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ORIGINAL PAPER

Changes in Multisensory Integration Following Brief State Induction and Longer-Term Training with Body Scan Meditation

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Abstract

Objectives The objective was to examine the impact of state and trait mindfulness cultivated through body scan meditation, on bodily multisensory integration, in order to explore effects of increased non-judgmental/accepting attention to ambiguous bodily sensations.

Methods Multisensory integration was operationalised through the rubber hand illusion, which was measured through subjective questionnaires, proprioceptive drift and skin conductance to perceived threat. State mindfulness was induced through a 20-min body scan meditation. Trait mindfulness was enhanced through a 14-day training programme of 10–15-min body scan meditation each day. An active control group engaged in relaxed listening. Trait mindfulness and trait bodily awareness were measured through questionnaires.

Results The state mindfulness induction was associated with a stronger reported rubber hand illusion than relaxed listening. In contrast, both 14 days of mindfulness training and of relaxed listening were associated with a decrease in reported rubber hand illusion, with a larger decrease after mindfulness training compared to relaxed listening.

Conclusions A state mindfulness induction increased participants' experience of the bodily illusion, while longer-term mindfulness training dampened the illusion, suggesting state and trait mindfulness via body scan meditation may have differential relationships with bodily multisensory integration. We discuss this finding in terms of initial attention-mediated salience of ambiguous somatosensory signals, followed by acceptance.

Keywords Mindfulness meditation · Body scan · Rubber hand illusion · Bodily ownership · Multisensory integration · Causal inference

One proposed mechanism for mediating the beneficial health effects of mindfulness meditation is increased bodily awareness. Many mindfulness-based interventions, such as mindfulness-based stress reduction (MBSR, Kabat-Zinn, 2003) and mindfulness-based cognitive therapy (MBCT, Segal et al., 2002), deliberately seek to cultivate an aware, non-judgmental relationship with bodily sensations. Recent meta-analyses have found that mindfulness meditation leads to small but significant improvements in accuracy of bodily awareness (Treves et al., 2019), and that mindfulness meditation has no relation to heartbeat-related interoceptive accuracy (Khalsa et al., 2020); a review of the effect of mindfulness interventions on self-related processes found mixed results for embodiment and interoception (Britton et al., 2021).

Body scan meditation is a form of mindfulness practice employed in many mindfulness-based interventions. It involves participants sequentially and non-judgmentally focusing their attention on parts of the body. This specific focus on the body distinguishes it from other mindfulness practices that can involve bodily sensations but also instruct participants to attend only to the breath, to sounds or more generally to the environment and to thoughts and emotions. Body scan meditation involves focused attention on bodily sensations, including interoception, touch and

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proprioception (see, e.g. Carmody & Baer, 2008; for review, see Gibson, 2019). Body scan meditation has been associated with increased sensitivity to tactile bodily sensations (Fox et al., 2012; Mirams et al., 2013) and non-reactivity to physical sensations (Benzo et al., 2018).

Only few studies have examined the effects of brief, body scan meditation interventions on bodily awareness. Mirams et al. (2013) found 15 min of body scan meditation reduced tactile misperception and increased sensitivity during the somatic signal detection task. Ussher et al. (2014) found 10 min of body scan meditation led to a significant reduction in ratings of pain-related distress and for pain interfering with social relations. Importantly, the effects of body scan meditation evolve with experience so a full appreciation of how body scan meditation relates to bodily awareness requires examining effects over time. To our knowledge, no prior research has attempted to contrast the differential effects of brief state inductions and longer-term, training-induced trait mindfulness on processes relating to bodily awareness.

Most research on the basic mechanism by which body scan meditation may mediate these varied bodily effects has focused on interoception (e.g. heartbeat) and fewer studies have looked at other aspects of embodiment (e.g. sense of ownership and agency; Britton et al., 2021). Since body scan meditation engages a constellation of sensory and cognitive processes across interoceptive and also tactile and proprioceptive inputs, it may be useful to focus on multisensory integration in the bodily domain and ask how body scan meditation might modulate this basic somatosensory mechanism, which is a key component of bodily awareness.

One potentially informative way of exploring the relationship between body scan meditation and bodily multisensory integration is by examining the effect of body scan meditation on the rubber hand illusion (Botvinick & Cohen, 1998). The rubber hand illusion involves a participant placing their hand into a box such that they cannot see their real hand but instead see a fake rubber hand. A brush is used to synchronously stroke both the unseen real hand and the seen fake hand. Seeing the rubber hand being stroked in synchrony with feeling one's own hand being stroked commonly creates perceptual effects (measured through questionnaires). These effects include a sense of ownership in the rubber hand as well as a perception that touch is being felt on the rubber hand rather than the real hand. Asynchronous stroking lessens or abolishes these effects. Objective measures often include proprioceptive drift (misperception of the spatial position of the participant's real hand towards the location of the rubber hand) and skin conductance responses to 'threats' to the rubber hand (e.g. hitting it with a hammer or bending a finger to an acute angle) (see, e.g. Ehrsson, 2012, 2020; Kilteni et al., 2015; Makin et al., 2008; Tsakiris et al., 2010; Tsakiris & Haggard, 2005).

The rubber hand illusion fundamentally results from multisensory integration, where visual, proprioceptive and tactile cues (in the synchronous as opposed to the asynchronous context) are integrated to form a coherent (but false) representation of the world (Chancel & Ehrsson, 2020; Ehrsson, 2012; Hohwy, 2013; Kilteni et al., 2015; Samad et al., 2015). The illusion involves several aspects that contribute to our broader bodily awareness and that are relevant for mindfulness meditation, including body ownership, body representation and mapping of personal and peripersonal space, and proprioception (for a review, see Kilteni et al., 2015).

The mechanism underlying multisensory integration relies on precision-weighted perceptual inference, which appears to be Bayes-optimal, including for visuo-proprioceptive integration (Alais & Burr, 2004; Chancel et al., 2016; Ernst & Banks, 2002; Körding et al., 2007; Reuschel et al., 2010; van Beers et al., 1999; for review, see Noppeney, 2021). Multisensory illusions arise when there is conflict between cues, which is resolved by adopting a false but coherent representation of the causal structure of the world. The factors that determine multisensory perceptual inference then include the following: the precision of sensory cues (i.e. how variable or noisy they are or are expected to be), how this precision may fluctuate over time (e.g. through adaptation), endogenous control of precision (through attentional allocation), the salience of the multisensory conflict (conceived as the divergence between the cues, determined by the means and precisions of the probability distributions representing them), prior beliefs and task-relevant salience of contextual spatiotemporal congruence (e.g. synchronicity, distance), and the availability of perceptual representations (generative causal models) to resolve such conflict. Recent psychophysical research and computational modelling of the rubber hand illusion has provided evidence that this illusion, and hence aspects of body ownership, bears the hallmarks of Bayes-optimal multisensory perceptual inference (Chancel, Ehrsson, et al., 2021; Chancel & Ehrsson, 2020).

Body scan meditation has two canonical components that can lead to predictions for the rubber hand illusion, conceived as multisensory perceptual inference (Bishop et al., 2004). First, attention to touch and proprioception prompted by the meditation instructions (see Supplementary Materials), which should increase the gain and hence precision of these perceptual cues in multisensory integration. Second, acceptance (i.e. attitudes of non-judgment and non-reactivity), which should dynamically modulate the response to (conflicting) multisensory input. Body scan meditation is thus of considerable interest to our mechanistic understanding of bodily multisensory integration and its influence on body representation and body ownership. Conversely, the rubber hand illusion provides a potentially fertile testing ground for understanding how body scan meditation interacts with fundamental sensory processing and perceptual inference under uncertainty, which can help understand the broader effects of mindfulness meditation in various settings.

