

Wandering minds, sleepy brains: lapses of attention and local sleep in wakefulness

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28 **Data and Code Availability:**

29 Raw data: https://osf.io/ey3ca/?view_only=680c39e7065649c3b783a4efec0a1a94

30 Code used for analyses: <https://github.com/andrillon/wanderIM>
31

32 **This file includes:**

33 Main Text

34 Figures 1 to 5
35

36 **Abstract**

37 Attentional lapses are ubiquitous and can negatively impact performance. They correlate with
38 mind wandering, or thoughts that are unrelated to ongoing tasks and environmental demands. In
39 other cases, the stream of consciousness itself comes to a halt and the mind goes blank. What
40 happens in the brain that leads to these mental states? To understand the neural mechanisms
41 underlying attentional lapses, we cross-analyzed the behavior, subjective experience and neural
42 activity of healthy participants performing a task. Random interruptions prompted participants to
43 indicate whether they were task-focused, mind-wandering or mind-blanking. High-density
44 electroencephalography revealed the occurrence of spatially and temporally localized sleep-like
45 patterns of neural activity. This “local sleep” accompanied behavioral markers of lapses and
46 preceded reports of mind wandering and mind blanking. Furthermore, the location of local sleep
47 distinguished sluggish versus impulsive behaviors, mind wandering versus mind blanking. Despite
48 contrasting cognitive profiles, attentional lapses could share a common physiological origin: the
49 appearance of local islets of sleep within the awake brain.

50

51 **Introduction**

52 The human brain sustains the stream of our conscious experiences. Attention can direct cognitive
53 resources toward the external world and enable the selection and amplification of information
54 relevant to an individual's current behavioral goals¹. But attention can also turn inward, as is the
55 case when we focus on internally generated task-unrelated thoughts, a phenomenon usually
56 referred to as mind wandering². Recent investigations have also shown that the stream of thoughts
57 can also come to a pause, as when individuals who are awake are left with the feeling of an empty
58 mind (mind blanking)³.

59 Mind blanking and mind wandering can occur spontaneously without our knowledge or will⁴,
60 which raises the question of what are the neuronal mechanisms that control the focus of attention.
61 In fact, a characteristic feature of directed attention is its fleeting nature and the difficulty to
62 maintain it on a task for long periods of time^{1,5}. In this paper, we define lapses of attention as the
63 shift of the focus of thoughts away from the task at hand or environmental demands. The
64 consequences of attentional lapses are very diverse. At the behavioral level, they can result in a
65 lack of responsiveness or sluggish reactions, but they can also result in impulsive responses⁶.
66 Curiously, these behavioral failures can be accompanied by a lack of conscious awareness and the
67 absence of mental activity (mind blanking³), or rich, spontaneous mental activity (mind
68 wandering²).

69 It is yet unclear whether these different types of attentional lapses (sluggish vs. impulsive
70 behaviors; mind-blanking vs. mind-wandering) belong to a disparate family of behavioral and
71 phenomenological events^{7,8}, each of them associated with different physiological causes^{9,10} or
72 whether they can be traced back to common underlying physiological causes¹¹. Previous models

73 of mind wandering have proposed that mind wandering and mind blanking might arise in distinct
74 neurophysiological states^{3,9,10}. However, the fact that both sluggish and impulsive responses
75 increase following sleep deprivation^{12,13} and in individuals with attentional deficits^{6,14} implies a
76 common mechanism. Likewise, sleepiness has been associated with both mind wandering and
77 mind blanking^{15,16} despite these two mind states being phenomenologically distinct³. Furthermore,
78 investigations of the sleep onset period (hypnagogia) also indicate that subjective experiences
79 resembling mind wandering (focus on internally generated contents) and mind blanking (loss of
80 awareness) can co-exist at the border between wakefulness and sleep^{17,18}. Interestingly, these
81 studies seem to associate lapses with pressure for sleep, suggesting an involvement of fatigue in
82 the occurrence of lapses.

