reflect a moment of cognition (Changeux and Michel, 2004), and a sequence of microstates a representation of the evolution of these moments as they unfold over time, our current findings suggest that the mental simulations undertaken when generating compassion for varying classes of others are distinct from one another, particularly in the case of the difficult other. While this does not provide insight into the exact neurocognitive processes at play, it establishes microstate sequence analysis as a potentially useful tool for examining the similarity of the simulations ostensibly undertaken when generating compassion for varying classes of others.

Previous findings in these same participants demonstrating increases in other-oriented care and concern (Rosenberg et al., 2015) and greater self-relevance of others' suffering (King et al., *in prep*). Despite this, the current findings offer no evidence that three months of intensive meditation training reduced differentiation between close and difficult others. Other recent works have pointed out the dualistic view of compassion that is embedded in much of Western compassion training and research (Quaglia et al., 2021), and have called for a return to the relational core of compassion training to overcome barriers to compassion (Condon & Makransky, 2020). The current data demonstrate that these are essential questions to grapple with if we are to take seriously the project of learning to collectively expand our circles of care.

Strengths, Limitations, and Future Directions

The current study conveys several strengths. The waitlist control design includes a builtin replication in the form of Retreat 2, allowing greater confidence in findings that are consistent across both retreat interventions. Further, the intensity of the intervention itself potentially allows us to identify effects that may not be obvious in less immersive settings. The current analysis includes direct comparisons between rest and meditation, which allows for greater interpretability of training effects. Finally, the richness of data available on this cohort of participants allows for a rare level of contextualization of the data in the present analysis. Crucially, all core analyses were preregistered, offering transparency and increased confidence in the observed effects.

There are also a number of limitations to the current analysis. This study relies on a relatively small sample size of experienced meditators. This means that we may not have the statistical power to detect smaller effects, and our results may be specific this population. Additionally, the compassion meditation epochs proceeded in the same order for all participants at all assessments. This means that we cannot rule out the possibility that observed sequence differences are driven by order effects. The choice of microstate analysis as a method also implies several limitations. In preparation for microstate analysis, continuous EEG data are subjected to a high degree of filtering and downsampling, which may mask effects that are carried by higher frequency bands or unfold on a faster timescale. Indeed, microstate topographies are thought to primarily reflect activity in the alpha envelope (Milz et al., 2017), but meditation training has been shown to influence oscillatory activity across a broad range of frequencies (Cahn & Polich, 2006; Lomas et al., 2015) including the gamma band (e.g., Lutz et al., 2004; Schoenberg et al., 2018). In the current analysis, we defined our global centroids

across all conditions, meditation epochs, assessments, and groups. This enabled us to compare across these factors, but also means that our analysis would be insensitive to topographic reconfigurations such as have been recently observed following meditation training (Brechet et al., 2021).

One way to examine topographic variation, while still maintaining the ability to compare parameters and sequences across groups, would be to examine the spatial correlations between centroid topographies from each group of participants that were assigned to the same global cluster. Additionally, tests to see if the current findings have any relationship to compassionrelevant behavioral or self-report measures would help to clarify our interpretations. Generally, a primary challenge in studying brain activity during meditative practices is that it is impossible to know exactly what a person is doing at any given moment, particularly without in-depth phenomenological reporting (e.g., Kok & Singer, 2017; Petitmengin et al., 2019; Przyrembel & Singer, 2018). Including approaches that address the phenomenological gap between third and first person measures may be an important aspect of future studies attempting to capture and interpret the variation and richness of meditative experience (Lutz et al., 2015; Lutz & Thompson, 2003; Varela, 1996).

Conclusion

The current study adds to a series of findings from these residential retreat interventions that demonstrate task-general changes in large-scale brain processes that may regulate network excitability. These changes appear to permeate across quiet rest (Skwara et al., *in revision*; Zanesco et al., 2021), concentrative breath meditation (Saggar et al., 2012), and guided compassion meditation. As a whole, these studies offer converging evidence that a primary effect of this intensive retreat training is a generalized increase in the lability and sensitivity of

neurocognitive systems, which may in turn support greater flexibility in responding to the demands of the present moment (Bressler & Kelso, 2016; Zanesco et al., 2021). We also present the first-known evidence that epochs of compassion meditation can be distinguished based on the target of compassion. This establishes microstate sequence analysis as a potentially useful tool for quantifying some aspects of the mental operations engaged during compassion generation for various others. While these findings should be considered preliminary, they may have implications for approaches to training compassion, particularly when working to extend the circle of care.

References

- Abbott, A., & Tsay, A. (2000). Sequence analysis and optimal matching methods in sociology: Review and prospect. *Sociological Methods & Research, 29(1)*, 3-33. https://doi.org/10.1177/0049124100029001001
- Allport, G. (1954). The nature of prejudice. Addison-Wesley.
- Ashar, Y. K., Andrews-Hanna, J. R., Yarkoni, T., Sills, J., Halifax, J., Dimidjian, S., & Wager, T. D. (2016). Effects of compassion meditation on a psychological model of charitable donation. *Emotion*, 16(5), 691.
- Ashar, Y. K., Andrews-Hanna, J. R., Halifax, J., Dimidjian, S., & Wager, T. D. (2021). Effects of compassion training on brain responses to suffering others. *Social Cognitive and Affective Neuroscience*, 16(10), 1036-1047.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology, 59*, 617–645. https://doi.org/10.1146/annurev.psych.59.103006.093639
- Barsalou, L. W. (2009). Simulation, situated conceptualization, and prediction. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1521), 1281–1289. https://doi.org/10.1098/rstb.2008.0319
- Bates D, Mächler M, Bolker B, Walker S (2015). "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software*, 67(1), 1–48. doi: <u>10.18637/jss.v067.i01</u>.
- Belouchrani, A., Abed-Meraim, K., Cardoso, J. F., & Moulines, E. (1997). A blind source separation technique using second-order statistics. *IEEE Transactions on Signal Processing*, 45(2), 434-444. <u>https://doi.org/10.1109/78.554307</u>
- Blackburn, S. (2003). Ethics: A very short introduction (Vol. 80). Oxford University Press.
- Böckler, A., Tusche, A., Schmidt, P., & Singer, T. (2018). Distinct mental trainings differentially affect altruistically motivated, norm motivated, and self-reported prosocial behaviour. *Scientific Reports*, 8(1), 1–14. https://doi.org/10.1038/s41598-018-31813-8
- Brechet, L., Brunet, D., Birot, G., Gruetter, R., Michel, C. M., & Jorge, J. (2019). Capturing the spatiotemporal dynamics of task-initiated thoughts with combined EEG and fMRI. *Neuroimage*, 194, 82-92. https://doi.org/10.1016/j.neuroimage.2019.03.029
- Bréchet, L., Ziegler, D. A., Simon, A. J., Brunet, D., Gazzaley, A., & Michel, C. M. (2021). Reconfiguration of electroencephalography microstate networks after breath-focused, digital meditation training. *Brain Connectivity*, 11(2), 146-155.

- Bressler, S. L., & Kelso, J. A. S. (2016). Coordination dynamics in cognitive neuroscience. *Frontiers in Neuroscience*, 10, 397. https://doi.org/10.3389/fnins.2016.00397
- Bressler, S.L., & Menon, V. (2010). Large-scale brain networks in cognition: emerging methods and principles. *Trends in Cognitive Sciences*, 14, 277–290.
- Brewer, M. B. (1999). The psychology of prejudice: Ingroup love or outgroup hate?. *Journal of Social Issues*, *55*, 429-444.
- Brown, R. (2011). Prejudice: Its social psychology. John Wiley & Sons.
- Brunet, D., Murray, M. M., & Michel, C. M. (2011). Spatiotemporal analysis of multichannel EEG: CARTOOL. Computational Intelligence and Neuroscience, 2011, 2. https://doi.org/10.1155/2011/813870
- Cahn, B. R., & Polich, J. (2006). Meditation states and traits: EEG, ERP, and neuroimaging studies. *Psychological Bulletin*, 132(2), 180-211. https://doi.org/10.1037/00332909.132.2.180
- Changeux, J. P., & Michel, C. M. (2004). Mechanisms of neural integration at the brain-scale level: The neuronal workspace and microstate models. In S. Grillner & A. M. Graybiel (Eds.), *Microcircuits: The interface between neurons and global brain function* (347-370). The MIT Press.
- Chödrön, P. (2001). Tonglen: The path of transformation. Vajradhatu Publications.
- Cikara, M., Bruneau, E. G., & Saxe, R. R. (2011). Us and them: Intergroup failures of empathy. *Current Directions in Psychological Science*, 20(3), 149-153.
- Condon, P., Desbordes, G., Miller, W. B., & DeSteno, D. (2013). Meditation increases compassionate responses to suffering. *Psychological Science*, *24*(10), 2125–2127. https://doi.org/10.1177/0956797613485603
- Condon, P., & Makransky, J. (2020). Recovering the relational starting point of compassion training: a foundation for sustainable and inclusive care. *Perspectives on Psychological Science*, *15*(6), 1346-1362.
- Custo, A., Van De Ville, D., Wells, W. M., Tomescu, M. I., Brunet, D., & Michel, C. M. (2017). Electroencephalographic resting-state networks: Source localization of microstates. *Brain Connectivity*, 7(10), 671-682. https://doi.org/10.1089/brain.2016.0476