The attentional component of body scan meditation would be expected to increase proprioceptive precision. The immediate hypothesis is that this will weaken the rubber hand illusion, since the true hand location is then better represented and harder to ignore. This would be consistent with previous research showing that individuals with higher proprioceptive acuity experience a weaker rubber hand illusion (Horváth et al., 2020; Pyasik et al., 2019). Changes to the relative precisions of sensory cues will affect the RHI according to these principles (Chancel, Ehrsson, et al., 2021). However, in the overall context of the rubber hand illusion, the attentional component will increase precision of the tactile cue as well as of proprioception. This will sharpen neural representation and therefore enhance the overall multisensory conflict between the visual, tactile and proprioceptive cues. This should in turn strengthen the imperative to resolve the conflict through perceptual inference on the basis of a causal model that could (falsely or veridically) explain the situation. This causal inference perspective (for review, see Noppeney, 2021; for discussion of the rubber hand illusion, see Hohwy, 2013; for psychophysics and modelling of the rubber hand illusion, see Chancel, Ehrsson, et al., 2021) leads to an alternative prediction with more complex nonlinearities that depend on whether stroking of the real and rubber hand is synchronous or asynchronous. Synchronous strokes suggest there must be a common cause of the cues so body scan meditation will strengthen the illusion. Asynchronous strokes suggest distinct causes of the visual and tactile cues so the illusion will be further weakened by body scan meditation. Whereas a dampening of the rubber hand illusion is the most intuitive prediction, suggested by previous research, there are thus two competing predictions for the attentional component of mindfulness meditation.

The acceptance component of body scan meditation would weaken the imperative to resolve the multisensory conflict by judging that the rubber hand is (or isn't) one's own. This leads to the prediction that the rubber hand illusion would be weakened during synchronous tapping, and also that there would be less strong disconfirmation of the illusion during asynchrony. However, these canonical mindfulness meditation components may dissociate temporally (Desbordes et al., 2015), such that attentional effects are seen first, and acceptance is cultivated later, after some training. Indeed, a week-by-week examination of differential changes on the Five Facet Mindfulness Questionnaire by Baer et al. (2012) found that changes on 'observing', 'acting with awareness' and 'non-reacting' preceded changes in 'non-judgment' during an MBSR programme.

Exploring this topic and investigating the relative contributions of attention and acceptance is important for designing successful mindfulness meditation interventions. Given such a temporal dissociation, it is of interest to investigate first an initial phase of state induction, which should be marked by attentional enhancement of bodily signals (noting that even brief amounts (10 min) of body scan meditation improves allocation of attention resources in novice meditators (Norris et al., 2018)), and then a post-training phase marked more by acceptance. The immediate prediction for the first phase would be dampening of the illusion, though noting the alternative prediction indicated above, followed by increased dampening in later phases, as acceptance emerges.

There have been only a few studies of mindfulness meditation and rubber hand illusion. Cebolla et al. (2016) found less sense of agency over the rubber hand in long-term meditators, and Xu et al. (2018) found mindfulness meditators to have a weaker subjective ownership experience of the rubber hand. This is consistent with the idea that acceptance after meditation training weakens the illusion. Neither of these studies found differences in other subjective experiences of the rubber hand illusion, nor in 23. Neither study was designed to test the hypotheses discussed above, around multisensory integration nor for dissociating the attention and acceptance components of mindfulness meditation. Lewis (2015) also takes a multisensory integration approach to the connection between mindfulness meditation and the rubber hand illusion. She reports no difference between groups in a pre/post, active control design testing the effects of a short (2–6 days) duration of mindfulness meditation on the rubber hand illusion. This suggests the extent of meditation training may have a dosage effect but we are unaware of any studies which also examine the immediate effects of a state mindfulness induction on the rubber hand illusion.

The aim of the present study was to elucidate the effects of state mindfulness induction and longer-term mindfulness training on bodily multisensory integration and body ownership. Specifically, we examined subjective and objective measures of the rubber hand illusion in a group who did body scan meditation and an active control group. State induction was assessed in an initial lab session and contrasted with longer-term effects after each group trained for 14 days in body scan meditation or the control exercise. We hypothesised that the body scan group would increase trait mindfulness more than the control group, and that only the participants who did the body scan meditations would demonstrate increased self-reported bodily awareness. We also hypothesised that body scan state induction would decrease the rubber hand illusion, though we note an alternative hypothesis here too, where the illusion is strengthened. We further predicted that after training, trait mindfulness would dampen the rubber hand illusion.

Methods

Participants

Thirty-three adult participants were recruited from Monash University, including students, staff and the wider community. All participants were novices to meditation, right-handed, neurotypical and healthy. Three participants failed to attend the second testing session, leaving a final sample of 30 participants, 16 in the mindfulness group (7 female-identifying, mean age = 25.8 years, (S)tandard (D)eviation = 11.2) and 14 active control participants (8 female-identifying, mean age = 21.7 years, SD = 5.5). Participants received monetary compensation of $20 for their time and travel expenses for each testing session. All study protocols were approved by the Monash University Human Research Ethics Committee (ID 2017–3290-7915) and all participants gave informed, written consent.

Procedures

After completing baseline assessments, participants were randomly allocated in a 1:1 ratio into either the body scan or the active control group. All participants were seated at a bench containing a black-out box such that the rubber hand apparatus was not visible. Each participant was asked to place their left hand into the box and their middle and index fingers were fitted with galvanic skin-conductance response (SCR) receptors. They were then instructed to keep their hand as still as possible. A black cloth was also placed over the participant's left shoulder and the left side of the box to obscure their left arm from vision.

Meditation

Both the body scan and active control groups were then asked to close their eyes while seated and listen to either a 20-min recording of a guided body scan meditation, or an audio recording of a TED talk on the topic of health and wellbeing (although specifically not mindfulness related; see Fig. 1a). The body scan meditation explicitly encouraged accurate perception of somatosensory experience and non-reactivity to physical sensations. The guidance was designed and recorded by an experienced mindfulness meditation teacher (RC). For the body scan meditation sessions, participants were asked to bring their awareness to different parts of their body and simply notice what sensation arose. When attention naturally drifted to thinking about other things, participants were asked to gently bring the attention back in an accepting and friendly manner. They were also encouraged to have an attitude of curiosity in regard to the sensations rather than one of judgment. During the meditation training session, the audio instructed them to systematically scan their attention through their whole body, including the left hand which was used as part of the rubber hand illusion induction (excerpts from the body scan meditation transcript are provided in the Supplementary Material). The experimenter left the room during this period and re-entered after a bell was rung by the participant upon the tape's completion. To minimise placebo effects and reporting bias, participants were unaware whether they were in the body scan or active control condition during this induction.

Rubber Hand Induction

The lights inside the box were then turned on to reveal a rubber left hand placed in front of the participant (under a semi-silvered mirror), aligned such that their shoulder was adjacent to the midpoint between the rubber hand and their true hand. The rubber hand was placed 22 cm from the real hand, and was a naturalistic prosthetic hand sourced from a local hospital prosthetics clinic; the hand had a light brown complexion and was not overtly male or female. The rubber hand had also been fitted with skin-conductance equipment similar to that placed on the participant's real left hand. Participants were instructed to keep their eyes fixed on the rubber hand while the experimenter stroked the rubber hand and the participant's real hand synchronously for 2 min with soft paint brushes. Strokes were approximately 2–5 cm along a finger on the hands, administered irregularly approximately every 1–2 s. Each pair of strokes was administered to the same spot on both hands, and different parts of the hand were touched over the 2-min trial. The same procedure was repeated for another 2 min of asynchronous stroking where the experimenter stroked the real and rubber hands asynchronously. Here, strokes were alternating irregularly in time to break the semblance of synchrony, with approximately a 0.5–1-s delay between strokes on the real hand and strokes on the rubber hand. The strokes in each condition were not counted but the experimenter was trained to deliver at approximately the same rate. Finally, synchronous and asynchronous trials were counterbalanced (see Fig. 1b: stroke). The synchronous stroking condition and asynchronous stroking were repeated two times each for a total of 6 trials per participant in the first session (see Fig. 1b). Each of the 6 stroking trials was followed by three measures, namely threat, drift and survey.