83 Indeed, each hour spent awake comes at the cost of mounting sleep pressure. Past research suggests
84 that the need for sleep might only be dissipated by sleep itself¹⁹ as sleep plays a vital role in neural
85 homeostasis²⁰. When individuals are prevented from sleeping for extended periods of time (as in
86 sleep deprivation studies), a subset of brain regions can start displaying electroencephalographic
87 (EEG) signatures of non-rapid eye-movement (NREM) sleep in the form of sleep-like slow waves
88 (within the delta (1-4 Hz) or theta (4-7 Hz) range), despite individuals being behaviorally and
89 physiologically awake^{21,22}. These sleep-like slow waves within wakefulness are referred to as
90 “local sleep” in contrast with the global whole-brain transition commonly observed at sleep
91 onset²²⁻²⁵.

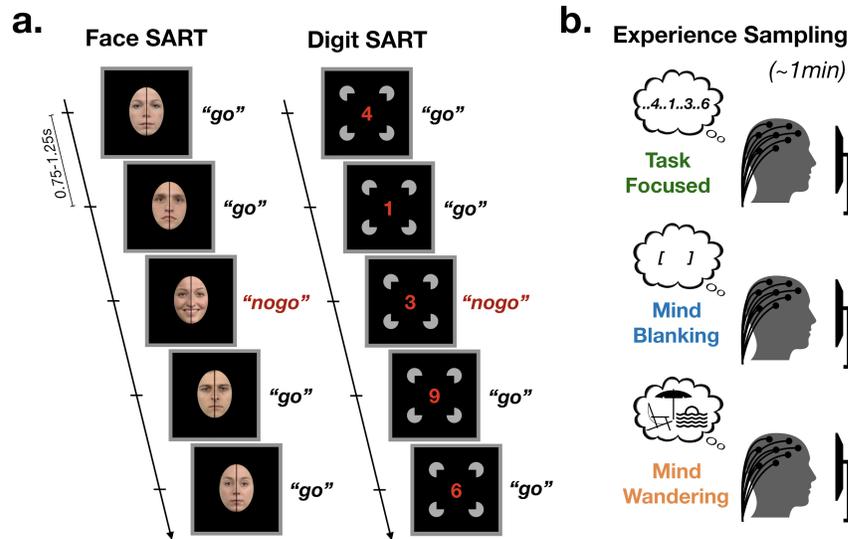
92 It has been proposed that local sleep could perturb brain functions and cause behavioral lapses²².
93 In fact, during sleep, slow waves are associated with episodes of widespread neural silencing²⁶,
94 which have been connected to behavioral unresponsiveness and the loss of consciousness^{27,28}.
95 Intracranial studies in humans and rodents showed that likewise, local sleep reduces neuronal

96 firing during waking and is associated with behavioral errors^{21,22}. Local sleep can also be detected
97 in human non-invasive recordings²⁹⁻³¹ and here again the amount of local sleep recorded in a given
98 brain region correlates with the number of errors performed in a task recruiting this specific brain
99 region^{29,30}. These results strongly suggest that local sleep could explain the behavioral component
100 of attentional lapses²². However, the impact of local sleep on phenomenology is still unclear.

101 In a recent review, we proposed that local sleep could not only explain the behavioral consequences
102 of attentional lapses, both regarding sluggish and impulsive responses, but also the
103 phenomenological profile of these lapses¹¹. We also argued that local sleep is not an extreme
104 phenomenon, occurring only when individuals are pushed to their limit, but could occur in well-
105 rested individuals³¹ and explain the occurrence of lapses in our everyday lives. To test this
106 framework, we formulate three different hypotheses as follows: (i) Can local sleep predict, at the
107 single trial level, both sluggish and impulsive behaviors in well-rested individuals? (ii) Is local
108 sleep associated with both mind blanking and mind wandering? (iii) Does the location of local
109 sleep (i.e. which brain regions are affected by a local sleep event) differentiate between
110 sluggishness and impulsivity, mind-blanking and mind-wandering? Through these hypotheses we
111 will test the idea that local sleep could act as a functional switch, transiently perturbing the
112 functioning of a given cortical network. Accordingly, a common physiological event (local sleep)
113 could lead to drastically different outcomes depending on its location within the brain.

114 To test these hypotheses, we cross-examined the behavioral performance, subjective reports and
115 physiological data from healthy individuals (N=26) performing an undemanding Go/NoGo tasks³²
116 (Figure 1a). We sampled participants' subjective experience by interrupting them during the task
117 and asking them a series of questions about their mental states prior to the interruption, including
118 whether they were focusing on the task, mind-wandering or mind-blanking (Figure 1b). Finally,

119 we recorded their brain activity using high-density scalp EEG and pupil size as an objective proxy
120 for participants' level of vigilance³³.