- Dahl, C. J., Lutz, A., & Davidson, R. J. (2015). Reconstructing and deconstructing the self: cognitive mechanisms in meditation practice. *Trends in Cognitive Sciences*, 19(9), 515-523.
- Dalai Lama & Chodron, T. (2017). *Buddhism: One teacher, many traditions*. Simon and Schuster.
- Dalai Lama & Kamalashila (2001). *Stages of meditation* (Geshe L. Jordhen, L. C. Ganchenpa, & J. Russell, Trans.). Snow Lion Publications.
- De Dreu, C. K., Greer, L. L., Van Kleef, G. A., Shalvi, S., & Handgraaf, M. J. (2011). Oxytocin promotes human ethnocentrism. *Proceedings of the National Academy of Sciences*, *108*(4), 1262-1266.
- Deco, G., Jirsa, V. K., & McIntosh, A. R. (2011). Emerging concepts for the dynamical organization of resting-state activity in the brain. *Nature Reviews Neuroscience*, 12, 43-56. https://doi.org/10.1038/nrn2961
- Desbordes, G., Negi, L. T., Pace, T. W., Wallace, B. A., Raison, C. L., & Schwartz, E. L. (2012). Effects of mindful-attention and compassion meditation training on amygdala response to emotional stimuli in an ordinary, non-meditative state. *Frontiers in Human Neuroscience*, 6, 292.
- Donald, J. N., Sahdra, B. K., Van Zanden, B., Duineveld, J. J., Atkins, P. W., Marshall, S. L., & Ciarrochi, J. (2019). Does your mindfulness benefit others? A systematic review and meta-analysis of the link between mindfulness and prosocial behaviour. *British Journal* of Psychology, 110(1), 101-125.
- Engen, H. G., & Singer, T. (2015). Compassion-based emotion regulation up-regulates experienced positive affect and associated neural networks. *Social Cognitive and Affective Neuroscience*, *10*(9), 1291-1301.
- Engen, H. G., Bernhardt, B. C., Skottnik, L., Ricard, M., & Singer, T. (2018). Structural changes in socio-affective networks: multi-modal MRI findings in long-term meditation practitioners. *Neuropsychologia*, 116, 26-33.
- Faber, P. L., Travis, F., Milz, P., & Parim, N. (2017). EEG microstates during different phases of Transcendental Meditation practice. *Cognitive Processing*, 18(3), 307-314. https://doi.org/10.1007/s10339-017-0812-y
- Fiske, S. T. (2002). What we know now about bias and intergroup conflict, the problem of the century. *Current Directions in Psychological Science*, *11*(4), 123-128.

- Flew, A. (1979). Golden rule. A dictionary of philosophy, 134.
- Fries, P., 2005. A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*, 474–480.
- Gabadinho, A., Ritschard, G., Müller, N. S., & Studer, M. (2011). Analyzing and visualizing state sequences in R with TraMineR. *Journal of Statistical Software 40(4)*, 1-37. https://doi.org/10.18637/jss.v040.i04
- Gaesser, B., & Fowler, Z. (2020). Episodic simulation of prosocial interaction: Investigating the roles of memory and imagination in facilitating a willingness to help others. *Psychology* of Consciousness: Theory, Research, and Practice, 7(4), 376–387. <u>https://doi.org/10.1037/cns0000232</u>
- Gaesser, B. (2013). Constructing memory, imagination, and empathy: A cognitive neuroscience perspective. *Frontiers in Psychology*, 3. <u>https://doi.org/10.3389/fpsyg.2012.00576</u>
- Gobodo-Madikizela, P. (2016). *Breaking intergenerational cycles of repetition: A global dialogue on historical trauma and memory*. Barbara Budrich Publishers.
- Gyatrul Rinpoche (2008). Path of the Bodhisattva (S. Khandro, Trans.). Vimala Publishing.
- Halifax, J. (2012). A heuristic model of enactive compassion. *Current Opinion in Supportive and Palliative Care*, 6(2), 228-235.
- Hammond, R. A., & Axelrod, R. (2006). The evolution of ethnocentrism. *Journal of Conflict Resolution*, 50(6), 926-936.
- Hardwick, R. M., Caspers, S., Eickhoff, S. B., & Swinnen, S. P. (2018). Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. *Neuroscience* and Biobehavioral Reviews, 94, 31–44. <u>https://doi.org/10.1016/j.neubiorev.2018.08.003</u>
- Harris, L. T., & Fiske, S. T. (2011). Dehumanized Perception: A Psychological Means to Facilitate Atrocities, Torture, and Genocide?. *Zeitschrift fur Psychologie*, 219(3), 175– 181. https://doi.org/10.1027/2151-2604/a000065
- Hastorf, A. H., & Cantril, H. (1954). They saw a game; a case study. *The Journal of Abnormal* and Social Psychology, 49(1), 129.
- Helske, S., & Helske, J. (2019). Mixture hidden Markov models for sequence data: the seqHMM package in R. *Journal of Statistical Software*, 88(3), 1-32. https://doi.org/10.18637/jss.v088.i03

- Kang, Y., Gray, J. R., & Dovidio, J. F. (2014). The nondiscriminating heart: lovingkindness meditation training decreases implicit intergroup bias. *Journal of Experimental Psychology: General*, 143(3), 1306.
- King, B. G., Zanesco, A. P., Skwara, A. C., & Saron, C. D. (*in preparation*). Cultivating concern for others' well-being: Meditation training and the motivation to engage with human suffering.
- Kirby, J. N., Tellegen, C. L., & Steindl, S. R. (2017). A meta-analysis of compassion-based interventions: Current state of knowledge and future directions. *Behavior Therapy*, 48(6), 778-792.
- Klimecki, O. M., Leiberg, S., Lamm, C., & Singer, T. (2013). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex*, 23(7), 1552-1561.
- Klimecki, O. M., Leiberg, S., Ricard, M., & Singer, T. (2014). Differential pattern of functional brain plasticity after compassion and empathy training. *Social Cognitive and Affective Neuroscience*, 9(6), 873-879.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, *29*(2-3), 169-195. https://doi.org/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*(2), 73-76.
- Koenig, T., & Brandeis, D. (2016). Inappropriate assumptions about EEG state changes and their impact on the quantification of EEG state dynamics. *Neuroimage*, 125, 1104-1106. https://doi.org/10.1016/j.neuroimage.2015.06.035
- Koenig, T., Prichep, L., Lehmann, D., Sosa, P. V., Braeker, E., Kleinlogel, H., Isenhart, R., & John, E. R. (2002). Millisecond by millisecond, year by year: normative EEG microstates and developmental stages. *Neuroimage*, 16(1), 41-48.
- Koenig, T., Stein, M., Grieder, M., & Kottlow, M. (2014). A tutorial on data-driven methods for statistically assessing ERP topographies. *Brain Topography*, 27(1), 72-83.
- Kok, B. E., & Singer, T. (2017). Phenomenological fingerprints of four meditations: Differential states changes in affect, mind-wandering, meta-cognition, and interoception before and after daily practice across 9 months of training. *Mindfulness*, 8(1), 218-231. https://doi.org/10.1007/s12671-016-0594-9

- Kteily, N., Bruneau, E., Waytz, A., & Cotterill, S. (2015). The ascent of man: Theoretical and empirical evidence for blatant dehumanization. *Journal of Personality and Social Psychology*, 109(5), 901.
- Kteily, N., Hodson, G., & Bruneau, E. (2016). They see us as less than human: Metadehumanization predicts intergroup conflict via reciprocal dehumanization. *Journal* of Personality and Social Psychology, 110(3), 343.
- Lang, J. (2020). The limited importance of dehumanization in collective violence. *Current Opinion in Psychology*, 35, 17-20.
- Lehmann, D. (1971). Multichannel topography of human alpha EEG fields. *Electroencephalography and Clinical Neurophysiology*, *31*(5), 439-449. <u>https://doi.org/10.1016/0013-4694(71)90165-9</u>
- Lehmann, D., Ozaki, H., & Pál, I. (1987). EEG alpha map series: brain micro-states by spaceoriented adaptive segmentation. *Electroencephalography and Clinical Neurophysiology*, 67(3), 271-288.
- Lingpa, D. (2016). *Heart of the great perfection: Dudjom Lingpa's visions of the great perfection* (B.A. Wallace, Trans.). Simon and Schuster.
- Lomas, T., Ivtzan, I., & Fu, C. H. (2015). A systematic review of the neurophysiology of mindfulness on EEG oscillations. *Neuroscience & Biobehavioral Reviews*, 57, 401-410. <u>https://doi.org/10.1016/j.neubiorev.2015.09.018</u>
- Lutz, A., Brefczynski-Lewis, J., Johnstone, T., & Davidson, R. J. (2008). Regulation of the *Opinion in Psychology*, *35*, 17-20.neural circuitry of emotion by compassion meditation: effects of meditative expertise. *PloS one*, *3*(3), e1897.
- Lutz, A., Greischar, L. L., Perlman, D. M., & Davidson, R. J. (2009). BOLD signal in insula is differentially related to cardiac function during compassion meditation in experts vs. novices. *Neuroimage*, 47(3), 1038-1046.
- Lutz, A., Greischar, L. L., Rawlings, N. B., Ricard, M., & Davidson, R. J. (2004). Long-term meditators self-induce high-amplitude gamma synchrony during mental practice. *Proceedings of the national Academy of Sciences*, *101*(46), 16369-16373.
- Lutz, A., Jha, A. P., Dunne, J. D., & Saron, C. D. (2015). Investigating the phenomenological matrix of mindfulness-related practices from a neurocognitive perspective. *American Psychologist*, 70(7), 632-658. https://doi.org/10.1037/a0039585.

