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Mind-wandering and alterations to default mode network connectivity when listening to naturalistic versus artificial sounds

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Abstract

Naturalistic environments have been demonstrated to promote relaxation and wellbeing. We assess opposing theoretical accounts for these effects through investigation of autonomic arousal and alterations of activation and functional connectivity within the default mode network (DMN) of the brain while participants listened to sounds from artificial and natural environments. We found no evidence for increased DMN activity in the naturalistic compared to artificial or control condition, however, seed based functional connectivity showed a shift from anterior to posterior midline functional coupling in the naturalistic condition. These changes were accompanied by an increase in peak high frequency heart rate variability, indicating an increase in parasympathetic activity in the naturalistic condition in line with the Stress Recovery Theory of nature exposure. Changes in heart rate and the peak high frequency were correlated with baseline functional connectivity within the DMN and baseline parasympathetic tone respectively, highlighting the importance of individual neural and autonomic differences in the response to nature exposure. Our findings may help explain reported health benefits of exposure to natural environments, through identification of alterations to autonomic activity and functional coupling within the DMN when listening to naturalistic sounds.

1 Introduction

2 Naturalistic sounds and 'green' environments are empirically reported to be subjectively more pleasant than
3 artificial sounds and environments¹⁻³. The positive effects of exposure to naturalistic environmental stimuli
4 extend to health benefits, including improvements in the patient experience of general anaesthesia⁴,
5 enhanced post-operative recovery^{5,6}, and reduced pain and anxiety in hospice care⁷. These effects are
6 observed following controlled exposure to naturalistic stimuli re-created in an experimental setting. A
7 primary focus of research in this area relates to the 'restorative' effects of naturalistic stimuli, and assessing
8 the ability of nature exposure to promote recovery from physiological or psychological stress. These
9 restorative effects are framed in the context of two prevailing theories: 1) attentional restoration theory
10 (ART)⁸ and; 2) stress recovery theory (SRT)⁹. ART proposes that an artificial environment is saturated with
11 stimuli that impose a high level of cognitive and attentional demand. In contrast, stimuli derived from
12 natural environments are proposed to engage less with top-down drivers of 'directed attention'. Exposure to
13 naturalistic stimuli might thus provide temporal respite from attentional load, thereby promoting recovery
14 of attentional capacity. In contrast, SRT posits that physiological (autonomic) and psychological stress are
15 reduced within naturalistic compared to artificial environmental contexts as a consequence of human
16 evolutionary adaptation to naturalistic stimuli. SRT makes a more direct link between nature exposure and
17 physiological shifts in autonomic balance toward parasympathetic ('rest-digest') activation, with a
18 concomitant reduction in sympathetic ('fight-flight') activation within the cardiovascular system.

19 Increases in cognitive capacity (ART) are observed across specific domains following exposure to naturalistic
20 stimuli¹⁰⁻¹². These effects may be amplified in individuals experiencing high levels of self-reported cognitive
21 exhaustion¹¹. However, the cognitive benefits that are central to the ART model provide no proximate
22 explanation for the physiological effects induced by naturalistic environments¹³. Psychological factors do,
23 however, drive stress-related changes in bodily physiology. Techniques such as simulated interviews¹⁴ and
24 backwards counting tasks¹⁵ are used in experimental studies of mental stress and associated with states of
25 bodily arousal¹⁴. Exposure to naturalistic stimuli following psychological stress challenge can increase

1 parasympathetic activation¹⁴ and reduce sympathetic activation¹⁵, as indexed by electrodermal activity,
2 heart rate and blood pressure, or cortisol levels. These physiological changes are not always accompanied
3 by changes in subjective ratings of anxiety¹⁴.

4 Brain imaging studies can help determine the neurobiological mechanisms underlying these behavioural and
5 physiological observations. However, as yet there have been relatively few imaging investigations into the
6 restorative effects of nature exposure. A field study using electroencephalography identified an increase in δ
7 band power when participants transitioned from urban to natural environments¹⁶. This was interpreted as
8 demonstrating a reduction in neural correlates of arousal and frustration, and an increase in active
9 engagement in the naturalistic environment, thereby supporting the ART model. In a functional magnetic
10 resonance imaging (fMRI) study, participants were presented with images of beaches (naturalistic 'tranquil'
11 condition) or freeways (artificial 'non-tranquil' condition) while they listened to a soundtrack which could be
12 interpreted as both rolling waves or high speed traffic¹⁷. During the tranquil condition greater functional
13 neural coupling was observed between auditory cortex and medial prefrontal cortex, posterior cingulate,
14 temporo-parietal cortex and thalamus. The authors link the low attentional demands of the naturalistic
15 stimuli with increased 'default mode network' (DMN) activity. The DMN describes a set of regions where
16 activity is increased during 'task free' states of wakefulness, and is decreased during task performance
17 associated with external cognitive load. In line with ART, increased activation of posterior cingulate cortex
18 (PCC, a key DMN 'hub') was observed during the tranquil condition relative to a baseline no-stimulus
19 condition, yet surprisingly there were no supra-threshold differences when contrasting tranquil and non-
20 tranquil stimulation. A limitation in this study, however, is the lack of behavioural or physiological data to
21 support the interpretation of neural findings.

22 ART and SRT make clear predictions about brain activity in task free or 'mind-wandering' situations. If
23 exposure to naturalistic stimuli reduces cognitive load relative to artificial stimuli, as suggested by ART, one
24 might predict an increase in mind wandering and DMN activity in naturalistic versus artificial conditions,
25 consistent with an increase in task-free activity¹⁷. Alternately, if exposure to naturalistic versus artificial

1 stimuli results in more general stress reduction associated with alterations in autonomic activation, one
2 might observe DMN differences that mirror changes in parasympathetic-sympathetic balance. In the present
3 fMRI study, we measured changes in the activation and connectivity of the DMN during exposure to
4 naturalistic and artificial stimuli, along with a no-soundscape control condition, to investigate and test the
5 opposing ART and SRT hypotheses. We used whole brain seeded timecourse correlations with the PCC to
6 investigate DMN functional connectivity under each condition. We used the functional connectivity map of
7 the DMN under the control condition to test the ART hypothesis of increased activation in DMN areas during
8 naturalistic conditions, and assessed alterations in connectivity through comparison of connectivity maps
9 between conditions. We also conducted an exploratory analysis of anterior and posterior salience networks,
10 the dorsal attention network, and the executive control network¹⁸, to test whether alterations to
11 connectivity within these systems can account for the increased cognitive capacity observed following
12 exposure to naturalistic stimuli (ART).

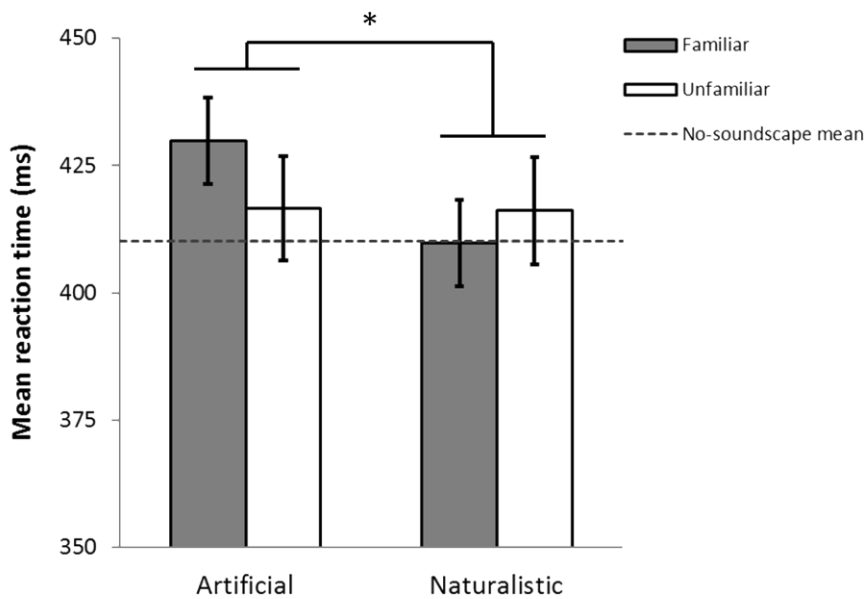
13 Participants were exposed to conditions of artificial and naturalistic 'soundscapes', comprised of equally
14 weighted familiar and unfamiliar sounds, which were rated for pleasantness, intensity and familiarity using a
15 visual analogue scale (VAS). The fMRI data acquisition was accompanied by behavioural measures of
16 attentional deployment using reaction times in performance of a low cognitive load tracking task, and
17 subjective indices of attentional capture in the form of VAS measures of task engagement, rumination,
18 distraction by thoughts and distraction by the soundscapes themselves. Neural, behavioural and subjective
19 data were complemented by physiological measurement of arousal indexed by changes in heart rate and
20 heart rate variability (HRV). HRV analysis involves spectral and temporal decomposition of the intervals
21 between successive heart beats. Interpretation of low frequency (0.04-0.15 Hz) components of HRV is
22 complicated by contributions from both sympathetic and parasympathetic responses¹⁹; we therefore
23 constrained our HRV analysis to assessment of the high frequency (0.15–0.4 Hz) component, as a reliable
24 index of cardiac parasympathetic activity^{20–24}. We hypothesised that reaction times would be increased in
25 the artificial condition compared to the naturalistic, suggesting a relative disengagement of attention from