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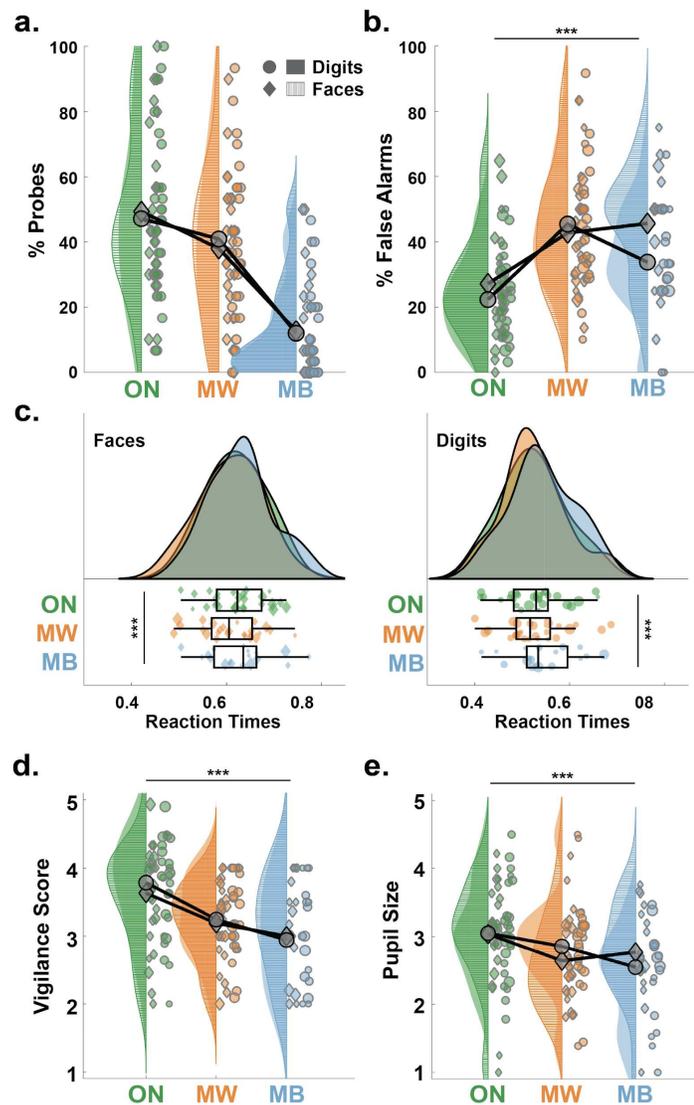
122 **Figure 1. Experimental design and hypotheses.**

123 **a:** Participants performed both a SART on faces stimuli (NoGo trials: smiling faces) and a SART
124 on digits (NoGo trials: “3”). Face/Digit presentation was continuous (new face/digit every 0.75-
125 1.25s). **b:** Every 30 to 70s, participants were interrupted and instructed to report their state of
126 mind (see Online and Supplementary Methods). Most importantly, they were asked to indicate
127 whether they were focusing on the task (task-focused: ON), thinking about nothing (mind-
128 blanking: MB) or thinking about something other than the task (mind-wandering: MW). High-
129 density EEG and pupil size were continuously recorded throughout the task.

130 Results

131 **Task performance and subjective experience.** The Go/NoGo tests (see Online Methods) require
132 participants' sustained attention, but our participants declared focusing on the task only in ~48%
133 of the probes (Face Task: $49.4 \pm 4.9\%$; Digit Task: $47.2 \pm 5.1\%$; mean \pm Standard Error of the
134 Mean (SEM) across N=26 participants; Figure 2a). In the rest of the time, they declared thinking
135 about something else (Mind Wandering (MW); Face: $38.0 \pm 4.3\%$; Digit: $40.9 \pm 4.8\%$; Figure 2a)

136 or thinking about nothing (Mind Blanking (MB); Face: $12.7 \pm 3.0\%$; Digit: $11.9 \pm 2.9\%$; Figure
 137 2a). These results are well in line with previous findings^{34,35} and highlight the prevalence of
 138 attentional lapses. Attentional lapses were also reflected in participants' poor accuracy on the
 139 Go/NoGo tests, notably regarding NoGo trials (Face: $35.3 \pm 1.3\%$ of false alarms (FA, i.e. errors
 140 on NoGo trials); Digit: $33.9 \pm 1.3\%$; Figure 2b).