- Lutz, A., & Thompson, E. (2003). Neurophenomenology: Integrating subjective experience and brain dynamics in the neuroscience of consciousness. *Journal of Consciousness Studies*, 10(9-10), 31-52.
- MacLean, K. A., Ferrer, E., Aichele, S. R., Bridwell, D. A., Zanesco, A. P., Jacobs, T. L., King, B. G., Rosenberg, E. L., Sahdra, B. K., Shaver, P. R., Wallace, B. A., Mangun, G. R., & Saron, C. D. (2010). Intensive meditation training improves perceptual discrimination and sustained attention. *Psychological Science*, 21(6), 829-839. <u>https://doi.org/10.1177/0956797610371339</u>
- Makransky, J. (2012). Compassion in Buddhist psychology. In C. Germer & R. D. Siegel (Eds.), *Wisdom and compassion in psychotherapy: Deepening mindfulness in clinical practice* (pp. 61–75). Guilford Publications.
- McArdle, B. H., & Anderson, M. J. (2001). Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology*, *82(1)*, 290-297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2
- McArtor, D. B. (2018). MDMR: Multivariate Distance Matrix Regression. R package version 0.5.1. <u>https://CRAN.R-project.org/package=MDMR</u>
- McArtor, D. B., Lubke, G. H., & Bergeman, C. S. (2017). Extending multivariate distance matrix regression with an effect size measure and the asymptotic null distribution of the test statistic. *Psychometrika*, 82(4), 1052-1077. https://doi.org/10.1007/s11336-016-9527-8
- Meehan, T.P., Bressler, S.L., 2012. Neurocognitive networks: findings, models, and theory. *Neuroscience and Biobehavioral Reviews*, *36*, 2232–2247.
- Michel, C. M., & Brunet, D. (2019). EEG source imaging: A practical review of the analysis steps. Frontiers in Neurology, 10:325. https://doi.org/10.3389/fneur.2019.00325
- Michel, C. M., & Koenig, T. (2018). EEG microstates as a tool for studying the temporal dynamics of whole-brain neuronal networks: A review. *Neuroimage*, 180, 577-593. <u>https://doi.org/10.1016/j.neuroimage.2017.11.062</u>
- Michel, C. M., Koenig, T., & Brandeis, D. (2009). Electric neuroimaging in the time domain. In C. M. Michel et al. (Eds.), *Electrical Neuroimaging* (pp. 111–144). Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511596889
- Milz, P., Pascual-Marqui, R. D., Achermann, P., Kochi, K., & Faber, P. L. (2017). The EEG microstate topography is predominantly determined by intracortical sources in the alpha band. *Neuroimage*, *162*, 353-361.

- Molenberghs, P. (2013). The neuroscience of in-group bias. *Neuroscience & Biobehavioral Reviews*, *37*(8), 1530-1536.
- Murray, M. M., Brunet, D., & Michel, C. M. (2008). Topographic ERP analyses: A step-by-step tutorial review. *Brain Topography*, 20(4), 249-264. https://doi.org/10.1007/s10548-008-0054-5
- Oyler, D. L., Price-Blackshear, M. A., Pratscher, S. D., & Bettencourt, B. A. (2021). Mindfulness and intergroup bias: A systematic review. *Group Processes & Intergroup Relations*, https://doi.org/10.1177/1368430220978694
- Panda, R., Bharath, R. D., Upadhyay, N., Mangalore, S., Chennu, S., & Rao, S. L. (2016). Temporal dynamics of the default mode network characterize meditation-induced alterations in consciousness. *Frontiers in Human Neuroscience*, 10, 372.
- Patrul Rinpoche. (1998). The words of my perfect teacher: A complete translation of a classic introduction to Tibetan Buddhism. Altamira Press.
- Pearson, J. (2019). The human imagination: The cognitive neuroscience of visual mental imagery. *Nature Reviews Neuroscience*, 20(10), 624–634. <u>https://doi.org/10.1038/s41583-019-0202-9</u>
- Petitmengin, C., van Beek, M., Bitbol, M., Nissou, J. M., & Roepstorff, A. (2019). Studying the experience of meditation through micro-phenomenology. *Current Opinion in Psychology*, 28, 54-59. https://doi.org/10.1016/j.copsyc.2018.10.009
- Pfurtscheller, G., & Lopes da Silva, F. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*(11), 1842-1857. <u>https://doi.org/10.1016/S1388-2457(99)00141-8</u>
- Przyrembel, M., & Singer, T. (2018). Experiencing meditation Evidence for differential effects of three contemplative mental practices in micro-phenomenological interviews. *Consciousness and Cognition*, 62, 82-101. https://doi.org/10.1016/j.concog.2018.04.004
- Quaglia, J. T., Soisson, A., & Simmer-Brown, J. (2021). Compassion for self versus other: a critical review of compassion training research. *The Journal of Positive Psychology*, 16(5), 675-690.
- Rosenberg, E. L., Zanesco, A. P., King, B. G., Aichele, S. R., Jacobs, T. L., Bridwell, D. A., MacLean, K. A., Shaver, P. R., Ferrer, E., Sahdra, B. K., Lavy, S., Wallace, B. A., & Saron, C. D. (2015). Intensive meditation training influences emotional responses to suffering. *Emotion*, 15(6), 775. <u>https://doi.org/10.1037/emo0000080</u>

- Saggar, M., King, B. G., Zanesco, A. P., MacLean, K. A., Aichele, S. R., Jacobs, T. L., Bridwell, D. A., Shaver, P. R., Rosenberg, E. L., Sahdra, B. J., Ferrer, E., Tang, A. C., Mangun, G. R., Wallace, B. A., Miikkulainen, R., & Saron, C. D. (2012). Intensive training induces longitudinal changes in meditation state-related EEG oscillatory activity. *Frontiers in Human Neuroscience*, *6*, 256. https://doi.org/10.3389/fnhum.2012.00256
- Sahdra, B. K., MacLean, K. A., Ferrer, E., Shaver, P. R., Rosenberg, E. L., Jacobs, T. L.,
 Zanesco, A. P., King, B. G., Aichele, S. R., Bridwell, D. A., Mangun, G. R., Lavy, S.,
 Wallace, B. A., & Saron, C. D. (2011). Enhanced response inhibition during intensive
 meditation training predicts improvements in self-reported adaptive socioemotional
 functioning. *Emotion*, 11(2), 299-312. https://doi.org/10.1037/a0022764
- Salzberg, S. (2002). *Lovingkindness: The revolutionary art of happiness*. Shambhala Publications.
- Schoenberg, P. L., Ruf, A., Churchill, J., Brown, D. P., & Brewer, J. A. (2018). Mapping complex mind states: EEG neural substrates of meditative unified compassionate awareness. *Consciousness and Cognition*, 57, 41-53.
- Schoenberg, P. L., & Vago, D. R. (2019). Mapping meditative states and stages with electrophysiology: concepts, classifications, and methods. *Current Opinion in Psychology*, 28, 211-217.
- Sherif, M., Harvey, O. J., White, B. J., Hood, W. R., & Sherif, C. W. (1961). *Intergroup conflict* and cooperation. The Robbers Cave experiment (Vol. 10). University of Oklahoma Book Exchange.
- Shāntideva (2006). *The way of the bodhisattva* (The Padmakara Translation Group, Trans.). Shambhala Publishing.
- Sheehan, D. V., Lecrubier, Y., Sheehan, K. H., Amorim, P., Janavs, J., Weiller, E., Hergueta, T., Baker, R., & Dunbar, G. C. (1998). The Mini-International Neuropsychiatric Interview (M.I.N.I): The development and validation of a structured diagnostic psychiatric interview for DSM-IV and ICD-10. *The Journal of Clinical Psychiatry*, 59(Suppl 20), 22–33.
- Shields, G. S., Skwara, A. C., King, B. G., Zanesco, A. P., Dhabhar, F. S., & Saron, C. D. (2020). Deconstructing the effects of concentration meditation practice on interference control: The roles of controlled attention and inflammatory activity. *Brain, Behavior, and Immunity*. <u>https://doi.org/10.1016/j.bbi.2020.06.034</u>

Singer, M. G. (1963). The golden rule. *Philosophy*, 38(146), 293-314.