1 the task (e.g. through distraction or mind-wandering), but that the neural and physiological data would
2 support SRT in providing evidence that exposure to naturalistic stimuli would enhance cardiac
3 parasympathetic activity (mediating reported health benefits associated with nature exposure), underpinned
4 by changes in functional neural connectivity which support the differences in phenomenological experience
5 of naturalistic and artificial exposure conditions.

6 **Results**

7 **Attentional monitoring**

8 The exposure conditions consisted of: 1) artificial familiar; 2) artificial unfamiliar; 3) naturalistic familiar; 4)
9 naturalistic unfamiliar; 5) no-soundscape (control). Each soundscape lasted 5 minutes 25 seconds, and was
10 presented in a randomised order while fMRI data were acquired and attention was monitored using a low
11 level reaction time task. Reaction times in the attentional monitoring task were significantly increased in the
12 artificial condition ($\mu = 423.22$ ms) compared to naturalistic condition ($\mu = 412.98$ ms) (main effect of
13 artificiality: $F_{(1,14)} = 5.94, p = 0.029$) (Figure 1). There was no main effect of familiarity ($F_{(1,14)} = 1.31, p = 0.272$),
14 and no artificiality-by-familiarity interaction ($F_{(1,14)} = 0.25, p = 0.623$). Post-hoc t-tests demonstrated a
15 significant difference between reaction times in the artificial familiar condition ($\mu = 432.98$ ms) compared to
16 the naturalistic familiar condition ($\mu = 415.04$ ms) ($t_{(16)} = 3.07, p = 0.007$). To minimise the number of
17 exploratory comparisons, the artificial familiar and naturalistic familiar conditions were taken forward for
18 further analysis of subjective, physiological and neural effects.



1

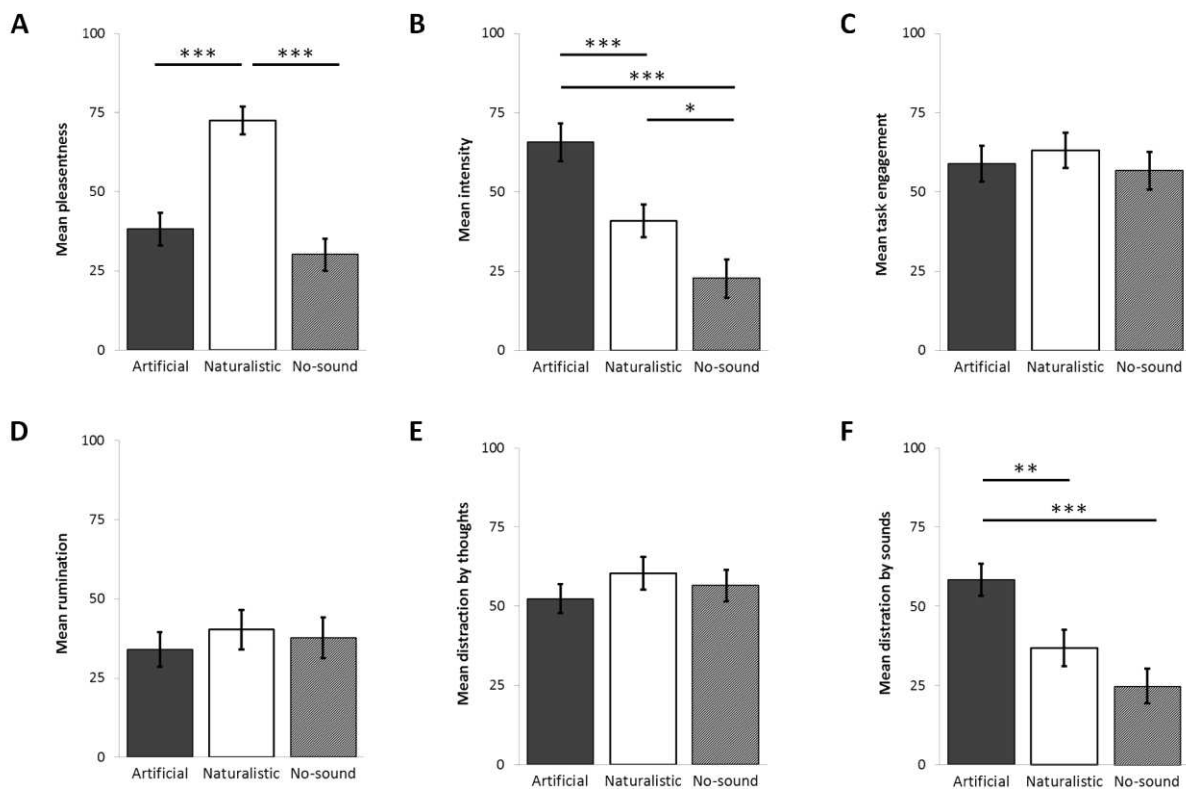
2 Figure 1. Mean reaction times in attentional monitoring task whilst listening to familiar and unfamiliar,
 3 artificial and naturalistic soundscapes. After controlling for variance in reaction times in the no-soundscape
 4 condition (dashed line), the main effect of artificiality indicates increased reaction times in artificial
 5 compared to naturalistic conditions ($p = 0.029$). * $p < 0.05$. Error bars $\pm 1SEM$.

6 Subjective ratings and physiological effects

7 At the end of each condition, participants completed a set of visual analogue scales to rate subjective
 8 experience. There was a significant effect of soundscape on pleasantness ($F_{(2,32)} = 35.57, p < 0.001$) (Figure
 9 2A) and intensity of the sounds ($F_{(2,32)} = 16.41, p < 0.001$) (Figure 2B), with the naturalistic familiar
 10 soundscape rated as more pleasant ($\mu = 74.30$) than both the artificial familiar ($\mu = 38.19$) ($t_{(16)} = 6.57, p <$
 11 0.001) and the no-soundscape control condition ($\mu = 28.94$) ($t_{(16)} = 6.34, p < 0.001$), and less intense ($\mu =$
 12 41.86) than the artificial familiar ($\mu = 65.73$) ($t_{(16)} = 4.42, p < 0.001$) and the no-soundscape condition ($\mu =$
 13 24.04) ($t_{(16)} = 5.18, p < 0.001$). There was no effect of soundscape on the subjective rating of perceived task
 14 engagement ($F_{(2,32)} = 0.42, p = 0.663$) (Figure 2C). In relation to thought content, there was no effect of
 15 soundscape on rumination ($F_{(2,32)} = 0.90, p = 0.420$) (Figure 2D), or distraction by thoughts ($F_{(2,32)} = 1.24, p =$

1 0.304) (Figure 2E). There was a significant effect of soundscape on distraction by sounds ($F_{(2,32)} = 15.54, p <$
 2 0.001) (Figure 2F) with the artificial familiar sounds ($\mu = 58.36$) being significantly more distracting than the
 3 naturalistic familiar sounds ($\mu = 36.82$) ($t_{(16)} = 3.27, p = 0.005$), and the no-soundscape control condition ($\mu =$
 4 24.77) ($t_{(16)} = 5.62, p < 0.001$). There was no difference in the distraction by sounds between the naturalistic
 5 familiar condition and the no-soundscape condition ($t_{(16)} = 2.11, p = 0.051$).