Threat Challenge to Rubber Hand

Next, the experimenter placed a finger on both the real and rubber index finger and then applied pressure to the rubber hand bending it back to an unnatural angle to provide a

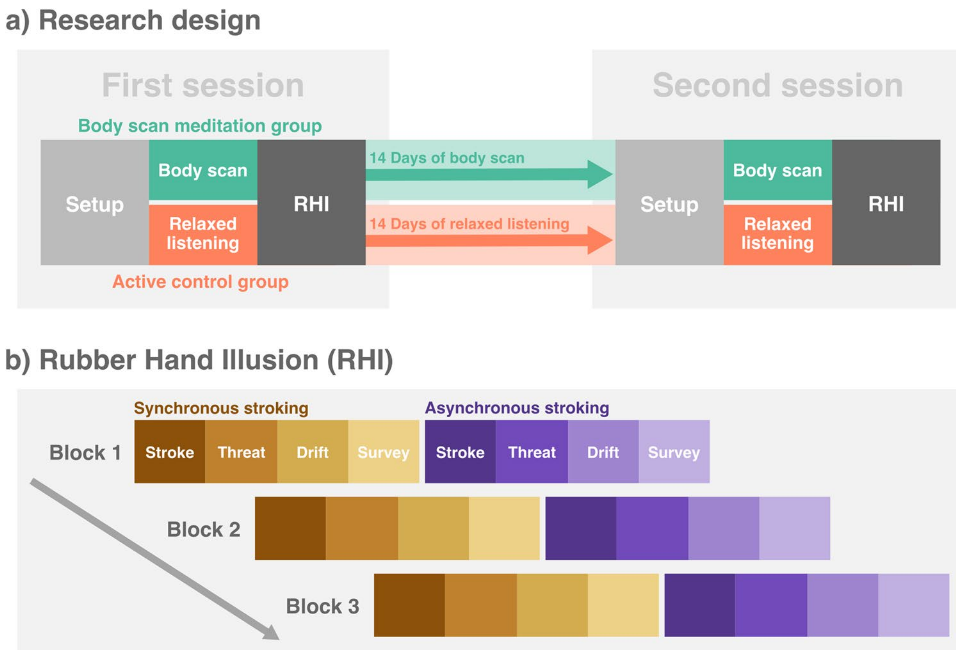

Fig. 1 Research design and rubber hand illusion procedure. **a** Between-subjects research design. Both groups conducted the same sequence of training and testing except that the Experimental intervention involved pre-recorded guided body scan meditation instructions and the active control intervention was an equivalent period of relaxed listening with TED Talks. Task instructions were read to each participant from the same script informing them that the study would involve 'mindfulness and relaxation'. Thus participants were blinded to the specific format of relaxation. RHI reflects three blocks of Rubber Hand Illusion. **b** Procedure for rubber hand illusion. First, the illusion was induced by stroking for two minutes (either synchronous or asynchronous movement with the actual and rubber-hand, order counterbalanced between-subjects). Second, the rubber hand was threatened to elicit a skin-conductance response. Third, drift was measured between the actual and perceived location of the participant's hand relative to the rubber hand. Fourth, a survey was completed that included both control and illusion questions. This sequence was duplicated for the alternate movement condition and the entire procedure was repeated for three blocks in both the first and second lab sessions. As such, participants had 12 exposures to the rubber hand illusion in total

threat stimulus (see Fig. 1b: threat). The level of response to this 'threat' was measured using skin-conductance response. Most prior research has used more drastic threats, such as knives and needles; the finger bending procedure has been used in Armel and Ramachandran (2003) and was used here to prevent moving the attentional focus from the body to some other non-body object.

Proprioceptive Drift Assessment

The box was then blacked out so that both hands were obscured. The experimenter then dragged a marker-block across a line on the surface of the box and the participant was asked to say 'stop' when they felt that the marker was placed above where it felt as if their middle finger was. The measurement of this distance from their actual middle finger (which was positioned on the same marker within the box for each participant) was then taken by the experimenter (Fig. 1b: drift).

Subjective Rubber Hand Illusion Assessment

Next, participants were asked to complete a series of questions which they answered using their right hand, marking each response on a sliding scale from agreement to disagreement (500 to −500) (Fig. 1b: survey). The statements inquired into the participant's experience of the illusion. They included three illusion and four control questions (see Table 1). These statements were adapted from the widely used questionnaire in Botvinick and Cohen (1998), and included control questions designed to speak to unusual experiences unrelated to the rubber hand illusion (such as the room changing temperature); versions of these questions have been used in several previous studies.

Between-Session Training Period

There were two lab sessions, spaced 14 days apart. Between sessions, the body scan group was asked to do body scan meditation in which they were instructed to attend to

Table 1 Subjective RHI questionnaire

Questionnaire item	Question
Illusion Q1	It seemed as if I was feeling the touch of the paintbrush in the location where I saw the rubber hand being touched
Illusion Q2	It felt as if the rubber hand were my hand
Illusion Q3	It seemed as though the touch I felt was caused by the paintbrush I could see
Control Q1	It seemed as if I was in two locations at the same time
Control Q2	I found the touch of the paintbrush on my hand was pleasant
Control Q3	I felt the room temperature change during the experiment
Control Q4	I found myself liking the rubber hand

different bodily sensations in a non-judgmental and accepting way (using a supplied audio meditation) for 10 min per day in the first week and then 15 min per day in the second week. The guidance was designed and recorded by an experienced mindfulness meditation teacher (RC), and was a shortened version of the 20-min state body scan meditation described above. The active control group was asked to listen to the audio feed of non-mindfulness related TED talks with a similar frequency and duration as the body scan group. Both groups were asked to fill in a homework sheet every day, indicating what time of day they practised and any observations from their experience to encourage accurate reporting. As a supplementary compliance measure in the body scan group, we also tracked the number of times each participant listened to each meditation recording (a similar check for the TED talks was not feasible).

Second Lab Session

Following 14 days of at-home body scan meditation or relaxed listening, participants returned for a second lab session. These followed an identical structure to the first, with the same measures, procedures and order. Participants completed survey measures before commencing the session.

Measures

Prior to each participant entering the lab, they were asked to complete a demographics questionnaire as well as survey measures of trait mindfulness and dispositional bodily awareness.

Five Facet Mindfulness Questionnaire

Trait mindfulness was measured using the Five Facet Mindfulness Questionnaire (FFMQ, Baer et al., 2008). The FFMQ is a 39-item self-report scale measuring five facets of mindfulness: Observing, Describing, Acting with awareness, Non-judging and Non-reacting. Participants rate the items on a 5-point Likert scale ranging from 1 ('never or very rarely true') to 5 ('very often or always true'). The scale is summed and higher scores (overall or on each facet) indicate higher levels of mindfulness. The FFMQ has consistently shown excellent psychometric properties (Baer et al., 2009), with high levels of construct validity and reliability (Choi, 2015).

Multidimensional Assessment of Interoceptive Awareness

Bodily awareness was measured using the Multidimensional Assessment of Interoceptive Awareness (MAIA, Mehling et al., 2012). The MAIA is a 32-item self-report scale measuring eight facets of interoceptive awareness: Noticing (awareness of uncomfortable, comfortable, and neutral body sensations), Not-distracting (avoiding the tendency to ignore or distract oneself from sensations of pain or discomfort), Not-worrying (avoiding emotional distress or worry with sensations of pain or discomfort), Attention regulation (the ability to sustain and control attention to body sensation), Emotional awareness (awareness of the connection between body sensations and emotional states), Self-regulation (the ability to regulate psychological distress by attention to body sensations), Body listening (actively listening to the body) and Trusting (experiencing one's body as safe and trustworthy). Participants rate the items on a 6-point Likert scale ranging from 0 ('never') to 5 ('always'). The scale is summed and higher scores (overall or on each facet) indicate higher levels of interoceptive awareness. The MAIA has good psychometric properties, with Cronbach's alpha varying among the subscales: Noticing (0.69), Not-distracting (0.66), Not-worrying (0.67), Attention regulation (0.87), Emotional awareness (0.82), Self-regulation (0.83), Body listening (0.82) and Trusting (0.79).

Skin Conductance Recording

Skin conductance was monitored continuously throughout the experiment using electrodermal conductors placed on the middle and index fingertips, and recorded to Lab Chart software at a 1000-Hz sample rate. Individuals with a mean skin-conductance response of less than 0.1 μS in both the synchronous and asynchronous movement conditions were considered to be non-responders and were excluded from our analysis (Armel & Ramachandran, 2003; Figner & Murphy, 2010). Two non-responders were identified, one participant from each group. Three additional participants (one from the body scan group and two from the active control group) were excluded from skin-conductance measurement due to excessive sweating. This left a final sample of 25 participants (14 in the body scan group and 11 in the active control group).