141

142

143 **Figure 2. Low arousal is associated with attentional lapses characterized by different**

144 **behavioral outcomes**

145 **a:** Proportion of mental states reported during probes categorized as task-focused (ON, green),
146 mind-wandering (MW, orange) and mind-blanking (MB, blue) during the tasks with Faces
147 (diamonds for each individual participant; filled surfaces for smoothed density plot) and Digits
148 (circles and surfaces with horizontal lines). Grey diamonds and circles show the average across
149 participants. **b:** Proportion of false alarms in the 20s preceding ON, MW and MB reports. The
150 markers' size is proportional to the number of reports for each participant (same for **c-e**). Grey
151 diamonds and circles show the average across participants, weighted by the number of reports
152 (same for **d** and **e**). **c:** Distribution of reaction times (RT) for Go Trials (left: Face; right: Digit) in
153 the 20s preceding ON, MW and MB reports. **d:** Vigilance scores (subjective ratings provided
154 during probes) associated with ON, MW and MB reports. **e:** Discretized pupil size (see Online
155 Methods) in the 20s preceding ON, MW and MB reports. In **b-e**, stars show the level of significance
156 of the effect of mind-states (Likelihood Ratio Test, see Online Methods; ***: $p < 0.005$).

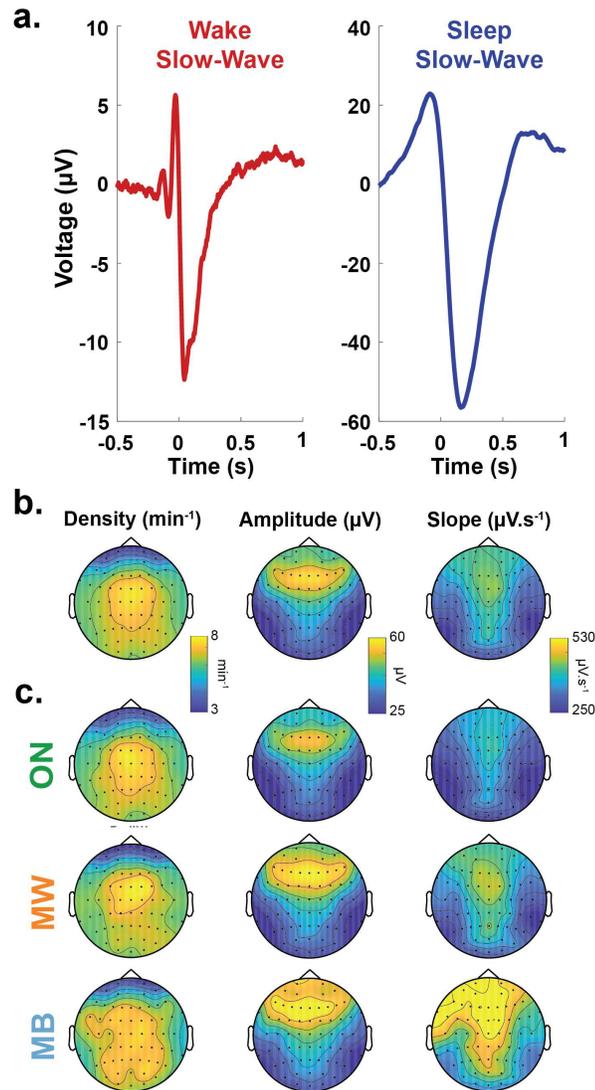
157 Next, we focused on the behavioral patterns preceding subjective reports of attentional lapses.
158 Specifically, we examined participants' behavior 20s before the onset of the probes that led to MW
159 and MB reports (see Online Methods). To quantify the impact of states of mind (i.e., ON, MW or
160 MB) on behavior, we compared statistical models that either did or did not include states of mind
161 as a predictor of behavior (see Online Methods and Supplementary Table 1). A significantly better
162 fit by the model incorporating mind states, assessed through a Likelihood Ratio Test, was
163 interpreted as evidence for the influence of mind states. To describe the size and direction of the
164 statistical effects, we report the estimates (β) of the contrasts of interest (MW vs ON, MB vs ON
165 and MB vs MW) and their 95% confidence-interval (CI). Accordingly, we found a significant
166 effect of mind states on false alarms (model comparison: $\chi^2(2)=115.9$, $p < 10^{-16}$; see Figure 2b), with
167 an increase for both MW and MB compared to ON (MW vs ON: $\beta=0.21$, CI: [0.17, 0.24]; MB vs
168 ON: $\beta=0.17$, CI: [0.12, 0.23]), but similar levels of false alarms for MB and MW (MB vs MW:
169 $\beta=-0.028$, CI: [-0.084, 0.028]). Misses were also modulated across mind states (model comparison:
170 $\chi^2(2)=36.0$, $p=1.5 \times 10^{-8}$). Specifically, MW and MB were associated with an increase in misses