6



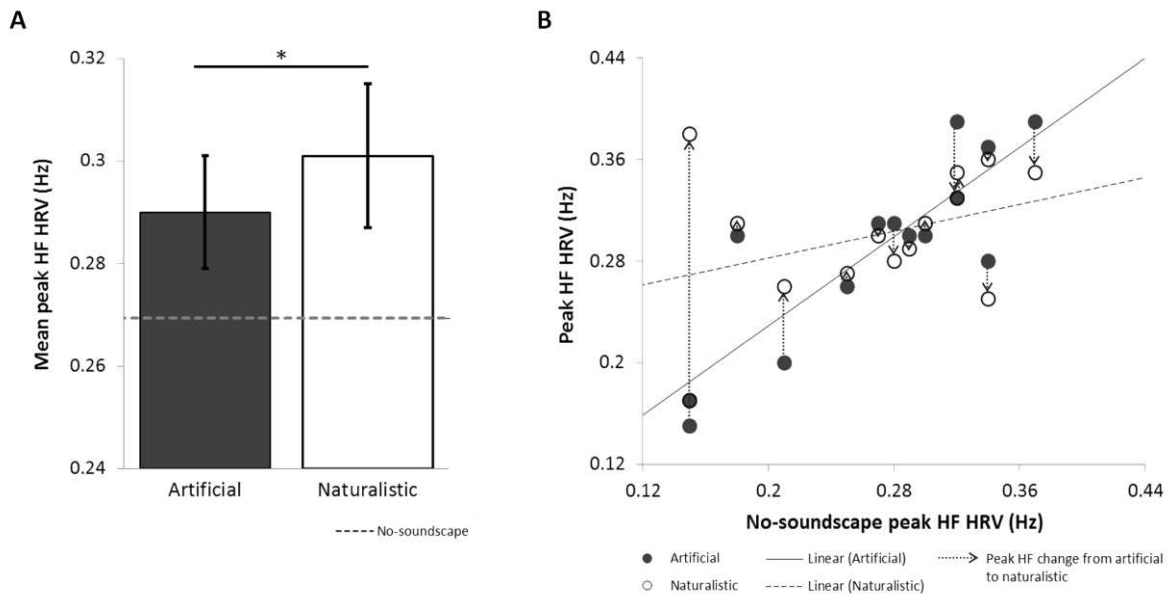
7 Figure 2. Subjective ratings of (A) pleasantness, (B) intensity of sounds, (C) task engagement, (D) rumination,
 8 (E) distraction by thoughts, and (F) distraction by sounds, for artificial familiar, naturalistic familiar and no-
 9 soundscape conditions. Error bars \pm 1SEM. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

10

11 During the experiment cardiac activity was continuously monitored using pulse oximetry. There was no
 12 main effect of soundscape on heart rate ($F_{(2,28)} = 3.06, p = 0.063$), suggesting there were no significant
 13 differences in broad arousal between the artificial familiar ($\mu = 65.75$ bpm), naturalistic familiar ($\mu = 67.31$

1 bpm) and no-soundscape condition ($\mu = 68.24$ bpm). However, after controlling for baseline heart rate
2 variability, there was a significant increase in the peak frequency of the high frequency band (peak HF) in
3 the naturalistic familiar compared to artificial familiar condition ($F_{(1,12)} = 8.58, p = 0.013$), suggesting an
4 increase in parasympathetic activity in the naturalistic compared to artificial condition (Figure 3A). The large
5 variance in peak HF reflected the significant interaction between baseline peak HF and stimulus condition
6 ($F_{(1,12)} = 8.07, p = 0.015$), where individuals with low baseline peak HF experienced an increase in
7 parasympathetic activity in naturalistic compared to artificial conditions, while individuals with high baseline
8 peak HF experienced a decrease in parasympathetic activity in naturalistic compared to artificial conditions
9 (Figure 3B). There were no significant differences in absolute ($F_{(1,12)} = 0.19, p = 0.671$) or relative (percentage)
10 high frequency power ($F_{(1,12)} = 0.02, p = 0.897$).

11

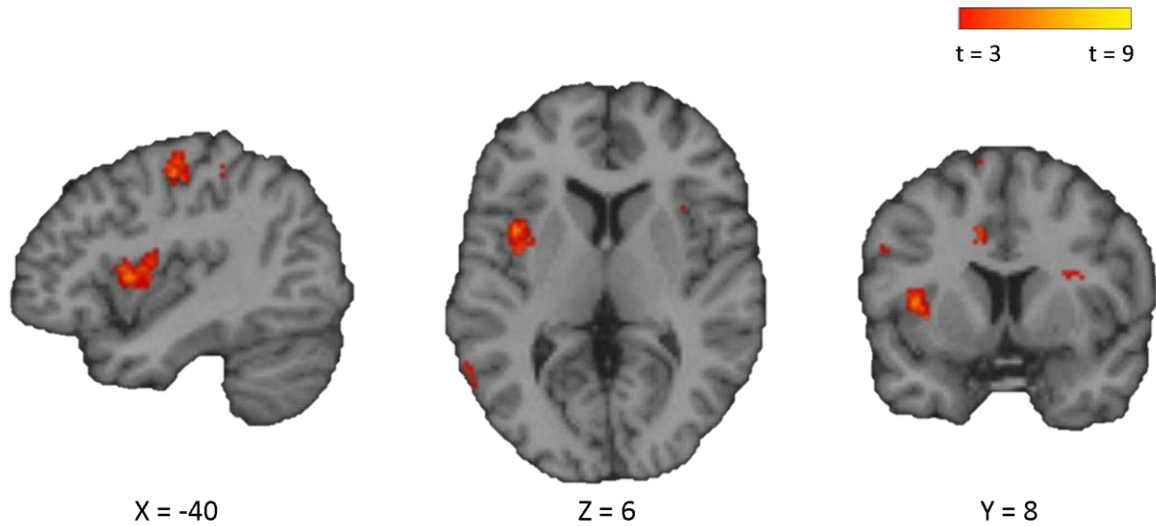


2 Figure 3. (A) Significant increase in the mean peak of the high frequency component of heart rate variability
 3 (peak HF HRV) in naturalistic familiar compared to artificial familiar conditions, after controlling for the
 4 baseline (no-soundscape) high frequency peak. Error bars ± 1 SEM. $*p < 0.05$ (B) Interaction between
 5 baseline (no-soundscape) peak HF and artificial familiar (dark circle, solid line) and naturalistic familiar (white
 6 circle, dashed line) peak HF. Individuals with low baseline peak HF show an increase in parasympathetic tone
 7 from artificial to naturalistic conditions (upwards arrow); individuals with high baseline peak HF show a
 8 decrease in parasympathetic tone from artificial to naturalistic conditions (downwards arrow).

9 Functional brain imaging findings

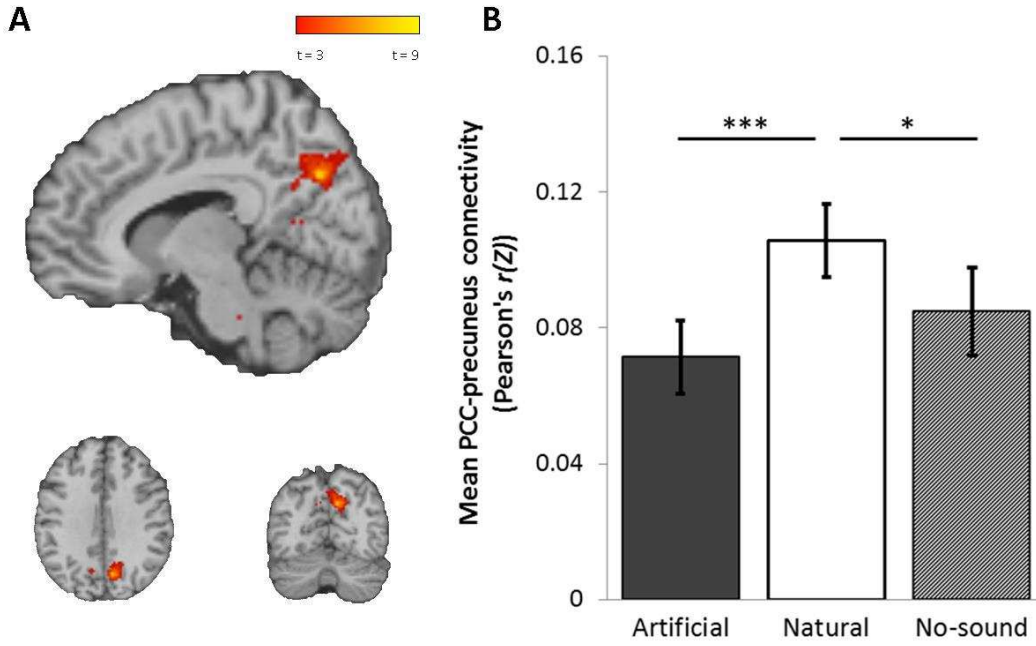
10 Neural data were acquired using fMRI during each of the experimental and control conditions. For general
 11 linear model analysis of evoked changes in neural activity within the DMN, a canonical DMN mask was
 12 generated using seed based functional connectivity with the PCC during the no-soundscape control
 13 condition. There were no suprathreshold differences of activation within the DMN masked area between the
 14 artificial familiar and naturalistic familiar conditions ($p_{(FWE\ peak)} > .05$, $p_{(FWE\ clus.)} > .05$). There was, however, a
 15 region of significantly increased activation during in the naturalistic familiar condition compared to the

1 artificial familiar condition outside of DMN areas, in the middle insula of the left hemisphere ($p_{(FWE\ clus.)} =$
2 0.002, $k = 96$, $p_{(FWE\ peak)} = 0.979$, $Z = 4.09$, [40, 8, 6]) (Figure 4).