During the experiment, the experimenter flagged the start and the end of each threat epoch with a key press. To compute the skin-conductance response to each threat, data were pre-processed according to the procedure outlined by Taschereau-Dumouchel et al. (2018). Baseline skin conductance was determined for each threat response by calculating the mean electrodermal activity over a four-second time window prior to the start of each threat epoch. This baseline value was then subtracted from the maximum skin-conductance response recorded over the threat epoch to determine each threat response. Finally, threat responses were square-root transformed to correct for skewness of the distribution.

Time-stamping the RHI

The start of the stroking period, the end of the stroking period and the administration of the threat stimulus, taking the drift measurement and question responses, were all time stamped using Lab Chart within the SCR data.

Data Analyses

The personality inventories, bodily awareness survey, proprioceptive drift and skin-conductance data were each analysed using frequentist and Bayesian mixed-effects model comparison in R (R Core Team, 2021). We adopted mixed-effects analysis because it allowed us to account for the hierarchical structure of our research design in ways that cannot be captured using traditional techniques such as repeated-measures ANOVA (Meteyard & Davies, 2020). Models were computed using the *lme4* package (Bates et al., 2015). We included random intercepts for each subject and random slopes for each fixed factor in all models. Interaction terms were included to capture any differences between the body scan and active control groups. Frequentist statistics were computed using the *lmerTest* (Kuznetsova et al., 2017) package which calculates *p*-value estimates using Satterthwaite approximation. Residual plots confirmed that assumptions of normality and homoscedasticity were not violated.

Bayesian analyses were performed using the *BayesFactor* (Morey et al., 2015) and *BayesTestR* (Makowski et al., 2019) packages. Bayes factors quantify evidence in favour of both the alternative and null hypotheses. For example, a Bayes factor $BF_{10} = 15$ indicates the observed data are fifteen times more likely to be observed under the alternative hypothesis (H1) than the null (H0). Conversely, when $BF_{10} = .25$, the observed data are four times more likely to be observed under the null than the alternative hypothesis. We included subjects as a random intercept in all models. Consequently, the null model (H0) for all comparisons was a model including the grand-mean but also the subject's mean as an additive factor. We used a Jeffreys-Zellner-Siow (JZS) prior to calculate Bayes factors (Rouder et al., 2009). The JZS is a conservative prior that minimises assumptions about the range of effects by combining a Cauchy prior on effect size and Jeffreys prior on variance. Specifying the scale of the prior in Bayesian analysis optimises Bayes factors for effects of particular pre-specified magnitude. We specified a conservative, medium scale ($r = 0.5$) for all fixed effects and 'nuisance' scale ($r = 1$) for random effects (Rouder et al., 2012).

RHI Magnitude: a Measure of Illusory Experience in the Rubber Hand Illusion

Studies that induce the rubber hand illusion using both synchronous and asynchronous stroking typically observe different illusory experiences for one versus the other stroking type (Botvinick & Cohen, 1998; Chancel & Ehrsson, 2020; Kilteni et al., 2015; Samad et al., 2015). The illusion is enhanced when visuotactile stimulation is synchronous and is weaker, or even inhibited, when stroking is asynchronous. This has become a central explanandum for theories of the rubber hand illusion and asynchronous stroking is commonly used as a control condition in studies that employ the paradigm.

Observing opposing effects for each stroking type could complicate the overall picture that emerges about mindfulness training and the rubber hand illusion. To account for this, we computed an overall measure of illusory experience that reflects the difference between synchronous and asynchronous stroking. Specifically, our measure of illusion experience, RHI magnitude, was computed by subtracting subjective ratings in the asynchronous stroking condition from ratings in the synchronous stroking condition.

Results

First Session

Rubber Hand Illusion Induction

We used the conventional method to test whether the rubber hand illusion was induced, comparing participant's agreement with control and illusion questions when stroking of the rubber hand and real hand was synchronous or asynchronous (stroking type). A significant effect of stroking type was observed ($BF_{10} = 2.66 \times 10^{43}$, $F(1,7.63) = 32.48$, $p < 0.001$, $e_p^2 = 0.81$) that was moderated by an interaction between stroking type and question type ($BF_{10} = 3.87 \times 10^{22}$, $F(1,981.85) = 177.29$, $p < 0.001$, $e_p^2 = 0.15$). Tukey-adjusted pairwise contrasts revealed a significant difference between stroking type for illusion questions ($t(9.64) = 8.84$, $p_{tukey} < 0.001$), synchronous stroking associated with higher ratings than asynchronous stroking, but not control questions ($t(8.63) = 1.98$, $p_{tukey} = 0.27$), as shown in Supplementary Fig. 1. These results are consistent with successful induction of the rubber hand illusion. In our next set of analyses, we investigated whether differences were observed between the groups for each measure of the rubber hand illusion.

Survey

To test whether subjective experience of the rubber hand illusion differed for each group (body scan mediation or active control) after their first exposure to meditation or the relaxed listening control task, we examined ratings for illusion questions only. These were compared between groups for each stroking type. We observed a significant main effect of stroking type ($BF_{10} = 9.34 \times 10^{76}$, $F(1,8.78) = 47.72$, $p < 0.001$, $e_p^2 = 0.84$) that was moderated by an interaction between stroking type and group ($BF_{10} = 6.98 \times 10^{8}$, $F(1,28) = 6.96$, $p = 0.013$, $e_p^2 = 0.20$). Tukey-adjusted pairwise contrasts were used to examine the interaction. Synchronous stroking was associated with stronger experience of the illusion than asynchronous stroking for both groups (each $p_{tukey} < 0.005$) but the difference between stroking types was largest for the group that performed 20 min of body scan meditation.

Body scan meditation participants had higher ratings on average than control participants when stroking was synchronous (body scan group: (M)ean = 256.06, (S)tandard (D)eviation = 274.96) vs. active control group: $M = 161.94$, SD = 340.83) and lower ratings when stroking was asynchronous (body scan group: M = −269.83, SD = 274.97) vs. active control group: $M = -123.38$, SD = 297.52), although these differences were not statistically significant after correction for multiple comparisons (each $p_{tukey} > 0.25$), as shown in Fig. 2.

To clarify the effects of group (body scan meditation or active control) between stroking conditions, we conducted a between group comparison using our novel measure of illusory experience: RHI magnitude (see 2). The effect of group was significant ($BF_{10} = 4.34$, $t(27.39) = 2.64$, $p = 0.013$, $d = 0.97$), and illusory experience was greater for the body scan group ($M = 525.88$, SD = 332.08) than the active control group ($M = 285.32$, SD = 309.86), as shown in Fig. 3. Despite a large degree of individual variability, these results

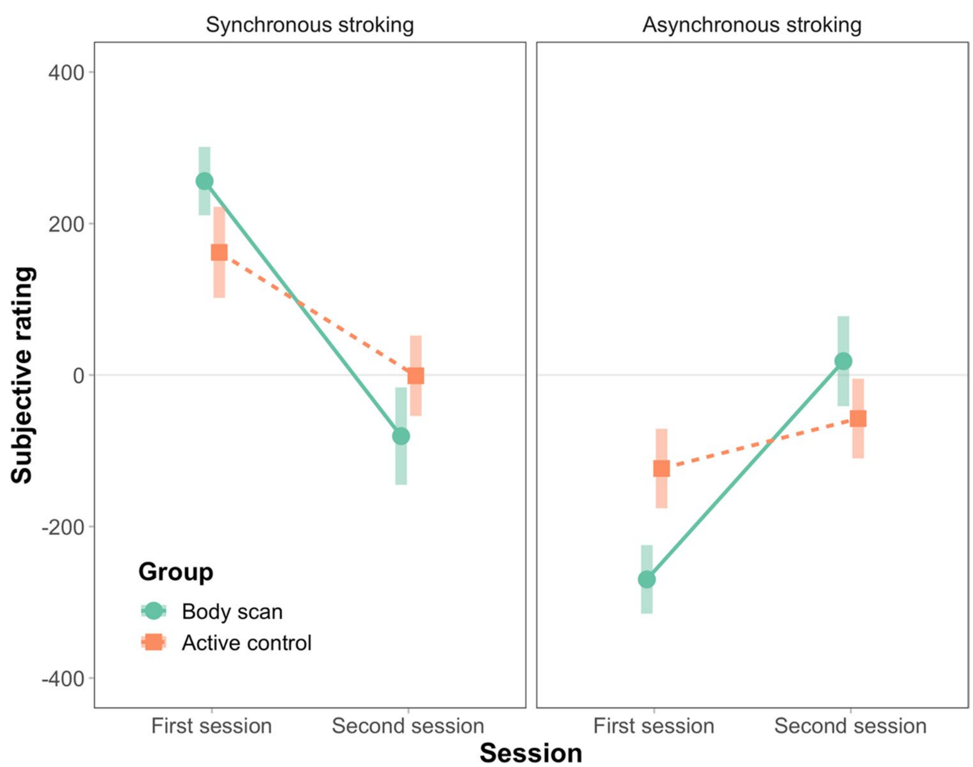

Fig. 2 Mean ratings of illusion questions as a function of group, session and stroking type. Error bars are 95% confidence intervals