- Skrandies, W. (1990). Global field power and topographic similarity. *Brain Topography*, 3(1), 137-141. <u>https://doi.org/10.1007/BF01128870</u>
- Skwara, A. C., King, B. G., & Saron, C. D. (2017). Studies of training compassion: What have we learned; what remains unknown. In E. M. Seppälä, E. Simon-Thomas, S. L. Brown, M. C. Worline, C. D. Cameron, & J. R. Doty (Eds.), *The Oxford handbook of compassion science* (pp. 219-236). Oxford University Press.
- Skwara, A. C., King, B. G., Zanesco, A. P., & Saron, C. D. (*in revision*). Shifting baselines: Longitudinal reductions in beta oscillatory power characterize resting brain activity with intensive meditation.
- Struch, N., & Schwarz, S. H. (1989). Intergroup aggression: Its predictions and distinctness from in-group bias. *Journal of Personality and Social Psychology*, 56, 364–373.
- Studer, M., & Ritschard, G. (2016). What matters in differences between life trajectories: a comparative review of sequence dissimilarity measures. *Journal of the Royal Statistical Society*, 179(2), 481-511. https://doi.org/10.1111/rssa.12125
- Studer, M., Ritschard, G., Gabadinho, A., & Müller, N. S. (2011). Discrepancy analysis of state sequences. Sociological Methods & Research, 40(3), 471-510. https://doi.org/10.1177/0049124111415372
- Tang, A. C., Sutherland, M. T., & McKinney, C. J. (2005). Validation of SOBI components from high-density EEG. *NeuroImage*, 25(2), 539-553. <u>https://doi.org/10.1016/j.neuroimage.2004.11.027</u>
- Turner, J. C., Oakes, P. J., Haslam, S. A., & McGarty, C. (1994). Self and collective: Cognition and social context. *Personality and Social Psychology Bulletin*, 20(5), 454-463.
- Van de Ville, D., Britz, J., & Michel, C. M. (2010). EEG microstate sequences in healthy humans at rest reveal scale-free dynamics. *Proceedings of the National Academy of Sciences*, 107(42), 18179-18184.
- Varela, F. (1996). Neurophenomenology: A methodological remedy for the hard problem. Journal of Consciousness Studies, 3, 330–349.
- Viki, G. T., Osgood, D., & Phillips, S. (2013). Dehumanization and self-reported proclivity to torture prisoners of war. *Journal of Experimental Social Psychology*, 49(3), 325-328.

- Wallace, B. A. (1999). *The four immeasurables: Practices to open the heart*. Snow Lion Publications.
- Wallace, B. A. (2006). *The attention revolution: Unlocking the power of the focused mind*. Simon and Schuster.
- Wattles, J. (1996). The golden rule. Oxford University Press.
- Weng, H. Y., Fox, A. S., Hessenthaler, H. C., Stodola, D. E., & Davidson, R. J. (2015). The role of compassion in altruistic helping and punishment behavior. *PloS one*, 10(12), e0143794.
- Weng, H. Y., Fox, A. S., Shackman, A. J., Stodola, D. E., Caldwell, J. Z., Olson, M. C., Rogers, G. M., & Davidson, R. J. (2013). Compassion training alters altruism and neural responses to suffering. *Psychological Science*, 24(7), 1171-1180.
- Weng, H. Y., Lapate, R. C., Stodola, D. E., Rogers, G. M., & Davidson, R. J. (2018). Visual attention to suffering after compassion training is associated with decreased amygdala responses. *Frontiers in Psychology*, 9, 771.
- Wilson-Mendenhall, C., Dunne, J., & Davidson, R. (2021). Visualizing compassion: Episodic simulation as contemplative practice. *MindRxiv*. <u>https://doi.org/10.31231/osf.io/zbu6k</u>
- Wilson-Mendenhall, C. D., Henriques, A., Barsalou, L. W., & Barrett, L. F. (2019). Primary interoceptive cortex activity during simulated experiences of the body. *Journal of Cognitive Neuroscience*, 31(2), 221–235. https://doi.org/10.1162/jocn a 01346
- Zanesco, A. P., King, B. G., Skwara, A. C., & Saron, C. D. (2020). Within and between-person correlates of the temporal dynamics of resting EEG microstates. *NeuroImage*, 211(1), 116631. https://doi.org/10.1016/j.neuroimage.2020.116631
- Zanesco, A. P., Skwara, A. C., King, B. G., Powers, C., Wineberg, K., & Saron, C. D. (2021). Meditation training modulates brain electric microstates and felt states of awareness. *Human Brain Mapping*, 42(10), 3228-3252. https://doi.org/10.1002/hbm.25430
- Zapala, M. A., & Schork, N. J. (2012). Statistical properties of multivariate distance matrix regression for high-dimensional data analysis. *Frontiers in Genetics*, *3*, 190. <u>https://doi.org/10.3389/fgene.2012.00190</u>
- Zarka, D., Cevallos, C., Ruiz, P., Cebolla, A. M., Petieau, M., Bengoetxea, A., & Cheron, G. (2021). Trait and state mindfulness modulate EEG microstates. *MedRxiv*. <u>https://doi.org/10.1101/2021.11.22.21266675</u>

Tables and Figures

Table 3.1

Descriptive Statistics of Microstate Parameters during Compassion Meditation Retreat 1

	Training Group			Waitlist Control Group		
	Pre	Mid	Post	Pre	Mid	Post
N	30	30	29	30	30	30
GEV (%)						
А	6.63 (3.69)	6.84 (3.48)	6.81 (3.3)	5.15 (3.09)	4.79 (2.84)	5.1 (2.46)
В	6.42 (2.74)	7.19 (3.24)	6.76 (2.83)	6.08 (3.74)	6.03 (3.48)	6.07 (2.76)
С	20.38 (7.72)	20.16 (7.16)	20.39 (7.9)	24.99 (11.27)	26.6 (12.89)	24.3 (9.41)
D	11.38 (6.3)	12.22 (6.3)	11.96 (6.11)	9.81 (4.61)	10.61 (4.77)	10.3 (3.91)
Е	11.04 (5.11)	9.52 (4.26)	10.24 (3.93)	11.3 (5.97)	9.81 (5.33)	11.44 (4.54)
Total	55.85 (4.24)	55.94 (3.75)	56.16 (4.23)	57.33 (5.02)	57.83 (5.34)	57.2 (4.74)
Duration	(ms)					
А	70.88 (4.8)	70.2 (4.08)	69.94 (4.85)	70.19 (6.24)	69.41 (8.93)	70.82 (6.02)
В	71.58 (5.46)	71.31 (4.15)	69.84 (4.53)	71.34 (5.88)	70.57 (9.99)	72.27 (6.89)
С	84.43 (10.53)	82.62 (8.84)	82.88 (9.72)	89.68 (13.4)	89.03 (12.8)	89.61 (10.46)
D	77.64 (7.85)	76.86 (6.23)	76.64 (6.56)	77.16 (8.14)	76.44 (10.25)	78.08 (7.61)
Е	76.97 (7.49)	75.15 (6.63)	74.86 (5.7)	78.57 (8.97)	75.76 (10.03)	79.15 (8.92)
Average	76.3 (5.13)	75.23 (4.28)	74.83 (4.49)	77.39 (5.29)	76.24 (8.34)	77.99 (5.98)
Occurren	ce (count/sec)					
А	1.64 (0.62)	1.69 (0.52)	1.7 (0.5)	1.37 (0.54)	1.32 (0.49)	1.39 (0.45)
В	1.62 (0.49)	1.78 (0.55)	1.74 (0.53)	1.51 (0.52)	1.53 (0.53)	1.55 (0.45)
С	2.68 (0.47)	2.71 (0.43)	2.75 (0.49)	2.86 (0.72)	3.17 (1.61)	2.8 (0.64)
D	2.41 (0.63)	2.53 (0.73)	2.46 (0.65)	2.22 (0.59)	2.31 (0.74)	2.27 (0.55)
Е	2.23 (0.6)	2.11 (0.53)	2.22 (0.52)	2.21 (0.51)	2.05 (0.65)	2.21 (0.39)
Total	10.58 (1.04)	10.81 (0.89)	10.87 (0.93)	10.16 (1.07)	10.37 (1.33)	10.22 (1.09)
GFP (µV)						
А	5.4 (1.32)	5.15 (1.31)	5.19 (1.3)	6.3 (2.05)	6.21 (1.9)	6.13 (2)
В	5.39 (1.33)	5.13 (1.3)	5.18 (1.27)	6.5 (2.01)	6.4 (1.99)	6.26 (1.92)
С	6.37 (1.85)	6.04 (1.75)	6.09 (1.81)	7.93 (2.67)	7.84 (2.48)	7.64 (2.61)
D	5.52 (1.38)	5.3 (1.38)	5.37 (1.38)	6.61 (2.05)	6.6 (2.01)	6.43 (2.06)
Е	5.64 (1.53)	5.24 (1.46)	5.38 (1.48)	6.88 (2.24)	6.63 (2.15)	6.64 (2.07)
Average	5.66 (1.44)	5.37 (1.4)	5.44 (1.41)	6.84 (2.17)	6.74 (2.07)	6.62 (2.11)

Note. Means and *SD*s of microstate parameters during compassion meditation are provided for each configuration. Additionally, a summary statistic (total or average) across configurations is provided for each parameter.