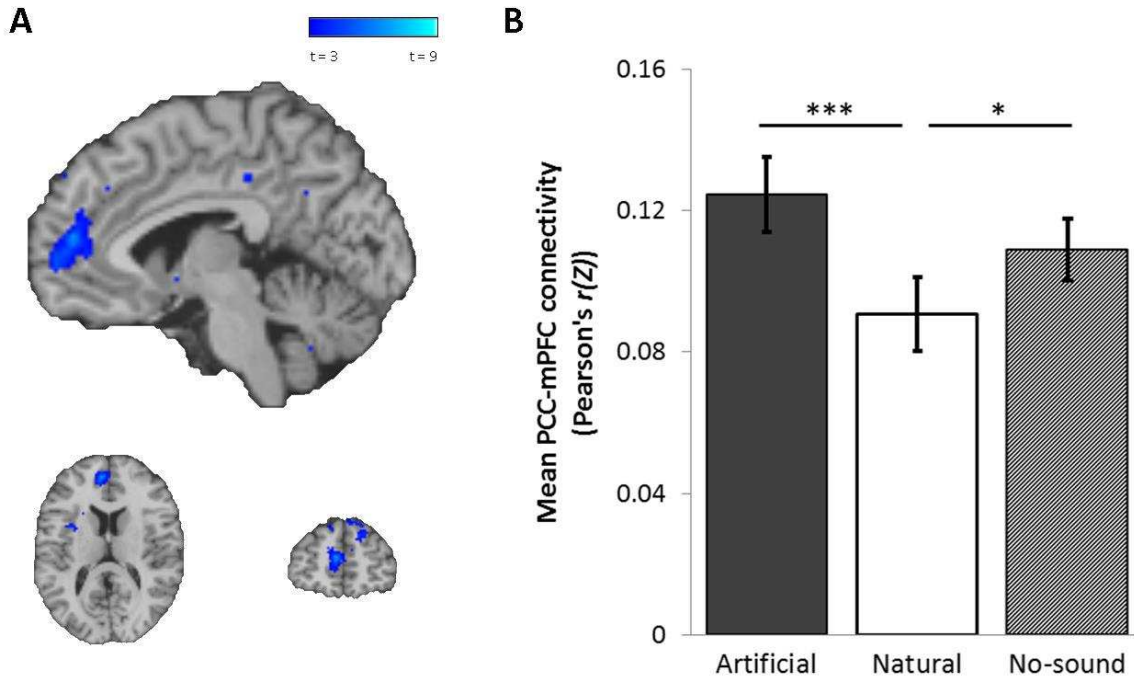
3
4 Figure 4. Region of significantly increased activation in the naturalistic familiar condition compared to the
5 artificial familiar condition in the middle insula of the left hemisphere ($p_{(FWE\ clus.)} = 0.002$, $k = 96$, $p_{(FWE\ peak)} =$
6 0.979, $Z = 4.09$, [-40, 8, 6]). Note precentral cluster in the sagittal view does not survive FWE correction ($p_{(FWE$
7 $clus.)} = 0.050$, $k = 55$, $p_{(FWE\ peak)} = 0.986$, $Z = 4.05$, [-36,-14, 62]).

8 In functional connectivity analysis, the DMN was identified separately for each condition by the extraction of
9 timecourse activation data from the PCC, and entered into regression analysis against all voxels to identify
10 significant correlations between the PCC and all other regions of the brain. In contrasting the DMN
11 functional connectivity maps, the naturalistic familiar condition was associated with a significant increase in
12 connectivity between PCC and the precuneus ($p_{(FWE\ clus.)} < 0.001$, $k = 183$, $p_{(FWE\ peak)} = 0.058$, $Z = 4.98$, [10, -68,
13 34]) (Figure 5), and a decrease in connectivity between the PCC and the medial prefrontal cortex (mPFC)
14 ($p_{(FWE\ clus.)} < 0.001$, $k = 185$, $p_{(FWE\ peak)} = 0.770$, $Z = 4.29$, [-4, 52, 14]) (Figure 6), when compared to the artificial
15 or no-sound control conditions.



1

2 Figure 5. (A) FWE corrected significant region of increased local functional connectivity between the PCC
 3 seed region and the precuneus in the naturalistic familiar condition compared to artificial familiar condition
 4 ($p(\text{FWE clus.}) < 0.001$, $k = 183$, $p(\text{FWE peak}) = 0.058$, $Z = 4.98$, $[10, -68, 34]$). (B) Main effect of soundscape
 5 demonstrated in the extracted connectivity scores between the PCC and precuneus ($F(2,32) = 10.96$, $p =$
 6 0.001), with increased connectivity in the naturalistic familiar (μ Pearson's $r(Z) = 0.11$) compared to the
 7 artificial familiar (μ Pearson's $r(Z) = 0.07$) ($t(16) = 6.35$, $p < 0.001$) and no-soundscape condition (μ Pearson's
 8 $r(Z) = 0.85$) ($t(16) = 2.94$, $p = 0.010$). Error bars ± 1 SEM. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

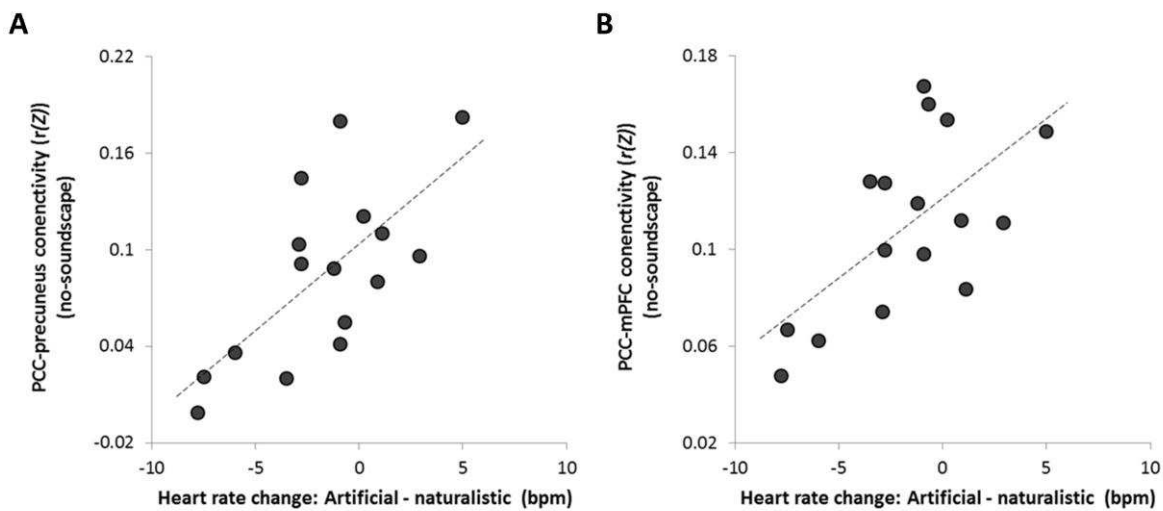


1

2 Figure 6. (A) FWE corrected significant region of reduced functional connectivity between the PCC seed and
 3 the mPFC in the naturalistic familiar condition compared to the artificial familiar condition ($p_{(FWE\ clus.)} < 0.001$,
 4 $k = 185$, $p_{(FWE\ peak)} = 0.770$, $Z = 4.29$, $[-4, 52, 14]$). (B) Main effect of soundscape on extracted connectivity
 5 scores between the PCC and mPFC ($F(2,32) = 9.94$, $p < 0.001$), with decreased connectivity in the naturalistic
 6 familiar condition (μ Pearson's $r(Z) = 0.91$) compared to the artificial familiar (μ Pearson's $r(Z) = 0.13$) ($t(16) =$
 7 4.90 , $p < 0.001$) and no-soundscape condition (μ Pearson's $r(Z) = 0.11$) ($t(16) = 2.35$, $p = 0.032$). Error bars ± 1
 8 SEM. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

9

1 Finally, relationships were explored between the change in arousal (artificial heart rate – naturalistic heart
2 rate) and functional connectivity. There was a significant positive correlation between the change in arousal
3 and baseline (no-soundscape) functional connectivity between the PCC and the precuneus (Pearson's $r =$
4 $0.68, p = 0.003$) (Figure 7A), and between the change in arousal and baseline PCC and mPFC connectivity
5 (Pearson's $r = 0.63, p = 0.009$) (Figure 7B).