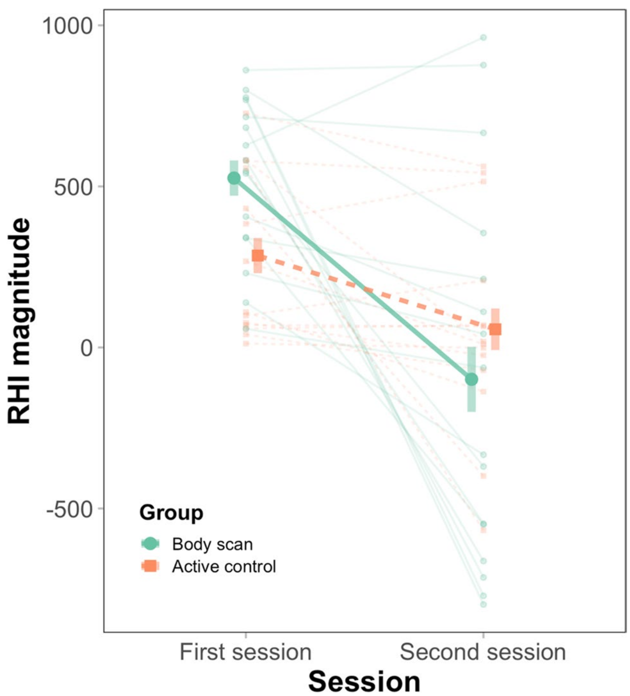

Fig. 3 Body scan meditation is associated with a dampening in subjective experience of the rubber hand illusion. Mean RHI magnitude (synchronous ratings—asynchronous ratings) as a function of session and group. Individual subject data plotted in background. Error bars are 95% confidence intervals

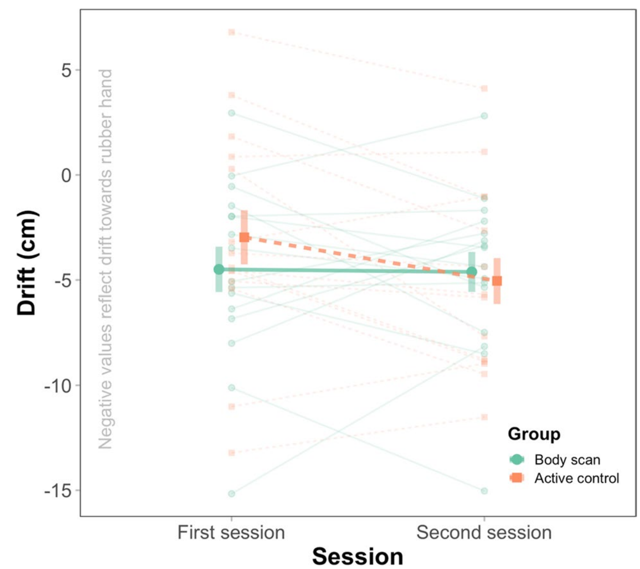

Fig. 4 Bayesian analysis indicates greater proprioceptive drift for control participants but not for body scan meditators after training. Individual subject data plotted in background. Zero reflects the position of each participant's actual index finger. Negative values are illusory proprioceptive drift—misperceiving the position of the real hand as being closer to the rubber hand. Error bars are 95% confidence intervals

are consistent with the conclusion that subjective experience of the rubber hand illusion was greater on average for participants who performed 20 min of body scan meditation than controls.

Proprioceptive Drift

Consistent with previous findings of proprioceptive drift in the RHI, participants exhibited a large displacement in the perceived location of their real hand, approximately 3.78 cm (SD = 4.84) towards the rubber hand on average (test against zero: $t(29) = 4.28$, $p < 0.001$, $d = 0.78$). To test whether proprioceptive drift differed as a function of group, we examined drift between groups for each stroking type. The main effect of stroking type was significant ($BF_{10} = 103$, $F(1,28) = 8.68$, $p = 0.006$, $e_p^2 = 0.24$), and drift towards the rubber hand was larger for synchronous stroking ($M = 4.69$, SD = 6.17) than asynchronous stroking ($M = 2.88$, SD = 4.97). Drift towards the rubber hand was not significantly different between the body scan group ($M = 4.50$, SD = 5.33) and the active control group (M = 2.97, SD = 5.94) ($BF_{10} = 0.47$, $F(1,28) = 0.73$, $p > 0.25$, $e_p^2 = 0.03$), as shown in Fig. 4.

Skin Conductance

Participants exhibited a pronounced skin conductance response when the rubber hand was threatened, approximately 1.26μS (SD = 1.24) on average (test against zero: $t(26) = 5.33$, $p < 0.001$, $d = 1.03$). To test whether the threat response differed as a function of group, we examined skin conductance between groups for each stroking type after excluding two non-responders (one from each group, see 15). The null hypothesis was supported for all effects (each $BF_{10} < 0.33$, $p > 0.25$). Threat response was equivalent for both stroking types and did not differ between groups, as shown in Fig. 5.

Second Session and Pre/Post Analyses

Compliance

Homework results for meditators were crosschecked against the plays listed for each individual audio link to confirm that participants completed the instructed level of training. In the body scan group, 87.5% of participants completed at least 50% of training sessions. The average number of body scan meditation sessions completed per participant was 10.13 (SD = 3.90) with an average duration of 12.19 min each. In

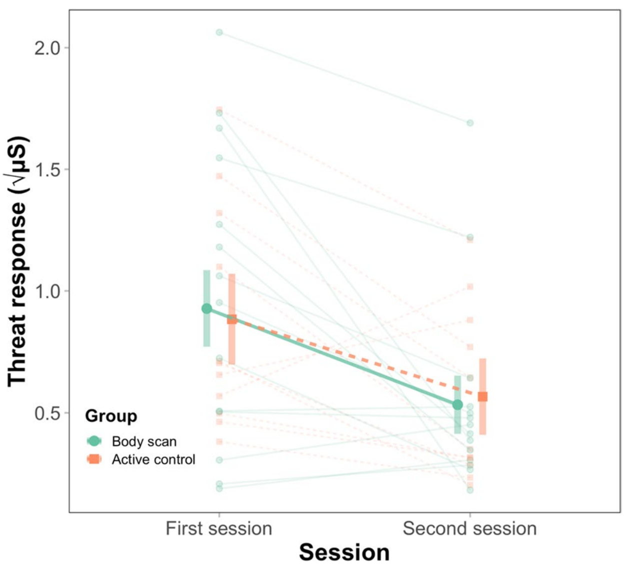

Fig. 5 Threat response is statistically equivalent for the body scan and active control groups. Bayesian analysis supports the null hypothesis for the interaction between session and group. Threat response computed using the method outlined in Taschereau-Dumouchel et al. (2018), (see 15 in the '2' section). Individual subject data are plotted in the background. Errorbars are 95% confidence intervals

Table 2 Scale reliability statistics for the first and second session

	First session		Second session	
	ω	α	ω	α
FFMQ				
Observing	0.72	0.70	0.80	0.79
Describing	0.92	0.92	0.93	0.93
Acting with awareness	0.91	0.91	0.90	0.91
Non-judging	0.93	0.93	0.92	0.92
Non-reactivity	0.82	0.79	0.77	0.75
MAIA				
Noticing	0.77	0.76	0.75	0.75
Not worrying	0.99	0.60	0.82	0.78
Emotional awareness	0.69	0.69	0.74	0.75
Body listening	0.86	0.86	0.84	0.83
Not distracting	0.80	0.80	0.17	0.35
Attention regulation	0.86	0.85	0.87	0.86
Self-regulation	0.87	0.87	0.91	0.91
Trusting	0.99	0.88	0.86	0.85

ω, McDonald's omega; α, Cronbach's alpha

total, participants meditated for an average of 123.44 min each (SD = 51.79) over the course of the training period. Training was not recorded for each individual participant in the active control group but homework sheets were examined to ensure this group completed the instructed level of training (100% of participants completed at least 50% of relaxed listening sessions). Data from all participants were included in the analyses reported in this paper. We note that the same pattern of results were observed when statistics were re-computed with only those participants that completed at least 50% of training sessions.