Descriptive Statistics of Microstate Parameters during Compassion Meditation Retreat 2					
	Pre	Mid	Post		
N	29	29	29		
GEV (%)					
А	4.81 (2.31)	5.05 (2.52)	4.78 (2.56)		
В	6.06 (2.76)	6.14 (3.04)	6.26 (2.99)		
С	24.59 (9.71)	26.13 (9.26)	26.29 (10.44)		
D	10.38 (4.39)	11.36 (4.82)	10.67 (4.38)		
Е	11.15 (5.38)	9.38 (3.75)	10.46 (4.31)		
Total	57 (5.15)	58.06 (4.93)	58.46 (5.01)		
Duration (ms))				
A	70.81 (7.69)	66.86 (6.98)	66.01 (6.32)		
В	72.05 (7.58)	67.79 (5.9)	68.39 (5.97)		
С	88.83 (9.4)	86.84 (11.03)	87.7 (11.47)		
D	77.76 (8.87)	74.54 (8.43)	73.85 (7.78)		
Е	78.74 (9.9)	72.66 (6.13)	74.18 (6.66)		
Average	77.64 (6.73)	73.74 (5.47)	74.03 (5.05)		
Occurrence (count/sec)				
А	1.34 (0.43)	1.43 (0.5)	1.37 (0.53)		
В	1.56 (0.44)	1.65 (0.55)	1.65 (0.52)		
С	2.84 (0.71)	3.11 (0.55)	3.07 (0.59)		
D	2.32 (0.57)	2.49 (0.57)	2.4 (0.57)		
Е	2.21 (0.46)	2.13 (0.53)	2.23 (0.51)		
Total	10.26 (1.07)	10.81 (1.18)	10.72 (1.11)		
GFP (µV)					
А	6.26 (2.16)	6.13 (1.95)	6.11 (2.11)		
В	6.46 (2.17)	6.26 (1.86)	6.34 (2.08)		
С	7.92 (2.79)	7.65 (2.42)	7.7 (2.72)		
D	6.6 (2.21)	6.52 (1.96)	6.5 (2.09)		
Е	6.83 (2.25)	6.53 (2.11)	6.67 (2.3)		
Average	6.82 (2.29)	6.62 (2.03)	6.67 (2.23)		

Note. Means and *SD*s of microstate parameters during compassion meditation are provided for each configuration. Additionally, a summary statistic (total or average) across configurations is provided for each parameter.

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Retreat 1						
	Training Group			Waitlist Control Group		
	Pre	Mid	Post	Pre	Mid	Post
N	30	30	29	30	30	30
GEV (%)						
А	6.61 (3.99)	6.61 (3.8)	6.55 (3.73)	5.52 (3.79)	5.11 (3.41)	4.79 (2.62)
В	6.04 (3.01)	7.32 (3.15)	7.19 (3.24)	6.18 (3.57)	6.36 (4.37)	6.25 (3.37)
С	21.94 (8.48)	20.29 (7.47)	21.3 (8.47)	25.36 (11.81)	27.62 (15.06)	25.91 (11.96)
D	10.58 (7.29)	11.2 (5.61)	11.09 (6.82)	9.14 (4.07)	9.45 (4.24)	9.26 (4.55)
Е	11.09 (5.19)	10.7 (4.54)	10.44 (4.3)	11.45 (6)	9.4 (5.65)	11.44 (5.59)
Total	56.27 (4.85)	56.12 (3.69)	56.57 (4.24)	57.65 (5.41)	57.95 (6.32)	57.65 (5.63)
Duration	(ms)					
А	72.28 (7.03)	69.66 (7.55)	69.66 (7.17)	71.81 (8.73)	69.12 (11.66)	71.78 (8.32)
В	72.88 (7)	72.46 (6.43)	68.76 (6.4)	72.76 (9.34)	70.04 (13.47)	72.76 (9.19)
С	87.93 (13.21)	84.39 (10.81)	82.71 (11.01)	91.12 (18.74)	90.93 (15.44)	92.41 (17.96)
D	75.73 (9.97)	76.47 (7.86)	76.25 (8.55)	75.47 (7.08)	75.12 (11.41)	77.02 (9.38)
Е	76.94 (9.61)	75.84 (7.66)	75.57 (8.21)	79.1 (11.12)	NA (NA)	79.53 (11.94)
Average	77.15 (6.15)	75.76 (5.63)	74.59 (5.24)	78.05 (6.38)	NA (NA)	78.7 (7.34)
Occurren	ce (count/sec)					
А	1.62 (0.7)	1.68 (0.62)	1.68 (0.69)	1.42 (0.66)	1.35 (0.57)	1.3 (0.51)
В	1.53 (0.5)	1.75 (0.55)	1.82 (0.58)	1.52 (0.54)	1.54 (0.59)	1.57 (0.51)
С	2.79 (0.47)	2.7 (0.5)	2.82 (0.63)	2.87 (0.7)	3.22 (1.66)	2.82 (0.72)
D	2.25 (0.74)	2.38 (0.75)	2.34 (0.72)	2.13 (0.69)	2.19 (0.66)	2.11 (0.68)
Е	2.24 (0.65)	2.25 (0.56)	2.21 (0.64)	2.16 (0.56)	1.99 (0.69)	2.2 (0.56)
Total	10.42 (1.16)	10.75 (1.08)	10.87 (1.01)	10.1 (1.39)	10.29 (1.34)	10 (1.39)
GFP (μV)					
А	5.9 (1.62)	5.27 (1.39)	5.47 (1.34)	6.72 (2.04)	6.47 (2.06)	6.71 (2.05)
В	5.76 (1.45)	5.31 (1.42)	5.57 (1.38)	7.02 (2.16)	6.67 (2.06)	6.9 (2.13)
С	6.91 (2.04)	6.19 (1.88)	6.55 (1.94)	8.45 (2.67)	8.12 (2.46)	8.42 (2.58)
D	5.95 (1.59)	5.39 (1.3)	5.67 (1.51)	6.99 (2.09)	6.79 (2.01)	6.91 (1.97)
Е	6.09 (1.66)	5.49 (1.55)	5.76 (1.6)	7.36 (2.29)	6.8 (2.1)	7.26 (2.18)
Average	6.12 (1.63)	5.53 (1.47)	5.8 (1.51)	7.31 (2.2)	6.97 (2.08)	7.24 (2.13)

Note. Means and *SD*s of microstate parameters during pre-meditation rest are provided for each configuration. Additionally, a summary statistic (total or average) across configurations is provided for each parameter.

Retreat 2					
	Pre	Mid	Post		
N	29	29	29		
GEV (%)					
А	4.53 (2.05)	4.57 (2.31)	4.87 (2.68)		
В	5.74 (2.91)	5.79 (3.08)	6.43 (3.41)		
С	26.23 (10.77)	27.49 (10.48)	26.36 (11.25)		
D	9.49 (4.64)	10.33 (4.17)	10.81 (5.56)		
Е	11.35 (5.68)	10.05 (3.75)	10.59 (4.62)		
Total	57.33 (5.5)	58.24 (5.2)	59.07 (5.12)		
Duration (ms	5)				
А	72.03 (13.45)	66.55 (8.29)	66.31 (8.21)		
В	71.88 (11.14)	68.4 (8.92)	68.68 (7.89)		
С	91.02 (13.13)	89.86 (17.65)	88.66 (14.26)		
D	76.57 (9.29)	73.37 (9.64)	75.14 (10.5)		
Е	79.99 (13.24)	72.37 (7.47)	74.18 (8.18)		
Average	78.3 (8.41)	74.11 (5.99)	74.59 (6.17)		
Occurrence ((count/sec)				
А	1.28 (0.4)	1.34 (0.49)	1.39 (0.57)		
В	1.55 (0.49)	1.56 (0.54)	1.64 (0.55)		
С	2.91 (0.78)	3.18 (0.57)	3.04 (0.61)		
D	2.17 (0.7)	2.38 (0.66)	2.35 (0.73)		
Е	2.2 (0.54)	2.23 (0.57)	2.2 (0.53)		
Total	10.1 (1.25)	10.69 (1.44)	10.63 (1.29)		
GFP (µV)					
А	6.8 (2.42)	6.26 (1.99)	6.34 (2.19)		
В	6.89 (2.23)	6.39 (1.94)	6.54 (2.09)		
С	8.48 (2.68)	7.84 (2.52)	7.94 (2.71)		
D	7.02 (2.22)	6.6 (1.98)	6.65 (2.02)		
Е	7.28 (2.27)	6.76 (2.17)	6.92 (2.27)		
Average	7.29 (2.33)	6.77 (2.09)	6.88 (2.22)		

Note. Means and *SD*s of microstate parameters during pre-meditation rest are provided for each configuration. Additionally, a summary statistic (total or average) across configurations is provided for each parameter.