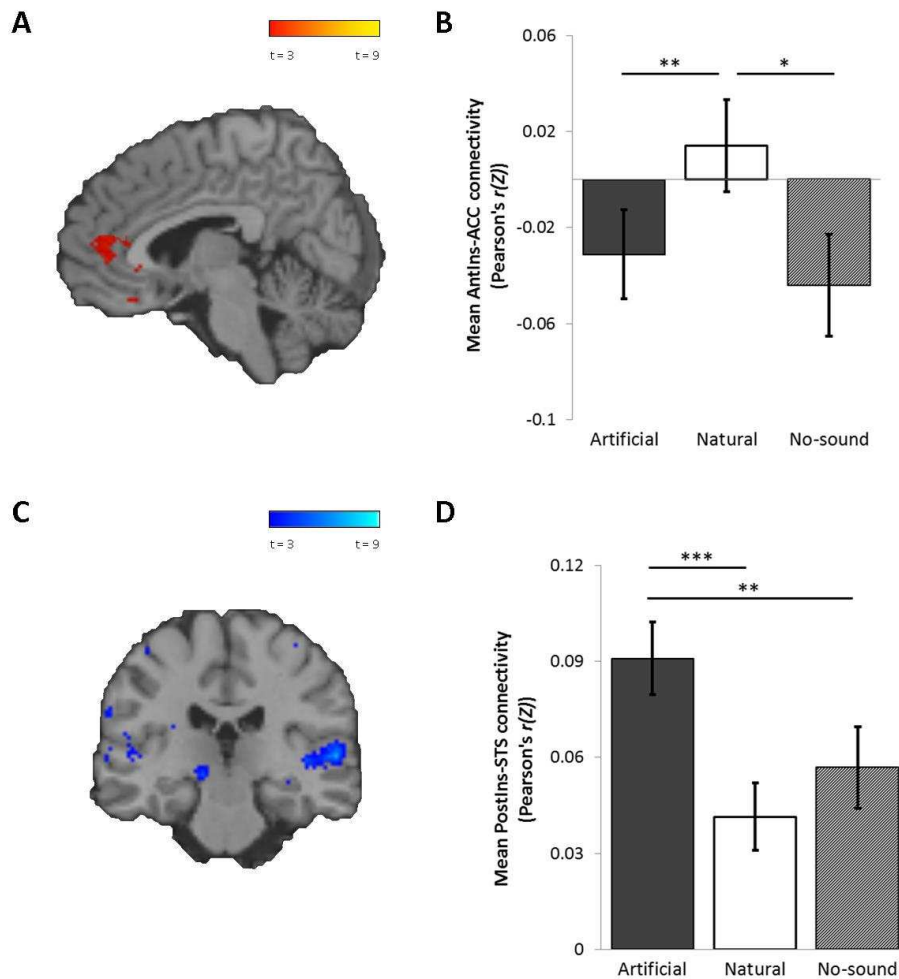


6

7 Figure 7. Correlation between changes in arousal (change in heart rate between the artificial familiar and
8 naturalistic familiar condition) and functional connectivity scores in the baseline no-soundscape condition
9 between the PCC seed and (A) the precuneus (Pearson's $r = 0.68, p = 0.003$) and (B) the mPFC (Pearson's $r =$
10 $0.628, p = 0.009$).

11 In exploratory analysis of functional connectivity in the salience (bilateral anterior and posterior insula
12 seeds), dorsal attention (right supramarginal gyrus seed) and executive control networks (left and right
13 dorsolateral prefrontal cortex seeds), we found differential effects of naturalistic and artificial soundscapes
14 in the salience networks only (see Figure 8). All other differences were non-significant after FWE correction
15 at the cluster or peak level. In the anterior salience network there was a significant increase in connectivity
16 in the naturalistic familiar condition compared to the artificial condition, between bilateral anterior insula
17 and the anterior cingulate cortex (ACC) ($p_{(FWE\ clus.)} = 0.021, k = 84, p_{(FWE\ peak)} = 0.995, Z = 3.88, [2, 46, 4]$) (Figure

1 8A). In the posterior salience network there was a significant increase in connectivity in the artificial familiar
2 condition compared to the naturalistic condition, between bilateral posterior insula and a region of the right
3 superior temporal sulcus (STS) ($p_{(FWE\ clus.)} = 0.002$, $k = 121$, $p_{(FWE\ peak)} = 0.511$, $Z = 4.54$, $[60, -24, 4]$) (Figure 8B).
4 Analysis of the extracted connectivity strength for the anterior salience network from each condition shows
5 the activation timecourse in the anterior insula to be positively correlated with the timecourse of the
6 anterior cingulate in the naturalistic familiar condition (μ Pearson's $r(Z) = 0.01$), while activity in the anterior
7 insula is negatively correlated with the anterior cingulate in the artificial (μ Pearson's $r(Z) = -0.03$) and no-
8 soundscape control conditions (μ Pearson's $r(Z) = -0.04$). There was a significant increase in connectivity
9 between the anterior insula and the anterior cingulate in the naturalistic condition compared to the artificial
10 ($t_{(16)} = 2.71$, $p = 0.016$) and no-soundscape control condition ($t_{(16)} = 3.09$, $p = 0.007$). In the posterior salience
11 network, there was a significant increase in positive connectivity between the posterior insula and the
12 superior temporal sulcus in the artificial condition (μ Pearson's $r(Z) = 0.09$) compared to the naturalistic (μ
13 Pearson's $r(Z) = 0.04$, $t_{(16)} = 5.01$, $p = <0.001$) and no-soundscape control condition (μ Pearson's $r(Z) = 0.06$,
14 $t_{(16)} = 2.85$, $p = 0.012$). There were no significant correlations between baseline connectivity scores and the
15 change in heart rate or HRV measures after controlling for multiple comparisons ($p > 0.05$).



1

2 Figure 8. Exploratory connectivity analysis of salience networks, seeded from (A&B) bilateral anterior insula;
 3 and (C&D) bilateral posterior insula. (A) The anterior insula show increased functional connectivity with the
 4 ACC ($p_{(FWE\ clus.)} = 0.021$, $k = 84$, $p_{(FWE\ peak)} = 0.995$, $Z = 3.88$, $[2, 46, 4]$) in the naturalistic compared to artificial
 5 condition. (B) Main effect of soundscape on extracted connectivity scores for between the anterior insula
 6 and ACC, with increased functional connectivity in the naturalistic condition compared to the artificial ($t_{(16)} =$
 7 2.71 , $p = 0.016$) and no-soundscape control condition ($t_{(16)} = 3.09$, $p = 0.007$). (C) The posterior insula show
 8 increased functional connectivity with a region of the right STS ($p_{(FWE\ clus.)} = 0.002$, $k = 121$, $p_{(FWE\ peak)} = 0.511$, Z
 9 $= 4.54$, $[60, -24, 4]$) in the artificial condition compared to the naturalistic condition. (D) Main effect of
 10 soundscape on extracted connectivity scores between the posterior insula and the right STS, with increased
 11 functional connectivity in the artificial condition compared to the naturalistic ($t_{(16)} = 5.01$, $p < 0.001$) and no-
 12 soundscape control condition ($t_{(16)} = 2.85$, $p = 0.012$). Error bars ± 1 SEM. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

1 Discussion

2 We tested from a neurobiological perspective two competing theoretical accounts of the reported
3 restorative effects of exposure to naturalistic environmental stimuli. We assessed activation and functional
4 connectivity within the DMN when participants were listening to naturalistic familiar and artificial familiar
5 soundscapes, encompassing regions whose activity reduces with externally directed attention and cognitive
6 load. We further explored changes in connectivity within the salience, dorsal attention and executive control
7 networks. Behavioural results showed that artificial soundscapes were associated with poorer attentional
8 monitoring compared to naturalistic soundscapes (Figure 1). Subjective reports indicated that the largest
9 differences between artificial familiar and naturalistic familiar conditions were observed in ratings of
10 pleasantness (Figure 2A), intensity (Figure 2B), and distraction by the sounds themselves (Figure 2F). We also
11 observed a significant increase in the high frequency peak of HRV during the naturalistic familiar compared
12 to artificial familiar condition (Figure 3A), indicating an increase in cardiac parasympathetic activity.
13 Importantly, the shift in high frequency peak between conditions was dependant on the baseline peak level:
14 individuals with low baseline parasympathetic activity showed an increase in parasympathetic activity in the
15 naturalistic condition. In contrast, individuals with high baseline parasympathetic activity showed a relative
16 decrease in parasympathetic activity in the naturalistic condition (Figure 3B). We observed no significant
17 difference in the absolute and relative power of high frequency HRV, however this effect may have been
18 masked by difference in respiratory activity²⁰.