Effects of Training on Trait Mindfulness and Bodily Awareness

To examine the effects of training on trait mindfulness and bodily awareness, we compared responses on the FFMQ and MAIA between the first and second lab sessions. Scale reliability was high in both sessions (Table 2). We observed a significant increase in trait mindfulness in the lab session after body scan meditation training, driven by changes in the observing, describing and non-reactivity facets, with no significant difference between groups (Table 3).

Bodily awareness, as measured by the MAIA, was broadly unchanged for both groups (Table 4). The null hypothesis was supported for four of eight subscales which indicates these dimensions did not change between the first and second session. However, we observed a significant increase in the second session for one subscale of the MAIA (not distracting—the tendency not to ignore or distract oneself from bodily sensation of discomfort and pain). Increases in this subscale were observed in both groups.

Rubber Hand Illusion

We also tested whether the rubber hand illusion was induced in the second lab session. For this, we used the same method as in the first session—comparing ratings for each question type and stroking type. A small but significant interaction was observed between stroking type and question type ($BF_{10} = 1.24$, $F(1,548.11) = 8.58$, $p = 0.004$, $e_p^2 = 0.02$). After correction for multiple comparisons, pairwise contrasts revealed that the difference between stroking types was not significant for either illusion questions ($t(32.43) = -0.48$, $p_{tukey} > 0.25$) or control questions ($t(31) = 0.88$, $p_{tukey} > 0.25$) (Supplementary Fig. 1 and Supplementary Fig. 2). These results are consistent with an effect that is small at the level of single events but potentially more ultimately consequential (Funder & Ozer, 2019). Nevertheless, it represents dampening of the illusion in the second lab session compared to the first, which we examine in the following analyses.

The Effect of Pre/Post Session and Group on Rubber Hand Illusion Experience

To examine the effects of the 14-day body scan meditation training or control exercise on subjective experience of the

Table 3 Means, standard deviations and *F* statistics for the Five Facet Mindfulness Questionnaire (FFMQ)

	Body scan		Active control		Session	Group	Session × group
	First session	Second session	First session	Second session			
Observing	3.42 (.54)	3.71 (.45)	3.09 (.55)	3.26 (.76)	**5.45***	**4.24***	.35
Describing	3.32 (.74)	3.54 (.71)	3.15 (.76)	3.33 (.86)	**5.71***	.55	.12
Acting with awareness	2.82 (.72)	2.88 (.67)	3.10 (.75)	3.02 (.81)	**< .01**[NE]	.61	.73
Non-judging	2.65 (.72)	3.01 (.83)	3.15 (.98)	3.13 (.94)	3.04	1.06	4.10
Non-reactivity	3.07 (.52)	3.33 (.51)	2.91 (.65)	3.03 (.54)	**4.32***	1.57	.52
Total	15.28 (1.50)	16.48 (1.69)	15.40 (2.33)	15.76 (2.47)	**7.79****	.20	2.25

Standard deviations are in parentheses. *$p < .05$; **$p < .01$; [NE]$BF_{10} < 0.33$

Table 4 Means, standard deviations and *F* statistics for Multidimensional Assessment of Interoceptive Awareness (MAIA)

	Body scan		Active control		Session	Group	Session × group
	First session	Second session	First session	Second session			
Noticing	3.11 (.81)	3.00 (1.08)	3.06 (1.14)	2.93 (1.08)	**.27**[NE]	.03	**< .01**[NE]
Not worrying	2.42 (.86)	2.52 (.85)	2.18 (.99)	2.36 (1.26)	.83	.51	.12
Emotional awareness	3.09 (.91)	3.18 (1.13)	3.25 (.83)	3.40 (.97)	**.27**[NE]	.49	.02
Body listening	2.06 (1.08)	2.75 (1.09)	2.03 (1.28)	2.33 (1.27)	3.16	.39	.56
Not distracting	1.67 (.83)	2.48 (.97)	2.13 (.95)	2.21 (.76)	**5.12***	.16	3.51
Attention regulation	2.57 (.77)	2.74 (1.16)	2.44 (.72)	2.44 (.80)	**.23**[NE]	.50	.42
Self-regulation	2.83 (.90)	3.17 (1.18)	2.58 (1.14)	2.91 (1.22)	2.57	.39	.03
Trusting	3.38 (.61)	3.23 (1.12)	3.18 (1.30)	3.64 (1.22)	**.90**[NE]	.07	3.06

Standard deviations are in parentheses. *$p < .05$, [NE]$BF_{10} < 0.33$

rubber hand illusion and whether these effects differed as a function of group, we contrasted ratings for groups (body scan meditation or active control), session (first or second) and stroking types (synchronous or asynchronous) (Fig. 2). To be consistent with the first session, we included only illusion questions in this analysis. We observed a three-way interaction between group, session and stroking type ($BF_{10} = 8.65 \times 10^7$, $F(1,984) = 63.48$, $p < 0.001$, $e_p^2 = 0.06$). Tukey-adjusted pairwise contrasts were used to examine the interaction. In the body scan group, we observed a significant change in subjective ratings between lab sessions for both synchronous ($t(24.9) = 11.12$, $p_{tukey} < 0.001$) and asynchronous ($t(24.9) = -9.52$, $p_{tukey} < 0.001$) stroking. In the active control group, subjective ratings differed between lab sessions for synchronous ($t(28.9) = 5.05$, $p_{tukey} < 0.001$) but not asynchronous ($t(28.9) = -2.05$, $p_{tukey} = 0.47$) stroking, as shown in Fig. 2.

To clarify the effects of body scan meditation training over both stroking conditions, we used our novel measure of illusory experience: RHI magnitude (see the '2' section). The measure was modelled as a function of group and session. We observed a main effect of session ($BF_{10} = 6.54 \times 10^{34}$, $F(1,506) = 221.5$, $p < 0.001$ $e_p^2 = 0.30$) moderated by an interaction between session and group ($BF_{10} = 5.52 \times 10^8$, $F(1,506) = 47.65$, $p < 0.001$, $e_p^2 = 0.09$). Tukey-adjusted pairwise contrasts revealed a reduction in RHI magnitude between sessions for both groups (each $p_{tukey} < 0.05$) but reduction was greatest for the body scan group ($t(20.21) = 4.92$, $p_{tukey} < 0.001$) compared to the active control group ($t(18.7) = 1.77$, $p_{tukey} = 0.32$), as shown in Fig. 3.

The Effect of Pre/Post Session and Group on Proprioceptive Drift

In the second lab session, participants continued to exhibit a large proprioceptive drift of approximately 4.82 cm ($SD = 4.19$) towards the rubber hand (test against zero: $t(29) = 6.29$, $p < 0.001$, $d = 1.15$). To clarify this result, we analysed drift for both groups (body scan meditation or active control), session (first or second) and stroking types (synchronous or asynchronous). Drift towards the rubber hand was significantly larger for synchronous stroking ($M = 5.75$, $SD = 5.05$) than asynchronous stroking ($M = 3.88$, $SD = 4.45$; $BF_{10} = 6470.69$, $F(1,28) = 17.09$, $p < 0.001$, $e_p^2 = 0.38$).

Our Bayesian analysis indicated evidence for a small interaction between session and group ($BF_{10} = 5.29$, $F(1,28) = 2.27$, $p = 0.14$, $e_p^2 = 0.07$). Relative to the first lab session, pairwise contrasts demonstrated a slight increase in 23 in the second session for the active control group ($t(28) = 2.19$, $p_{tukey} = 0.151$, $p_{uncorrected} = 0.037$) but no change for the body scan group ($t(28) = 0.14$, $p_{tukey} = 0.999$, $p_{uncorrected} = 0.892$, as shown in Fig. 4.