171 compared to ON reports (MW vs ON: $\beta=0.011$, CI: [0.005, 0.016]; MB vs ON: $\beta=0.023$, CI:
172 [0.015, 0.032]) and misses were more frequent for MB compared to MW reports (MB vs MW:
173 $\beta=0.013$, CI: [0.005, 0.021]). Finally, mind states were associated with different patterns of
174 reaction times (RT; model comparison: $\chi^2(2)=16.3$, $p=2.9 \times 10^{-4}$; Figure 2c) with slower reaction
175 times for MB compared to both ON and MW reports (MB vs ON: $\beta=0.019$, CI: [0.009, 0.030];
176 MB vs MW: $\beta=0.022$, CI: [0.011, 0.032]). Taken together, these results suggest that MW and MB
177 can decrease performance through different ways: MW facilitates impulsivity, evidenced by faster
178 RT and more false alarms, whereas MB facilitates sluggishness, evidenced by slower RT and more
179 misses.

180 **Vigilance.** Although MW and MB differ according to their phenomenological definition and
181 associated behaviors, both states seem to occur in a similar context of low vigilance and sleepiness.
182 We quantified this by examining the correlation between participants' vigilance ratings and each
183 mind state (comparison between models including or not the information about mind-states:
184 $\chi^2(2)=144.8$, $p < 10^{-16}$; Figure 2d and Supplementary Table 1). Participants reported lower vigilance
185 ratings for both MW and MB compared to ON (MW vs ON: $\beta=-0.39$, CI: [-0.40, -0.37] and MB
186 vs ON: $\beta=-0.53$, CI: [-0.55, -0.50]). Vigilance ratings were even lower for MB compared to MW
187 (MB vs MW: $\beta=-0.13$, CI: [-0.24, -0.02]). We then examined a classical objective proxy for
188 vigilance: pupil size^{33,36}. Pupil size prior to probes (Figure 2e, N=25 participants here, see Online
189 Methods) was significantly modulated across mind-states (model comparison: $\chi^2(2)=18.0$,
190 $p=1.2 \times 10^{-4}$) with MW and MB associated with smaller pupils than ON probes (MW vs ON: $\beta=-$
191 0.29, CI: [-0.43, -0.15]; MB vs ON: $\beta=-0.22$, CI: [-0.45, -0.003]). Pupil size did not differ between
192 MW and MB (MB vs MW: $\beta=0.065$, CI: [-0.16, 0.29]).

193 **Local Sleep.** Critically, we examined the core hypothesis of our framework¹¹: whether apparently

194 distinct families of attentional lapses can be coherently explained by the occurrence of local sleep
 195 and its spatio-temporal characteristics. To do so, we first detected the occurrence of local sleep in
 196 each EEG electrode using an established approach for detecting slow waves in wakefulness and
 197 sleep (see^{30,31,37} and Online Methods). Operationally, we defined local sleep as the occurrence of
 198 large-amplitude waves within the delta ([1-4] Hz) range. Both the temporal profile and
 199 topographical distributions of local sleep detected during the tasks (Figure 3a-b) resemble the slow
 200 waves observed in NREM sleep^{37,38}. This is not trivial as our detection algorithm did not select
 201 this specific temporal profile or topographical distributions.