19 The behavioural and subjective data show partial support for ART, by demonstrating a reduced capacity for
20 external attentional monitoring and an increase in attentional capture by artificial soundscapes. The increase
21 attentional capture of the artificial soundscapes compared to naturalistic or control is also demonstrated in
22 exploratory analysis of the salience networks, which show increased connectivity with auditory cortex in the
23 artificial condition (Figure 8B), but increased connectivity with limbic structures in the naturalistic condition
24 (Figure 8A). However, our findings provide no evidence to support the ART-related hypothesis of an increase
25 in DMN (task free) activity in the naturalistic familiar condition compared to the artificial familiar condition,

1 or an increase in the subjective experience of rumination or mind wandering. Rather, the regional
2 localisation of alterations in functional connectivity of the DMN appears to reflect a shift in autonomic
3 balance in line with SRT, where we observed increased coupling between the PCC and precuneus in the
4 naturalistic familiar condition (Figure 5) and decreased coupling between the PCC and mPFC (Figure 6).
5 These differences were significant both in comparison to the artificial familiar condition, and when
6 comparing the naturalistic familiar with no-soundscape condition, suggesting these effects are induced
7 specifically by naturalistic familiar soundscapes. We note that the differences in functional connectivity are
8 strong even after controlling for differences in subjective ratings, suggesting that the neural effects are not
9 due perceived pleasantness, intensity or distraction by soundscapes.

10 Activity and connectivity of the DMN is coupled to changes in autonomic activation²⁵⁻²⁷. A recent meta-
11 analysis of fMRI investigations assessing the patterns of brain activity related to autonomic responses
12 suggested that sympathetic activation was associated with an increase in neural response in areas
13 associated with executive function and salience, while parasympathetic activation involved areas of the
14 DMN²⁵. Tasks which result in sympathetic activation evoked activity changes within regions including the
15 ventromedial prefrontal cortex and pregenual anterior cingulate, while tasks resulting in parasympathetic
16 activation identified clusters in the precuneus and dorsal PCC²⁵. Our interpretation that differential anterior
17 and posterior changes in DMN functional connectivity are directly coupled to physiology, notably specific
18 changes in parasympathetic cardiac drive during the naturalistic familiar condition, is supported by this
19 meta-analysis. Our findings also contribute to growing empirical description of brain mediators of stress-
20 related baroreflex suppression (hence sympathovagal balance)²⁸. However, ventromedial prefrontal cortex
21 (a component of the DMN) appears strongly antisympathetic²⁹⁻³¹ a role that does not come through in this
22 meta-analysis. Our neural data suggest that an increased capacity for external attentional monitoring in the
23 naturalistic condition is associated with the overall increase in parasympathetic activity compared to
24 artificial familiar conditions. This inference is also supported by the observed increase in peak high frequency
25 HRV in the naturalistic familiar condition. We note that the physiological arousal effects are correlated with

1 individual differences in baseline functional connectivity between the DMN hubs (Figure 7) and baseline
2 parasympathetic activity (Figure 3B). These individual differences suggest that arousal may be related to
3 basal state of neural connectivity and the participant's current autonomic state. This demonstration of
4 individual differences in physiological and neural response to naturalistic stimuli may be in part responsible
5 for inconsistencies with regard to arousal effects in previous investigations, and emphasise a need for further
6 investigation.

7 Our focus on the DMN was motivated by a desire to understand the task-free effects of naturalistic stimulus
8 exposure. Alterations in DMN functional connectivity are reported in association with disorders related to
9 psychological stress, including anxiety³², post-traumatic stress disorder³³ and depression³⁴. Dysfunctional
10 regulation of the DMN is linked to intrinsic alterations in functional connectivity within the network itself³⁵
11 and dysregulation in the competition between the DMN and anti-correlated task-positive networks. Anxiety
12 disorders are typically associated with an increase in functional connectivity or neural activity in the mPFC
13 and ACC^{33,34}, a region which is associated with metalizing³⁶, evaluative and self-referential
14 processing^{37,38} and sympathetic cardiovascular drive^{39,40}. These accounts suggest that increased
15 connectivity with mPFC and ACC subregions is associated with an increase in self-referential thought
16 processes. Our findings of decreased functional connectivity between the PCC and mPFC hubs of the DMN in
17 naturalistic familiar conditions may therefore correspond to an attenuation of self-referential thought
18 processes during exposure to naturalistic environmental stimuli. However, the increased functional
19 connectivity between the anterior insula and ACC identified in our exploratory analysis may suggest an
20 increase in emotional salience under natural conditions⁴¹. Conversely, the precuneus and PCC are thought
21 to support broad monitoring of external and internal self-generated experience⁴², including visuo-spatial
22 imagery⁴³ and working memory⁴⁴, with the precuneus specifically linked to relaxed states of
23 consciousness which involve higher order self-representation, as opposed to states of active task
24 engagement ^{43,45}. Our observation of increased functional connectivity between the PCC and precuneus

1 regions of the DMN during naturalistic familiar condition may suggest an increase in broad integrative
2 monitoring and visual working memory during naturalistic exposure.

3 This interpretation of differential connectivity of the anterior and posterior midline DMN structures is in
4 accord with the more general notion that the medial prefrontal cortex component of the DMN is associated
5 with inward-directed focus, in contrast to the precuneus/PCC which is association with outward-directed
6 focus of attentional processing^{46,47}. We found no statistical difference in the ratings of rumination or
7 distraction by internal thoughts to suggest a qualitative difference in the 'direction of thought focus'
8 between the conditions, however, this may be due to the relatively brief stimulation period (5 min 25
9 second) for each condition. It is possible that the short duration and switching between soundscapes was
10 sufficiently stimulating that mind wandering and internal thought processes were maintained at low levels
11 throughout. Future investigations of these effects may benefit from employing longer exposure durations, to
12 increase the likelihood of mind wandering. Extended exposure durations may also increase the likelihood of
13 detecting differences in the degree of DMN activation between artificial and naturalistic conditions,
14 alongside the more subtle differences in connectivity reported here.

15 ART proposes that naturalistic environments are restorative through the provision of respite from directed
16 attentional demands, which is anticipated to engage an increase in DMN (or task-free) activity¹⁷. Although
17 we identified an increase in attentional capacity during naturalistic familiar compared to artificial familiar
18 conditions, we found no evidence within the neural data for an increase in task-free activity during this
19 relatively short exposure to naturalistic familiar conditions. The primary claims of ART, however, relate to
20 post-exposure, rather than peri-exposure effects; a limitation in the present study may therefore be the
21 focus on neural, physiological and psychological alterations identified during naturalistic/artificial exposure
22 rather than after the exposure session. We also note that the differences in attentional monitoring capacity
23 were only significant for familiar and not unfamiliar conditions (Figure 1). This may suggest that the
24 attentional demand of artificial conditions is negated by the uncertainty of a naturalistic environment
25 comprised of unfamiliar stimuli.

1 The myriad of purported health benefits ascribed to exposure to naturalistic stimuli may have a physiological
2 homologue of 'comfort' in terms of a shift from sympathetic toward parasympathetic activation.
3 Psychological or physiological stress is associated with heightened sympathetic activation and a withdrawal
4 of peripheral parasympathetic tone. If the stress is chronic, this state of sustained autonomic imbalance is
5 detrimental to health, and is recognised to contribute to cardiovascular disease and cellular aging⁴⁸,
6 obesity⁴⁹, gastrointestinal disorders⁵⁰ and a spectrum of mental health conditions, particularly depression⁵¹
7 and anxiety disorders. According to SRT, naturalistic environments tend to evoke increased parasympathetic
8 tone as humans are evolutionarily adapted to natural environments. Thus SRT may provide a comprehensive
9 account of beneficial psychophysiological effects of nature exposure following heightened states of arousal.
10 Familiarity is likely to be an important mediator of the evoked psychophysiological comfort associated with
11 nature, indeed our strongest behavioural effects of attentional monitoring were observed when contrasting
12 the naturalistic and artificial familiar conditions only, and not the unfamiliar conditions.