Retreat 1						
	Training Group			Waitlist Control Group		
	Pre	Mid	Post	Pre	Mid	Post
N	30	30	29	30	30	30
GEV (%)						
А	6.35 (4.09)	7.2 (3.71)	7.29 (4.45)	5.51 (3.14)	5.41 (3.97)	5.2 (2.84)
В	6.1 (3.2)	8.32 (3.94)	7.41 (3.6)	6.27 (4.38)	6.15 (3.87)	6.26 (3.28)
С	21.65 (10.15)	18.89 (7.54)	19.9 (9.15)	25.05 (11.11)	27.26 (15.39)	25.18 (13.12)
D	11.77 (8.4)	12.25 (6.47)	12.05 (7.18)	9.72 (4.31)	9.91 (4.56)	10.05 (4.22)
Е	10.65 (4.75)	9.31 (3.75)	9.59 (4.83)	10.79 (5.74)	9.26 (6.39)	10.72 (4.87)
Total	56.52 (4.68)	55.97 (4.14)	56.24 (4.52)	57.35 (5.07)	57.99 (5.68)	57.41 (6.31)
Duration	(ms)					
А	71.37 (6.5)	70.56 (5.32)	71.99 (8.65)	71.93 (6.65)	70.76 (9.23)	71.16 (9.2)
В	69.87 (6.46)	73.49 (8.16)	71.47 (7.39)	71.37 (8.27)	71.81 (11.82)	71.82 (8.92)
С	86.3 (12.7)	82.09 (10.47)	82.54 (14.36)	90.1 (13.53)	91.73 (18.98)	92.6 (24.14)
D	79.17 (12.29)	77.41 (7.37)	75.41 (8.56)	78.18 (8.88)	76.13 (11.85)	77.38 (9.25)
Е	77.45 (9.09)	74.22 (8.01)	75.3 (9.86)	77.31 (10.18)	77.36 (10.67)	78.14 (8.82)
Average	76.83 (5.98)	75.55 (5.42)	75.34 (6.59)	77.78 (6.06)	77.56 (7.91)	78.22 (7.7)
Occurren	ce (count/sec)					
А	1.6 (0.74)	1.7 (0.63)	1.7 (0.65)	1.43 (0.64)	1.38 (0.61)	1.4 (0.55)
В	1.56 (0.57)	1.86 (0.64)	1.76 (0.63)	1.52 (0.58)	1.48 (0.59)	1.58 (0.53)
С	2.72 (0.7)	2.69 (0.5)	2.77 (0.52)	2.9 (0.79)	3.12 (1.55)	2.76 (0.72)
D	2.35 (0.73)	2.52 (0.75)	2.46 (0.72)	2.18 (0.66)	2.22 (0.72)	2.3 (0.69)
Е	2.13 (0.58)	2.08 (0.52)	2.1 (0.55)	2.17 (0.53)	1.9 (0.7)	2.15 (0.44)
Total	10.36 (1.35)	10.85 (1.05)	10.78 (1.28)	10.2 (1.2)	10.1 (1.48)	10.18 (1.57)
GFP (μV)					
А	5.74 (1.57)	5.47 (1.66)	5.27 (1.25)	6.65 (2.49)	6.52 (1.99)	6.41 (2.24)
В	5.67 (1.53)	5.55 (1.56)	5.3 (1.34)	6.77 (2.25)	6.65 (2.06)	6.54 (2.02)
С	6.78 (2.13)	6.2 (1.92)	6.14 (1.81)	8.23 (2.88)	8.13 (2.53)	7.99 (2.74)
D	5.87 (1.57)	5.56 (1.52)	5.4 (1.27)	6.87 (2.3)	6.78 (1.98)	6.65 (2.12)
Е	5.98 (1.77)	5.47 (1.58)	5.31 (1.55)	7.09 (2.45)	6.77 (2.02)	6.88 (2.18)
Average	6.01 (1.66)	5.65 (1.6)	5.48 (1.38)	7.12 (2.43)	6.97 (2.06)	6.89 (2.21)

Note. Means and SDs of microstate parameters during post-meditation rest are provided for each configuration. Additionally, a summary statistic (total or average) across configurations is provided for each parameter.

Descriptive Statistics of Microstate Parameters during Post-meditation Rest Retreat 2					
	Pre	Mid	Post		
N	29	29	29		
GEV (%)					
А	5.03 (2.59)	5.05 (3.04)	5.56 (3.04)		
В	5.83 (2.76)	6.18 (3.13)	6.49 (2.96)		
С	26.7 (12.6)	25.7 (11.77)	25.14 (10.66)		
D	9.63 (4.62)	11.19 (4.82)	11.14 (4.32)		
Е	10.08 (5.64)	9.98 (4.53)	9.56 (4.6)		
Total	57.27 (6.07)	58.11 (5.51)	57.9 (4.93)		
Duration (ms)				
А	71.49 (10.99)	68.31 (8.66)	67.51 (7.53)		
В	73.27 (11.96)	67.84 (7.8)	68.59 (7.58)		
С	92.79 (15.65)	88.3 (17.72)	86.39 (11.52)		
D	77.33 (10.37)	74.54 (10.42)	74.39 (7.27)		
Е	78.14 (11.35)	72.5 (10.27)	72.86 (7.68)		
Average	78.6 (8.48)	74.3 (6.78)	73.95 (5.02)		
Occurrence (count/sec)				
А	1.3 (0.48)	1.43 (0.6)	1.5 (0.6)		
В	1.52 (0.53)	1.65 (0.58)	1.63 (0.48)		
С	2.87 (0.72)	3.04 (0.64)	3.09 (0.67)		
D	2.23 (0.68)	2.48 (0.65)	2.47 (0.6)		
Е	2.09 (0.53)	2.16 (0.65)	2.13 (0.57)		
Total	10.01 (1.37)	10.75 (1.51)	10.81 (1.04)		
GFP (µV)					
А	6.71 (2.32)	6.23 (2.05)	6.13 (2.18)		
В	6.8 (2.17)	6.38 (2.05)	6.35 (2.13)		
С	8.44 (2.89)	7.75 (2.61)	7.6 (2.8)		
D	6.97 (2.24)	6.55 (2.01)	6.55 (2.21)		
Е	7.14 (2.26)	6.68 (2.17)	6.52 (2.32)		
Average	7.21 (2.34)	6.72 (2.14)	6.63 (2.3)		

Note. Means and *SD*s of microstate parameters during post-meditation rest are provided for each configuration. Additionally, a summary statistic (total or average) across configurations is provided for each parameter.
		Retreat 1			Retreat2	
Fixed Effects	Estimates	CI[2.5%, 97.5%]	df	Estimates	CI[2.5%, 97.5%]	df
Intercept	25.29 ***	24.11, 26.48	885.00	25.48 ***	24.62, 26.34	880.00
Configuration A	-20.28 ***	-21.95, -18.61	885.00	-20.53 ***	-21.75, -19.31	880.00
Configuration B	-19.24 ***	-20.91, -17.56	885.00	-19.37 ***	-20.59, -18.16	880.00
Configuration D	-15.06 ***	-16.73, -13.38	885.00	-14.96 ***	-16.18, -13.75	880.00
Configuration E	-14.45 ***	-16.12, -12.77	885.00	-14.88 ***	-16.10, -13.67	880.00
Training Group	-4.99 ***	-6.66, -3.31	885.00			
Training Group x Configuration A	6.73 ***	4.36, 9.11	885.00			
Training Group x Configuration B	5.72 ***	3.34, 8.09	885.00			
Training Group x Configuration D	6.60 ***	4.23, 8.98	885.00			
Training Group x Configuration E	4.41 **	2.03, 6.78	885.00			
Random Effects						
σ^2	32.69			34.06		
$ au_{00}$	0.00 Subject			0.00 Subject		
Ν	60 _{Subject}			30 _{Subject}		
Observations	895			885		
Marginal R ² / Conditional R ²	0.543 / NA	X		0.613 / NA	A	

Table 3.7 Global Explained Variance (%)

*p<0.01 **p<0.001 ***p<1e-04

Note. Model parameters from simplified mixed effects models of percent GEV during compassion meditation are provided. For each retreat, only effects that were significant in that retreat were retained. Effects are referenced to configuration C in the waitlist control group at the pre-retreat assessment. A cut-off of p < .01 is used to determine statistical significance; the 95% CI is provided for each parameter estimate.

		Retreat 1			Retreat2	
Fixed Effects	Estimates	CI[2.5%, 97.5%]	df	Estimates	CI[2.5%, 97.5%]	df
Intercept	89.44 ***	87.26, 91.62	123.19	89.83 ***	87.44, 92.21	66.87
Mid-assessment				-1.14	-2.73, 0.44	846.06
Post-assessment				0.60	-0.98, 2.19	846.06
Configuration A	-19.30 ***	-21.23, -17.37	826.99	-19.59 ***	-21.05, -18.13	846.06
Configuration B	-18.05 ***	-19.98, -16.12	826.99	-18.21 ***	-19.67, -16.75	846.06
Configuration D	-12.22 ***	-14.15, -10.28	826.99	-12.31 ***	-13.77, -10.85	846.06
Configuration E	-11.61 ***	-13.55, -9.68	826.99	-12.10 ***	-13.56, -10.64	846.06
Training Group	-6.08 **	-9.16, -2.99	123.75	0.37	-1.24, 1.97	847.04
Training Group x Mid-assessment				-2.76	-5.02, -0.49	846.06
Training Group x Post-assessment				-4.21 **	-6.47, -1.95	846.06
Training Group x Configuration A	6.33 ***	3.59, 9.07	826.99			
Training Group x Configuration B	5.65 ***	2.91, 8.39	826.99			
Training Group x Configuration D	5.95 ***	3.21, 8.69	826.99			
Training Group x Configuration E	3.97 *	1.23, 6.71	826.99			
Random Effects						
σ^2	43.60			48.97		
τ_{00}	21.83 _{Subjee}	t		26.45 _{Subjee}	t	
ICC	0.33			0.35		
Ν	60 _{Subject}			30 _{Subject}		
Observations	895			885		
Marginal R ² / Conditional R ²	0.351 / 0.5	67		0.402 / 0.6	12	
				* p<0.01	** p<0.001 ***	p<1e-04

Table 3.8 Mean Microstate Duration (ms)

Note. Model parameters from simplified mixed effects models of mean duration in milliseconds during compassion meditation are provided. For each retreat, only effects that were significant in that retreat were retained. Effects are referenced to configuration C in the waitlist control group at the pre-retreat assessment. A cut-off of p < .01 is used to determine statistical significance; the 95% CI is provided for each parameter estimate.