The Effect of Session and Group on Skin Conductance

In the second lab session, participants continued to exhibit a skin-conductance response when the rubber hand was threatened—approximately 0.49μS (SD = 0.72) on average (test against zero: $t(26) = 3.55$, $p = 0.001$, $d = 0.68$). To test whether this physiological response differed as a function of training, we analysed threat response for both groups (body scan meditation or active control), session (first or second) and stroking types (synchronous or asynchronous). Two non-responders were excluded from this analysis (one from each group). The difference in threat response between the first and second session was significant ($BF_{10} = 7.0 \times 10^5$, $F(1,23.48) = 13.66$, $p = 0.001$, $e_p^2 = 0.37$), and skin conductance to threatening the rubber hand was greater in the first than the second session, as shown in Fig. 5. No significant differences were observed between stroking types ($BF_{10} = 0.11$, $F(1,26.63) = 0.43$, $p > 0.25$, $e_p^2 = 0.02$). Critically, the null hypothesis was supported for the interaction between session and group ($BF_{10} = 0.21$, $F(1,23.49) = 0.42$, $p > 0.25$, $e_p^2 = 0.02$). This result indicates that the reduction in physiological response to threatening the rubber hand between sessions was equivalent for participants in both groups, as shown in Fig. 5.

Discussion

This study examined the relationship between state and trait body scan meditation on bodily multisensory integration, assessed via the rubber hand illusion; in addition, the study measured bodily awareness, via the MAIA. An experimental group undergoing a 20-min body scan meditation (leading to state mindfulness) was compared to an active control group undergoing a 20-min period of relaxed listening. These groups were then asked to do 10–15-min per day of body scan meditation training or relaxed listening to the audio feed of TED talks on non-mindfulness wellbeing topics, respectively, over a 14-day period to allow an examination of the effects of increased trait mindfulness.

The results are that state induction of body scan mindfulness strengthens the rubber hand illusion, compared to the control group, whereas 14 days of body scan meditation training dampens the subjective reports of the illusion, with the body scan group exhibiting a greater dampening of the rubber hand illusion than the control group after training. The body scan group did not exhibit a greater increase in trait mindfulness than the control group as both groups experienced an increase in self-reported mindfulness between the two testing sessions. Body scan participants did not demonstrate a greater increase in self-reported bodily awareness since we did not observe a significant difference between the groups in the second assessment session.

Effects of State Induction on the Rubber Hand Illusion

The rubber hand illusion was successfully induced for both the body scan meditation and active control groups. In both groups, synchronous stroking was associated with stronger subjective ratings than asynchronous stroking—the latter condition commonly resulting in a weaker experience of the illusion (Botvinick & Cohen, 1998). The body scan group demonstrated a larger difference between synchronous and asynchronous stroking than the control group after the state induction. This fails to support the most intuitive hypothesis—which would be in accordance with basic principles for multisensory integration—that endogenous attention enhances the precision of the proprioceptive cue. This in turn would hinder visual capture of touch such that body scan–mediated attention to proprioception should hinder the rubber hand illusion.

An alternative account, based on a more comprehensive perspective on multisensory integration and its role in causal inference, may help interpret the result. In this account, body scan meditation would also increase the precision on the tactile cue, leading to a more salient visuotactile-proprioceptive multisensory conflict. Such conflict signals uncertainty, which the perceiver must resolve by inferring a causal state of affairs that can best explain the sensory input (Körding et al., 2007; Noppeney, 2021); body scan meditation would initially therefore increase the imperative to resolve uncertainty. The spatiotemporal contextual cue provided by the synchronous and asynchronous stroking conditions would then distinguish between an illusory and a veridical inference: synchrony more convincingly binds the felt touch with the seen touch on the rubber hand, whereas asynchrony more clearly disambiguates between the seen touch and the felt touch. This constellation of effects would explain why the rubber hand illusion persists even if proprioception is strengthened. The fact that the illusion is stronger in the body scan group than in the control group can then be explained by the increased salience of the multisensory conflict and the corresponding effort needed to arrive at a satisfactory perceptual inference; slightly more technically, an inference that can resolve the increased uncertainty would be equivalent to a representation that accumulates more evidence in its own favour, leading to a stronger belief.

Proprioceptive drift is commonly, though not uniformly, positively correlated with the rubber hand illusion

(Abdulkarim & Ehrsson, 2016; Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2014; though see Rohde et al., 2011). Both groups demonstrated a considerable displacement towards the rubber hand, and this effect was larger for synchronous than asynchronous stroking. Though the body scan group had a more pronounced illusory experience, no substantial group difference in drift was observed.

Both groups exhibited a pronounced skin conductance response to 'threat' to the rubber hand, supporting the notion that participants experienced the rubber hand as their own. However, this response did not differ between synchronous and asynchronous stroking, nor did it differ significantly between groups. The failure to distinguish synchronous and asynchronous conditions limits skin conductance as an outcome measure in this experiment. It may have to do with our choice of the less commonly used finger bending threat (adapted from Armel & Ramachandran, 2003) instead of knife or needle threats (e.g. Ehrsson et al., 2007; Fan et al., 2021; Guterstam et al., 2011, 2013; Petkova & Ehrsson, 2009); this threat type was used to avoid directing attention to external objects and away from the body but may have interfered with the illusion itself. In addition, the study had repeated trials of the rubber hand illusion and skin conductance responses to repeated presentation of threat stimuli decreases with time (Andreassi, 2013), which may have made it harder to detect differences between conditions. Body scan meditation does explicitly encourage non-reactivity to physical sensations and mindfulness is linked with reduced reactivity generally (for review, see, Pascoe et al., 2017). It is possible that this has dampened the skin conductance response to threat for the otherwise more strongly felt illusion in the body scan group. In addition, prior research on mindfulness meditation and skin conductance has found diverging results in terms of skin conductance response, with no clear association for trait mindfulness and rare cases of changes in response following state mindfulness meditation induction (Paz et al., 2017; Scavone et al., 2020).

Effects of Training on the Rubber Hand Illusion

Our finding that the two weeks of daily body scan meditation training dampened the effects of the illusion concurs with previous research. For example, Cebolla et al. (2016) and Xu et al. (2018) found that experienced meditators reported a weaker rubber hand illusion than non-meditators. Body scan meditation explicitly aims to enhance bodily sensation through endogenous attention, and so it would be expected that 14 days of training would enable participants to more accurately discern their real hand from the rubber hand.

However, this more simplified interpretation is less attractive when the result is seen in the context of our full experimental design and other findings. First, we should consider that the control group also experienced a significantly reduced illusion in their second session compared to the first session, though the magnitude of the reduction was larger in the body scan group. This illusion reduction in the body scan group involved changes in ratings for both asynchronous as well as synchronous stroking (i.e. asynchronous stroking was less strongly associated with disconfirming the rubber hand illusion, and synchronous stroking was less strongly associated with confirming the illusion). Second, this larger dampening of the illusion in the body scan group emerges from a comparison between the first and second sessions (that is, before and after training), where the body scan group experienced a stronger rubber hand illusion in the first session (their illusion ratings were more extreme in both the synchronous condition and the asynchronous condition) compared to the control group, before decreasing in the second session. We therefore need to ask what might explain the constellation of results in the body scan group: enhanced rubber hand illusion in the first session, where mindfulness is induced as a state, and the concomitant larger reduction of the illusion in the second session, where mindfulness has been trained for 14 days?

One possible explanation relies on a temporal dissociation between the attentional and acceptance dimensions of mindfulness such that focused attention begins to develop earlier in mindfulness meditation practice than acceptance, which can take longer to cultivate (Baer et al., 2012; Desbordes et al., 2015). In our study, the enhanced rubber hand illusion in the first session may reflect an early attentional effect on bodily awareness, while the decreased illusion we observed in the body scan group compared to the control group during the second session may reflect the effects of acceptance.

Conceptually, this provides a distinctive account of the reduced rubber hand illusion after training. That is, the reduction was not due to increased bodily accuracy; rather, it was due to increased acceptance of the visuotactile-proprioceptive discrepancy induced by the rubber hand setup. In the first session, the body scan group attended to bodily signals and reacted strongly to the discrepancy, leading them to experience a strong rubber hand illusion in synchrony and to strongly disconfirm the illusion in asynchrony. In the second session, the attentionally enhanced sensory discrepancies were still there, but the body scan group were now more non-judging. That is, participants mindfully noticed the discrepancies but did not succumb to the illusion in synchronous stroking nor felt the need to disconfirm the illusion in asynchronous stroking. Although this explanation would conform to findings about attention and acceptance, more research is needed to fully explore it in the context of multisensory bodily integration.