13 In conclusion, we demonstrate that exposure to naturalistic familiar stimuli is associated with an increase in
14 parasympathetic tone and alterations in DMN which reflect a shift in the autonomic balance towards
15 parasympathetic activation in the naturalistic familiar condition and sympathetic activation in the artificial
16 familiar condition, in accord with SRT. Individual differences in the neural and physiological response to
17 naturalistic and artificial stimuli were associated with baseline autonomic state and baseline neural coupling.
18 Alterations in autonomic balance are associated with a wide range of health effects, suggesting that SRT may
19 provide a more complete account of the health benefits of nature exposure than ART. These data expand
20 our current understanding of the restorative effects of nature by demonstrating differences in functional
21 coupling between regions within the DMN, and suggest that environment plays a significant role in
22 modulating our physiological, neural and psychological activity. Future investigations of DMN activity will be
23 required to probe the specific shifts in thought patterns and content associated with changes in anterior and
24 posterior midline coupling, and relate these more precisely to alterations in sympathetic/parasympathetic
25 balance.

1 **Method**

2 **Participants**

3 All participants reported no history of significant medical, neurological or psychiatric illness and no long term
4 medication usage. Ethical approval for conduct of the study was provided by Brighton and Sussex Medical
5 School. All participants provided informed consent. All aspects of the investigation were performed in
6 accordance with the Declaration of Helsinki.

7 17 healthy volunteers (mean age 26 years, range 21-34 years; seven female; two left handed) participated in
8 fMRI data collection, during which time soundscapes were played, physiological data were recorded and
9 participants undertook a low level attentional monitoring task.

10 **Soundscapes**

11 The four distinct soundscapes of 5 minutes 25 second duration were comprised of seven individual sound
12 clips. All sound clips were recorded using a professional quality Zoom H4n digital sound recorder (Zoom
13 North America, New York, USA) with two Rode NTG1 Condenser Shotgun Microphones (RØDE Microphones,
14 Sydney, Australia). 100 original 15 second sound clips were recorded and equalised for peak volume levels.
15 Each clip was then rated for complexity (number of distinct sounds during each clip), consistency (number of
16 significant changes in volume during a clip), familiarity and subjective intensity using a visual analogue scale
17 (VAS). The 10 clips which scored the highest and lowest in familiarity were shortlisted for the familiar and
18 unfamiliar, naturalistic and artificial conditions. From each shortlist, seven clips were selected for the main
19 soundscape with intensity, complexity and consistency scores within the range of the mean \pm two standard
20 deviations of the combined shortlist average. These seven clips were looped and integrated to form the final
21 composition for each condition.

22

1 **Attentional monitoring**

2 Attentional capacity was assessed using a mind wandering task⁵² where participants monitor an unfilled
3 white circle as it traversed the horizontal length of the stimulus display screen. At random intervals, the
4 circle contour colour changed from white to red for 470 ms, then returned to white. Participants were
5 instructed to press a button when they detected the colour change. Reaction times were calculated as the
6 interval between the initiation of the colour change and the button press response. For each condition, the
7 circle completed nine horizontal transits of the display area and changed colour 14 times (the total task
8 duration was equal to the soundscape duration). Each participant completed five runs of the task with the
9 accompanying soundscape played throughout the task through MRI compatible in-ear headphones
10 (Etymotic Research Inc., Illinois, USA) or no soundscape for the control condition, assigned in a randomised
11 order. All reaction time data was normally distributed (Kolmogorov–Smirnov $p > 0.05$). Differences in
12 reaction times for each condition were assessed by a 2 x 2 ANCOVA with the factors ‘artificiality’ (artificial,
13 naturalistic) and ‘familiarity’ (familiar, unfamiliar), and mean reaction time of the no-soundscape condition
14 as a covariate. The artificial and naturalistic stimuli with the greatest difference in reaction time were taken
15 forward for subjective, physiological and fMRI analysis.

16 **Subjective ratings and physiological recording**

17 At the end of each run of fMRI data collection, participants provided feedback on their subjective experience
18 during the attentional monitoring task and associated soundscape. Participants rated the pleasantness and
19 intensity of the soundscape, their level of distraction attributed to the soundscape and their thoughts, their
20 level of rumination and the degree to which they felt focused on the attentional task, each on a separate
21 VAS.

22 Cardiac activity was recorded via pulse oximetry (8600FO Nonin Medical Inc., Minnesota, USA) during each
23 run of the attentional monitoring task and used to determine heart rate (beats per minute) for each

1 soundscape condition. Heart rate data was not available for two participants due to weak pulse oximetry
2 signal.

3 ***Statistical analysis***

4 All subjective and physiological data were assessed for normality using the Kolmogorov–Smirnov test and
5 found to be not significantly different from a normal distribution ($p > 0.05$ in all cases). Subjective ratings
6 were separately analysed using three-way ANOVAs, to assess differences between the no-soundscape
7 control condition and the artificial and naturalistic soundscape conditions selected for further analysis.
8 Change in subjective ratings and heart rate were calculated as the difference between artificial and
9 naturalistic conditions (naturalistic - artificial). HRV analysis was performed using the HRVAS toolbox⁵³, using
10 the Lomb-Scargle periodogram method^{54,55} due to its suitability in handling irregular sampling of beat
11 intervals^{56,57}. HRV values were entered into a two-way ANCOVA, with the no-soundscape value included as a
12 covariate. One participant was removed from HRV analysis as an outlier in the naturalistic familiar condition.
13 Appropriate corrections were performed where the assumption of sphericity was violated. All statistical
14 analyses were two-tailed with α set to $p < 0.05$.

15 **Magnetic resonance imaging**

16 Neuroimaging data were acquired on a 1.5T Siemens Avanto with 32 channel headcoil. Functional data
17 consisted of T2*-weighted echo planar images (EPI) sensitive to Blood Oxygenation Level Dependent (BOLD)
18 contrast (32 slices, 3 x 3 x 3 mm resolution, 20% inter-slice gap, TR = 2520 ms, TE = 43 ms), with 170 whole
19 brain volumes acquired per run (total scanning time 35 minutes). The contrast contained within the average
20 motion-correct EPI dataset from each participant was sufficient to infer corresponding structural anatomy at
21 the same 3 mm spatial resolution.

22

1 **Preprocessing**

2 Data were preprocessed using SPM12 (Wellcome Trust Centre for Neuroimaging, University College London,
3 UK) and in-house software implemented in MATLAB (The MathWorks Inc., MA, USA). The first five volumes
4 from each run were discarded to allow for T1 equilibration effects. Preprocessing consisted of slice time
5 correction, realignment and normalisation to the MNI template, and 8 mm FWHM smoothing. Additional
6 filtering for seed based connectivity consisted of global drift removal using a 3rd order polynomial fit, with
7 regression against: i) motion parameters; ii) mean white matter; iii) mean grey matter; iv) mean
8 cerebrospinal fluid signal⁵⁸. Finally, a phase-insensitive band-pass filter (pass band 0.01-0.08 Hz) was applied
9 to reduce the effect of low frequency drift and high frequency physiological noise.

10 **General linear model analysis**

11 Informed by our behavioural findings, neuroimaging analysis was focused on the naturalistic familiar and
12 artificial familiar soundscape conditions. To explore differences in neural activity (inferred from
13 haemodynamic changes in BOLD signal) within the DMN, random effects general linear model (GLM) analysis
14 was conducted on the first level BOLD activation maps contrasting the artificial familiar (AF) against the
15 naturalistic familiar (NF) conditions (AF>NF and NF>AF). An inclusive DMN mask was created from the
16 acquired datasets, operationalized as the map of regions showing significant ($p_{(FWE\ peak)} < 0.05$) functional
17 connectivity with the PCC seed in the no-sound control condition (see Method section: Seed based
18 connectivity analysis). This map showed good agreement with previously described DMN regions⁴².
19 Activation within the masked region was assessed for significant differences between the naturalistic and
20 artificial conditions (AF>NF and NF>AF). Variations in activation associated with differences in the subjective
21 ratings of pleasantness, intensity and distraction by the sounds themselves were removed from the model
22 by including the difference in these terms as a nuisance covariate in the group (2nd level) analysis. All 2nd
23 level maps were initially thresholded at $p_{(unc. peak)} < 0.001$, with a significance determined as a peak or cluster
24 which survived FWE correction at $p < 0.05$.