		Retreat 1			Retreat2	
Fixed Effects	Estimates	CI[2.5%, 97.5%]	df	Estimates	CI[2.5%, 97.5%]	df
Intercept	2.94 ***	2.81, 3.07	514.13	2.97 ***	2.86, 3.08	125.96
Configuration A	-1.58 ***	-1.76, -1.40	827.20	-1.60 ***	-1.73, -1.48	851.27
Configuration B	-1.41 ***	-1.59, -1.23	827.20	-1.40 ***	-1.52, -1.28	851.27
Configuration D	-0.68 ***	-0.85, -0.50	827.20	-0.64 ***	-0.76, -0.52	851.27
Configuration E	-0.78 ***	-0.96, -0.60	827.20	-0.80 ***	-0.93, -0.68	851.27
Training Group	-0.23	-0.42, -0.04	516.50			
Training Group x Configuration A	0.54 ***	0.28, 0.79	827.20			
Training Group x Configuration B	0.41 *	0.16, 0.67	827.20			
Training Group x Configuration D	0.43 **	0.17, 0.68	827.20			
Training Group x Configuration E	0.26	0.00, 0.51	827.20			
Random Effects						
σ^2	0.37			0.35		
τ_{00}	0.01 Subject	t		0.03 Subject		
ICC	0.03			0.08		
Ν	60 _{Subject}			30 _{Subject}		
Observations	895			885		
Marginal R ² / Conditional R ²	0.389/0.4	409		0.462 / 0.:	505	

Table 3.9 Occurrence per Second (count/sec)

*p<0.01 **p<0.001 ***p<1e-04

Note. Model parameters from simplified mixed effects models of occurrence per second during compassion meditation are provided. For each retreat, only effects that were significant in that retreat were retained. Effects are referenced to configuration C in the waitlist control group at the pre-retreat assessment. A cut-off of p < .01 is used to determine statistical significance; the 95% CI is provided for each parameter estimate.

		Retreat 1			Retreat2	
Fixed Effects	Estimates	CI[2.5%, 97.5%]	df	Estimates	CI[2.5%, 97.5%]	df
Intercept	7.95 ***	7.30, 8.60	63.21	7.91 ***	7.12, 8.70	30.68
Mid-assessment	-0.20 **	-0.30, -0.10	825.00	-0.15	-0.27, -0.03	847.99
Post-assessment	-0.25 ***	-0.35, -0.14	825.09	-0.19 *	-0.31, -0.07	847.99
Configuration A	-1.59 ***	-1.77, -1.40	825.00	-1.59 ***	-1.74, -1.44	847.99
Configuration B	-1.41 ***	-1.60, -1.23	825.00	-1.41 ***	-1.56, -1.26	847.99
Configuration D	-1.25 ***	-1.44, -1.07	825.00	-1.24 ***	-1.39, -1.08	847.99
Configuration E	-1.08 ***	-1.27, -0.90	825.00	-1.08 ***	-1.23, -0.93	847.99
Training Group	-1.65 **	-2.56, -0.73	62.18	-0.13 *	-0.23, -0.04	848.22
Training Group x Configuration A	0.67 ***	0.41, 0.93	825.00			
Training Group x Configuration B	0.48 **	0.21, 0.74	825.00			
Training Group x Configuration D	0.48 **	0.22, 0.75	825.00			
Training Group x Configuration E	0.34	0.07, 0.60	825.00			
Random Effects						
σ^2	0.40			0.53		
$ au_{00}$	3.01 Subject	ŧ		4.34 Subject	t	
ICC	0.88			0.89		
N	60 Subject			30 Subject		
Observations	895			885		
Marginal R^2 / Conditional R^2	0.155 / 0.5	901		0.062 / 0.3	898	
				* p<0.01	** p<0.001 ***	[•] p<1e-04

Table 3.10 Global Field Power at Peaks (μV)

Note. Model parameters from simplified mixed effects models of GFP in microvolts during compassion meditation are provided. For each retreat, only effects that were significant in that retreat were retained. Effects are referenced to configuration C in the waitlist control group at the pre-retreat assessment. A cut-off of p < .01 is used to determine statistical significance; the 95% CI is provided for each parameter estimate.

		Retr	eat 1		Retreat 2				
Source	df_{Num}	df_{Den}	F-value	р	df_{Num}	df _{Den}	F-value	р	
Condition	2	2595.00	0.02	.977	2	2536.38	0.03	.970	
Assessment	2	2595.00	0.00	.995	2	2536.38	0.13	.877	
Configuration	4	2595.00	659.51***	.000	4	2536.38	924.15***	.000	
Status	1	2595.00	1.37	.242	1	2561.43	0.06	.811	
Condition x Assessment	4	2595.00	0.00	1	4	2536.38	0.01	1	
Condition x Configuration	8	2595.00	0.78	.617	8	2536.38	0.64	.747	
Assessment x Configuration	8	2595.00	0.94	.478	8	2536.38	1.37	.207	
Condition x Status	2	2595.00	0.00	.999	2	2536.38	0.01	.995	
Assessment x Status	2	2595.00	0.05	.956	2	2536.38	0.09	.910	
Configuration x Status	4	2595.00	28.93***	.000	4	2536.38	0.65	.627	
Condition x Assessment x Configuration	16	2595.00	0.07	1	16	2536.38	0.09	1	
Condition x Assessment x Status	4	2595.00	0.01	1	4	2536.38	0.01	1	
Condition x Configuration x Status	8	2595.00	0.11	.999	8	2536.38	0.05	1	
Assessment x Configuration x Status	8	2595.00	1.35	.216	8	2536.38	0.39	.928	
Condition x Assessment x Configuration x Status	16	2595.00	0.12	1	16	2536.38	0.17	1	

Table 3.11 Global Explained Variance: Type III Tests of Fixed Effects Including Condition

Note. Type III tests of fixed effects are reported for mixed effects models of percent GEV incorporating condition (pre-meditation rest, compassion meditation, post-meditation rest). In Retreat 1, "Status" refers to the between-subjects effect of group (waitlist control, training); in Retreat 2, "Status" refers to the within-subjects effect of status (as R1 waitlist controls, in R2 training).Satterthwaite approximation is used to estimate degrees of freedom. A cut-off of p < .01 is used to determine statistical significance.

		Retr	eat 1		Retreat 2			
Source	df_{Num}	df _{Den}	F-value	p	df _{Num}	df _{Den}	F-value	р
Condition	2	2536.00	1.01	.366	2	2535.03	0.97	.378
Assessment	2	2537.20	4.21`	.015	2	2535.03	18.16***	.000
Configuration	4	2536.00	326.68***	.000	4	2535.03	405.57***	.000
Status	1	58.00	1.73	.193	1	2539.78	29.34***	.000
Condition x Assessment	4	2536.00	0.24	.917	4	2535.03	0.42	.794
Condition x Configuration	8	2536.00	0.85	.557	8	2535.03	0.79	.609
Assessment x Configuration	8	2536.00	0.49	.864	8	2535.03	0.77	.633
Condition x Status	2	2536.00	0.03	.970	2	2535.03	0.04	.958
Assessment x Status	2	2537.20	4.75*	.009	2	2535.03	13.97***	.000
Configuration x Status	4	2536.00	15.61***	.000	4	2535.03	0.37	.831
Condition x Assessment x Configuration	16	2536.00	0.40	.983	16	2535.03	0.14	1
Condition x Assessment x Status	4	2536.00	0.54	.707	4	2535.03	0.19	.943
Condition x Configuration x Status	8	2536.00	0.15	.997	8	2535.03	0.07	1
Assessment x Configuration x Status	8	2536.00	0.75	.648	8	2535.03	0.16	.996
Condition x Assessment x Configuration x Status	16	2536.00	0.34	.993	16	2535.03	0.29	.997

Table 3.12 Mean Duration: Type III Tests of Fixed Effects Including Condition

Note. Type III tests of fixed effects are reported for mixed effects models of mean microstate duration in milliseconds incorporating condition (pre-meditation rest, compassion meditation, post-meditation rest). In Retreat 1, "Status" refers to the between-subjects effect of group (waitlist control, training); in Retreat 2, "Status" refers to the within-subjects effect of status (as R1 waitlist controls, in R2 training).Satterthwaite approximation is used to estimate degrees of freedom. A cut-off of p < .01 is used to determine statistical significance.

		Ret	treat 1		Retreat 2			
Source	df _{Num}	df _{Den}	F-value	р	df _{Num}	df _{Den}	F-value	р
Condition	2	2537.05	0.27	.766	2	2536.12	0.37	.692
Assessment	2	2540.52	1.24	.291	2	2536.12	3.40`	.033
Configuration	4	2537.05	383.83***	.000	4	2536.12	564.13***	.000
Status	1	58.03	3.42	.069	1	2547.13	7.74*	.005
Condition x Assessment	4	2537.05	0.02	.999	4	2536.12	0.14	.967
Condition x Configuration	8	2537.05	0.85	.559	8	2536.12	0.69	.703
Assessment x Configuration	8	2537.05	1.79	.075	8	2536.12	2.66*	.007
Condition x Status	2	2537.05	0.01	.989	2	2536.12	0.00	.997
Assessment x Status	2	2540.52	0.83	.435	2	2536.12	2.55	.078
Configuration x Status	4	2537.05	12.30***	.000	4	2536.12	1.00	.406
Condition x Assessment x Configuration	16	2537.05	0.08	1	16	2536.12	0.09	1
Condition x Assessment x Status	4	2537.05	0.24	.916	4	2536.12	0.17	.952
Condition x Configuration x Status	8	2537.05	0.11	.999	8	2536.12	0.06	1
Assessment x Configuration x Status	8	2537.05	2.10`	.033	8	2536.12	1.13	.341
Condition x Assessment x Configuration x Status	16	2537.05	0.08	1	16	2536.12	0.13	1

Table 3.13 Occurrence per Second: Type III Tests of Fixed Effects Including Condition

Note. Type III tests of fixed effects are reported for mixed effects models of mean microstate duration in milliseconds incorporating condition (pre-meditation rest, compassion meditation, post-meditation rest). In Retreat 1, "Status" refers to the between-subjects effect of group (waitlist control, training); in Retreat 2, "Status" refers to the within-subjects effect of status (as R1 waitlist controls, in R2 training).Satterthwaite approximation is used to estimate degrees of freedom. A cut-off of p < .01 is used to determine statistical significance.