The objective measures of the rubber hand illusion, drift and skin conductance offer a complex picture in the second session. The drift measure did not change for the body scan group and increased slightly for the control group. It is unclear what may explain this result. Other researchers (Cebolla et al., 2016) have failed to find a significant difference between meditators and non-meditators in drift measures. Dissociations between subjective measures of the rubber hand illusion and drift have been observed (Rohde et al., 2011), and the connection questioned (Abdulkarim & Ehrsson, 2016). More research is thus needed to disentangle the effects of mindfulness meditation, and particularly body scan meditation, on proprioceptive drift. Skin conductance was reduced in the second session, across all groups and conditions. This is consistent with the overall dampening of the rubber hand illusion in the second session, with less extreme ratings in both synchrony and asynchrony as well as with the abovementioned general dampening of this response to repeated presentations.

Overall, the interpretation of the results from the state induction and the post-training session appears to cohere with recent psychophysical studies of ownership in the rubber hand illusion. This provides an important new avenue for understanding these phenomena, beyond the reliance on subjective questionnaire measures and indirect measures like drift and skin conductance. This recent work provides evidence that the rubber hand illusion arises as a result of common cause inference in multisensory integration, where the precision of bottom-up sensory cues and strength of spatiotemporal prior expectations (i.e. priors that manifest as expectations for the distance between hands to be relatively close and synchronous stroking to occur within an approximately 200 ms window) play a central role (see Chancel & Ehrsson, 2020). This speaks to the idea that body representation and ownership arises via perceptual inference, just like representations of other environmental causes of sensory input (e.g. 'Bayesian body'; Hohwy, 2013). The current study therefore suggests that body scan meditation interacts with these basic neurocomputational processes, such that the attention component in body scan meditation enhances precision of bottom-up signals and the acceptance component weakens the influence of top-down prior expectations and thereby the imperative to resolve uncertainty with (false or veridical) inference.

Recent developments in causal inference and predictive processing provide an interesting further perspective (for reviews, see Noppeney, 2021; Talsma, 2015; for relevant studies of the rubber hand illusion, see Chancel, Ehrsson, et al., 2021; Chancel, Hasenack, et al., 2021; Rossi Sebastiano et al., 2021). Specifically, Limanowski (2021) reviews the behavioural and neuroimaging literature of the rubber hand illusion from the perspective of active inference (in the sense of attention as active precision (or gain) control, where precision is the inverse of the variance of probability distributions, or the noise in the neural representation). The author argues that an actively controlled reduction in proprioceptive precision (in somatosensory cortices; S1 in particular) is associated with a stronger rubber hand illusion. The active inference reasoning would be that once the false rubber hand representation is selected, there will be a prediction that proprioception will not be informative, and the participant will attend less to proprioceptive information. This reduces proprioceptive precision, making it easier to accumulate evidence for the false inference (from the perspective of causal inference, see Noppeney, 2021, p. 460).

For the body scan state induction in the first session of the current study, where there is high initial attention to proprioception, the prediction would be that this active attention away from proprioception would be more pronounced (i.e. in body scan meditation, one should observe initial high level of activity in S1, followed by more pronounced reduction in the second session). In contrast, for the second session, there should still be increased attention to proprioception but the acceptance component predicts that the ensuing sensory uncertainty would remain unresolved and there would be no need to attend away from proprioception (i.e. in body scan meditation, one should observe more consistently high activity in S1 throughout the trial). In other words, it may be that the acceptance component facilitates a capacity to sustain bodily attention in body scan meditation. This lends an intriguing active inference lens to body scan meditation, consistent with recent deep hierarchical computational models of phenomena like meditation, focused on mental action as precision control through top-down expectations for uncertainty reduction (Sandved-Smith et al., 2021).

Effects of Training on Mindfulness and Bodily Awareness

Both groups exhibited a significant increase in trait mindfulness as measured by the FFMQ, especially the facets of observing, describing and non-reactivity. This was predicted for the body scan group between testing sessions, but was an unexpected finding for the active control group. There are a number of possible explanations for this result. First, when we consider that classical definitions of mindfulness include sustained attention to sensory objects (both body sensations and sounds), it is possible that relaxed listening may in fact overlap with a type of mindfulness exercise (that is, mindful listening) even though we did not specifically encourage the control group to listen to the TED Talk audio in a 'mindful' way (that is, paying sustained, non-judgmental attention).

Second, the active control was designed to mimic any expectancy effects that participants might experience from engaging in a 'wellbeing' exercise. The study was advertised as being about 'mindfulness and relaxation' and homework exercises encouraged participants to reflect on their own experience. Therefore, it is possible that control participants may have been more attuned to psychological characteristics akin to mindfulness when giving self-reports.

We failed to find significant overall increases in bodily awareness (as measured by the MAIA), for either the body scan or active control group. The null hypothesis was supported for four of the eight subscales. There was a significant increase in one subscale, 'not distracting', for both groups. This means that after the 14 days of training, both groups were less likely to ignore or distract themselves from unpleasant physical sensations. Overall, this is at odds with prior research that has shown a relationship between mindfulness and interoception (for review, see, Gibson, 2019). It is not clear why we found no effect in our study, though it is possible that the amount of meditation training the body scan group engaged in was sufficient to increase their levels of trait mindfulness but insufficient to increase interoception. Further research is needed to clarify the necessary dose of body scan meditation to increase interoception, which specific aspects of interoception are impacted by body scan meditation training (in particular when tactile sense is included in interoception), and how changes in interoception relate to bodily awareness more broadly, in particular those aspects relevant for the rubber hand illusion and bodily multisensory integration.

Limitations and Future Research

Not all participants exhibited high-level compliance in their meditation training. This could potentially be improved upon through the use of a mindfulness app or reminder prompts for participants. Though there are practical limitations to laboratory-based pre/post active control studies, it is possible that with a higher number of participants we would have better power to examine the FFMQ and achieve a broader range of skin conductance data.

The body scan training regime had relatively short sessions, of 10 min in week 1 and 15 min in week 2. This relatively low dose of body scan meditation may be reflected in our results and some of the failures to see some group differences for the rubber hand illusion as well as the MAIA. It is possible longer doses would change these results. The question of dose dependence in body scan and mindfulness meditation interventions is unresolved, with some studies suggesting short interventions can be effective (Strohmaier et al., 2021). Recent psychophysical studies of the rubber hand illusion (Chancel & Ehrsson, 2020; Chancel, Ehrsson, et al., 2021; Chancel, Hasenack, et al., 2021) have used short, 12 s trials, whereas this study used 2-min trials. It is possible that shorter trials would change the course of attentional processing and the manifestation of acceptance in body scan meditation.

Overall, this study suggests differential effects on bodily multisensory integration and body ownership of state and trait mindfulness meditation. Utilising the body scan meditation practice common to many mindfulness-based interventions, and with a pre/post design using an active control group, the changes in bodily awareness can be understood in terms of apparently dissociable processes of early attention to proprioceptive and tactile signals and later acceptance of multisensory discrepancies involving such signals. These results can be interpreted in terms of modulation of (Bayes-optimal) multisensory integration and active common cause inference. This study may thus help reveal underlying cognitive mechanisms of state and trait mindfulness meditation, in terms of modulations and interactions in the regulation of bottom-up and top-down signals.

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Author Contribution T. G. and J. R. M. contributed equally to this study. T. G.: collaborated in the design of the study, executed the study and wrote the paper. J. R. M.: analysed the data and wrote the paper. R. C.: collaborated in the design of the study, prepared the meditation instructions and wrote the paper. J. W.: collaborated in the design of the study and writing the paper. J. H.: collaborated in the design of the study, supervised the execution of the study and wrote the paper.

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Data availability All data are available at FigShare (https://doi.org/10.6084/m9.figshare.15080499.v3).

Declarations

All procedures performed in the current study were in accordance with the ethical standards of Monash University Human Research Ethics Committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study.

Conflict of interest The authors declare no competing interests.

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