1 **Seed based connectivity analysis**

2 The DMN was identified via seed based functional neural connectivity using a PCC anatomical mask
3 developed using whole-brain functional connectivity analysis of resting state networks in a large cohort of
4 healthy control participants¹⁸. For each participant and condition, the BOLD signal timecourse was extracted
5 from the region within the PCC mask, and averaged over all voxels. The seed signal was then entered as a
6 regressor in the 1st level model to identify regions with a significantly correlated BOLD timecourse over the
7 duration of the run. Whole brain PCC functional connectivity was then contrasted between the artificial and
8 naturalistic condition for each participant, with individual 1st level contrasts taken forward to 2nd level
9 random effect analysis. As with the GLM analysis, variations in connectivity associated with differences in
10 pleasantness, intensity and distraction by the sounds themselves were controlled for at the 2nd level by
11 including the difference in these terms between conditions as nuisance regressors. This method of 1st level
12 network identification and 2nd level comparison was also followed for exploratory analysis of the following
13 networks using published anatomical seed regions¹⁸ (given in parenthesis):

- 14 1) Anterior salience (bilateral anterior insula);
- 15 2) Posterior salience (bilateral posterior insula);
- 16 3) Dorsal attention / visuospatial (right supramarginal gyrus);
- 17 4) Left executive control (left dorsolateral prefrontal cortex);
- 18 5) Right executive control (right dorsolateral prefrontal cortex).

19 All 2nd level maps were initially thresholded at $p_{(unc. peak)} < 0.001$, with significance determined as a peak or
20 cluster which survived FWE correction at $p < 0.05$. Z-scores of connectivity strength (Pearson's correlation
21 with the BOLD signal timecourse of the seed) were extracted from the peak of significant clusters (averaged
22 over a 5 mm radius ROI) and entered into a separate three-way ANOVA for each network (naturalistic
23 familiar, artificial familiar and no-soundscape) to assess the direction of connectivity differences.
24 Appropriate corrections were performed where the assumption of sphericity was violated.

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1 **Figure captions**

2 Figure 1. Mean reaction times in attentional monitoring task whilst listening to familiar and unfamiliar,
3 artificial and naturalistic soundscapes. After controlling for variance in reaction times in the no-soundscape
4 condition (dashed line), the main effect of artificiality indicates increased reaction times in artificial
5 compared to naturalistic conditions ($p = 0.029$). $*p < 0.05$. Error bars ± 1 SEM.

6 Figure 2. Subjective ratings of (A) pleasantness, (B) intensity of sounds, (C) task engagement, (D) rumination,
7 (E) distraction by thoughts, and (F) distraction by sounds, for artificial familiar, naturalistic familiar and no-
8 soundscape conditions. Error bars ± 1 SEM. $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

9 Figure 3. (A) Significant increase in the mean peak of the high frequency component of heart rate variability
10 (peak HF HRV) in naturalistic familiar compared to artificial familiar conditions, after controlling for the
11 baseline (no-soundscape) high frequency peak. Error bars ± 1 SEM. $*p < 0.05$ (B) Interaction between
12 baseline (no-soundscape) peak HF and artificial familiar (dark circle, solid line) and naturalistic familiar (white
13 circle, dashed line) peak HF. Individuals with low baseline peak HF show an increase in parasympathetic tone
14 from artificial to naturalistic conditions (upwards arrow); individuals with high baseline peak HF show a
15 decrease in parasympathetic tone from artificial to naturalistic conditions (downwards arrow).

16 Figure 4. Region of significantly increased activation in the naturalistic familiar condition compared to the
17 artificial familiar condition in the middle insula of the left hemisphere ($p_{(FWE\ clus.)} 0.002$, $k = 96$, $p_{(FWE\ peak)} =$
18 0.979 , $Z = 4.09$, $[-40, 8, 6]$). Note precentral cluster in the sagittal view does not survive FWE correction ($p_{(FWE$
19 $clus.)} = 0.050$, $k = 55$, $p_{(FWE\ peak)} = 0.986$, $Z = 4.05$, $[-36, -14, 62]$).

20 Figure 5. (A) FWE corrected significant region of increased local functional connectivity between the PCC
21 seed region and the precuneus in the naturalistic familiar condition compared to artificial familiar condition
22 ($p_{(FWE\ clus.)} < 0.001$, $k = 183$, $p_{(FWE\ peak)} = 0.058$, $Z = 4.98$, $[10, -68, 34]$). (B) Main effect of soundscape
23 demonstrated in the extracted connectivity scores between the PCC and precuneus ($F_{(2,32)} = 10.96$, $p =$

1 0.001), with increased connectivity in the naturalistic familiar (μ Pearson's $r(Z) = 0.11$) compared to the
2 artificial familiar (μ Pearson's $r(Z) = 0.07$) ($t_{(16)} = 6.35, p < 0.001$) and no-soundscape condition (μ Pearson's
3 $r(Z) = 0.85$) ($t_{(16)} = 2.94, p = 0.010$). Error bars ± 1 SEM. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

4 Figure 6. (A) FWE corrected significant region of reduced functional connectivity between the PCC seed and
5 the mPFC in the naturalistic familiar condition compared to the artificial familiar condition ($p_{(FWE\ clus.)} < 0.001$,
6 $k = 185, p_{(FWE\ peak)} = 0.770, Z = 4.29, [-4, 52, 14]$). (B) Main effect of soundscape on extracted connectivity
7 scores between the PCC and mPFC ($F_{(2,32)} = 9.94, p < 0.001$), with decreased connectivity in the naturalistic
8 familiar condition (μ Pearson's $r(Z) = 0.91$) compared to the artificial familiar (μ Pearson's $r(Z) = 0.13$) ($t_{(16)} =$
9 $4.90, p < 0.001$) and no-soundscape condition (μ Pearson's $r(Z) = 0.11$) ($t_{(16)} = 2.35, p = 0.032$). Error bars ± 1
10 SEM. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

11 Figure 7. Correlation between changes in arousal (change in heart rate between the artificial familiar and
12 naturalistic familiar condition) and functional connectivity scores in the baseline no-soundscape condition
13 between the PCC seed and (A) the precuneus (Pearson's $r = 0.68, p = 0.003$) and (B) the mPFC (Pearson's $r =$
14 $0.628, p = 0.009$).

15 Figure 8. Exploratory connectivity analysis of salience networks, seeded from (A&B) bilateral anterior insula;
16 and (C&D) bilateral posterior insula. (A) The anterior insula show increased functional connectivity with the
17 ACC ($p_{(FWE\ clus.)} = 0.021, k = 84, p_{(FWE\ peak)} = 0.995, Z = 3.88, [2, 46, 4]$) in the naturalistic compared to artificial
18 condition. (B) Main effect of soundscape on extracted connectivity scores for between the anterior insula
19 and ACC, with increased functional connectivity in the naturalistic condition compared to the artificial ($t_{(16)} =$
20 $2.71, p = 0.016$) and no-soundscape control condition ($t_{(16)} = 3.09, p = 0.007$). (C) The posterior insula show
21 increased functional connectivity with a region of the right STS ($p_{(FWE\ clus.)} = 0.002, k = 121, p_{(FWE\ peak)} = 0.511, Z$
22 $= 4.54, [60, -24, 4]$) in the artificial condition compared to the naturalistic condition. (D) Main effect of
23 soundscape on extracted connectivity scores between the posterior insula and the right STS, with increased

1 functional connectivity in the artificial condition compared to the naturalistic ($t_{(16)} = 5.01, p < 0.001$) and no-
2 soundscape control condition ($t_{(16)} = 2.85, p = 0.012$). Error bars ± 1 SEM. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

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8 Conceptualization: SNG, HDC, and MW; Methodology: SNG and HDC; Software: AOP and CDGVP; Formal
9 Analysis: CDGVP; Investigation: OS and AM; Resources: MW; Writing – Original Draft: CDGVP, OS, AM;
10 Writing – Review & Editing: SNG, CO, HDC; Supervision: SNG; Funding Acquisition: MW, SNG, HDC.

11 **Competing financial interests**

12 The authors declare no competing financial interests.