		Retr	eat 1		Retreat 2			
Source	df _{Num}	df _{Den}	F-value	р	df_{Num}	df _{Den}	F-value	р
Condition	2	2537.01	63.13***	.000	2	2536.00	41.21***	.000
Assessment	2	2537.03	44.23***	.000	2	2536.00	35.76***	.000
Configuration	4	2537.00	261.96***	.000	4	2536.00	308.47***	.000
Status	1	58.00	7.84*	.007	1	2536.29	49.99***	.000
Condition x Assessment	4	2537.01	4.58*	.001	4	2536.00	3.74*	.005
Condition x Configuration	8	2537.00	0.44	.897	8	2536.00	0.30	.965
Assessment x Configuration	8	2537.00	0.70	.691	8	2536.00	0.48	.868
Condition x Status	2	2537.01	2.11	.121	2	2536.00	2.06	.128
Assessment x Status	2	2537.03	5.12*	.006	2	2536.00	4.52`	.011
Configuration x Status	4	2537.00	16.71***	.000	4	2536.00	0.21	.931
Condition x Assessment x Configuration	16	2537.00	0.07	1	16	2536.00	0.05	1
Condition x Assessment x Status	4	2537.01	0.56	.689	4	2536.00	1.80	.127
Condition x Configuration x Status	8	2537.00	0.10	.999	8	2536.00	0.05	1
Assessment x Configuration x Status	8	2537.00	0.41	.917	8	2536.00	0.32	.961
Condition x Assessment x Configuration x Status	16	2537.00	0.11	1	16	2536.00	0.07	1

Table 3.14Global Field Power: Type III Tests of Fixed Effects Including Condition

Note. Type III tests of fixed effects are reported for mixed effects models of GFP in microvolts incorporating condition (pre-meditation rest, compassion meditation, post-meditation rest). In Retreat 1, "Status" refers to the between-subjects effect of group (waitlist control, training); in Retreat 2, "Status" refers to the within-subjects effect of status (as R1 waitlist controls, in R2 training).Satterthwaite approximation is used to estimate degrees of freedom. A cut-off of p < .01 is used to determine statistical significance.

		Retreat 1			Retreat2	
Fixed Effects	Estimates	CI[2.5%, 97.5%]	df	Estimates	CI[2.5%, 97.5%]	df
Intercept	7.95 ***	7.29, 8.61	62.01	7.99 ***	7.20, 8.78	30.33
Pre Rest	0.46 ***	0.34, 0.58	2607.00	0.47 ***	0.34, 0.61	2612.00
Post Rest	0.31 ***	0.19, 0.43	2607.00	0.34 ***	0.20, 0.47	2612.00
Mid-assessment	-0.10	-0.23, 0.04	2607.00	-0.15	-0.29, -0.02	2612.00
Post-assessment	-0.17	-0.30, -0.03	2607.00	-0.19 *	-0.32, -0.05	2612.00
Configuration A	-1.63 ***	-1.75, -1.50	2607.00	-1.61 ***	-1.71, -1.51	2612.00
Configuration B	-1.45 ***	-1.57, -1.32	2607.00	-1.44 ***	-1.54, -1.34	2612.00
Configuration D	-1.35 ***	-1.47, -1.22	2607.00	-1.31 ***	-1.41, -1.21	2612.00
Configuration E	-1.16 ***	-1.28, -1.04	2607.00	-1.14 ***	-1.24, -1.04	2612.00
Pre Rest x Mid-assessment	-0.26 *	-0.43, -0.10	2607.00	-0.28 *	-0.47, -0.09	2612.00
Post Rest x Mid-assessment	-0.05	-0.22, 0.11	2607.00	-0.17	-0.36, 0.02	2612.00
Pre Rest x Post-assessment	0.03	-0.13, 0.20	2607.00	-0.05	-0.24, 0.14	2612.00
Post Rest x Post-assessment	-0.06	-0.22, 0.11	2607.02	-0.22	-0.41, -0.03	2612.00
Training Group	-1.59 *	-2.52, -0.66	60.67	-0.23 ***	-0.30, -0.17	2612.29
Training Group x Post-assessment	-0.17	-0.30, -0.03	2607.04			
Training Group x Mid-assessment	-0.21 *	-0.35, -0.08	2607.00			
Training Group x Configuration A	0.69 ***	0.52, 0.87	2607.00			
Training Group x Configuration B	0.51 ***	0.34, 0.69	2607.00			
Training Group x Configuration D	0.54 ***	0.37, 0.72	2607.00			
Training Group x Configuration E	0.39 ***	0.22, 0.57	2607.00			
Random Effects						
σ^2	0.54			0.69		
$ au_{00}$	3.16 _{SubID}			4.43 _{SubID}		
ICC	0.85			0.87		
Ν	60 _{SubID}			30 SubID		
Observations	2685			2655		
Marginal R ² / Conditional R ²	0.158 / 0.	877		0.0 7 0 / 0.	875	

Table 3.15 Global Field Power (μV) by Condition

* p<0.01 ** p<0.001 *** p<1e-04

Note. Model parameters from simplified mixed effects models of GFP in microvolts incorporating condition (premeditation rest, compassion meditation, post-meditation rest) are provided. For each retreat, only effects that were significant in that retreat were retained. Effects are referenced to configuration C in the waitlist control group during compassion meditation at the pre-retreat assessment. A cut-off of p < .01 is used to determine statistical significance; the 95% CI is provided for each parameter estimate.



Note. The five microstate configurations, global centroids A - E, resulting from the *k*-means clustering procedure are presented, along with the file-level centroid maps that were assigned to each cluster. Each global topography is the centroid of their respective clusters of maps. Four file-level centroid maps went unassigned. Maps are 2-D isometric projections with nasion upwards.

Figure 3.2 Individual Microstate Sequences (A) Retreat 1 Training



Note. Figure continued on next page.



Note. Two-page figure. Microstate sequences for each participant in each epoch (close other, difficult other, all others) at each assessment (pre, mid, post), organized by group (retreat 1 training, retreat 1 control, retreat 2 control) are depicted. Note that Retreat 1 Control and Retreat 2 Training sequences depict the same participants as waitlist controls and in retreat training, respectively.



Figure 3.3 Heatmaps of Pairwise Dissimilarities (A) Retreat 1

Note. The pairwise dissimilarities between sequences calculated based on optimal matching (OM) of spells are depicted in symmetrical matrices. Note that the Retreat 2 matrix compares participants to themselves as controls.



Figure 3.4





Note. (A) Centroid distances between each assessment and epoch are depicted for each group. Centroid distances are the dissimilarity between the multivariate distance centers of two groupings, and represent the overall dissimilarity between those groupings. (B) Sequence medoids in each epoch at each assessment are depicted by group. A sequence medoid is the individual sequence that has the lowest dissimilarity with all other sequences in its grouping, making it the most representative single sequence.

Appendix 3A

Guided Compassion Meditation Transcript

Introduction

"For the next 12 minutes, you will be engaging in a guided compassion meditation. Please begin by sitting comfortably with your spine erect. Take 3 deep, relaxing breaths into your lower abdomen, keeping the abdomen soft and flexible. There will be a few moments of silence, during which you may settle your mind and body. You will then receive further instructions..."

Epoch 1: Close Other

"Now direct your attention to someone you know and care about who is suffering from physical or psychological distress. Let this person fill your heart and mind. Attend to his or her experience, and if you know the causes of the person's grief or pain, be present with those causes. Imagine shifting your attention into his or her perspective, experiencing his or her difficulties. Then return to your own perspective, imagine the person being present, and think: 'May you be free from suffering and the causes of suffering. Imagine this person finding relief and being free to lead a happy and meaningful life. Take some time to remain with that wish."

Epoch 2: Difficult Other

"Now bring to mind another person who, despite wishing to be free of suffering him or herself, causes you a great deal of difficulty. Shift your perspective to this person's perspective, imagining what it is like, and then return to your own. With an understanding of the consequences of this person's troubling, difficult behavior, wish that he or she be free of the mental afflictions that contribute to it. Let the heartfelt wish arise: 'May you have a clear vision of the path to freedom from suffering.' And imagine this person free of the causes of suffering. Stay with this thought for a few moments."

Epoch 3: All Others

"Now let the scope of your awareness rove through the world, attending to those who suffer, whether from hunger and thirst, from poverty or the miseries of war, from social injustice, or the imbalances and afflictions of their own minds. We are all deserving of compassion, especially when we act out of delusion, harming ourselves and others. Let your heart embrace the world, with the aspiration: 'May we all be free of suffering and its true causes, may we all help ease each other's pain."