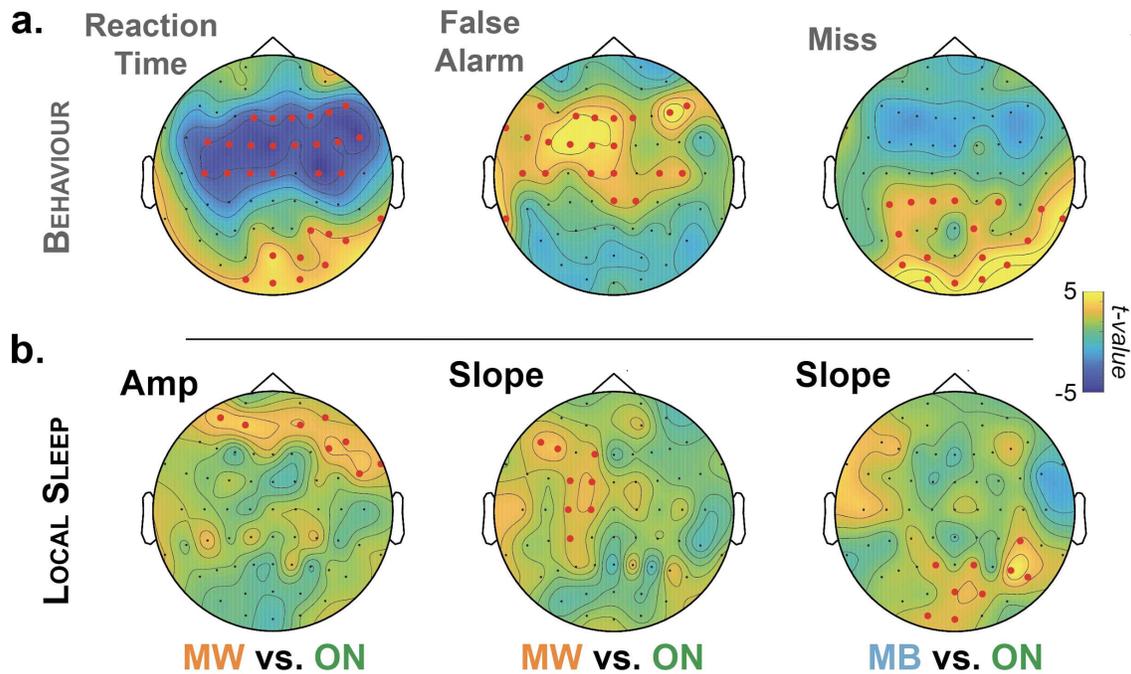
203 **Figure 3. Mind-Wandering, Mind-Blanking and Local Sleep**

204 **a:** Average waveform of the slow-waves detected over electrode Cz during the behavioral tasks
205 (red, left; N=26 participants). The average waveform of slow waves detected during sleep (blue,
206 right) extracted from another dataset (see Supplementary Methods) is shown for comparison. **b:**
207 Scalp topographies of wake slow-waves properties (left: temporal density; middle: peak-to-peak
208 amplitude; right: downward slope; see Online Methods) averaged across participants (N=26). **c:**
209 Scalp topographies for slow-waves Density (left), Amplitude (middle) and Slope (right) for the
210 different mind-states (ON, MW and MB).

211 Next, we checked whether local sleep indexes participants' level of sleepiness. For this analysis,
212 we quantified the amount and properties of local sleep across the entire scalp by averaging the
213 temporal density of local sleep (number of local sleep events per minute) as well as local sleep
214 amplitude and slope (see Online Methods) across all 63 electrodes. We verified that each of these
215 variables extracted prior to probe onset ([-20, 0]s) was negatively correlated with the subsequent
216 vigilance ratings obtained in each probe (model comparison between models with or without local
217 sleep density, amplitude or slope: density: $\chi^2(1)=13.1$, $p=3.9 \times 10^{-4}$, $\beta=-0.074$, CI: [-0.114, -0.034];
218 amplitude: $\chi^2(1)=33.1$, $p=8.5 \times 10^{-9}$, $\beta=-0.023$, CI: [-0.031, -0.015]; slope: $\chi^2(1)=82.1$, $p < 10^{-16}$, $\beta=-$
219 2.5×10^{-3} , CI: [-3.1×10^{-3} , -2.0×10^{-3}]).

220 In addition to vigilance ratings, local sleep also preceded subsequent reports of attentional lapses.
221 Topographical maps show that MW and MB reports seem preceded by larger and steeper slow
222 waves than ON reports (Figure 3c). This was confirmed by a mixed-effect model analysis focusing
223 on local sleep events before each probe and across all electrodes. We observed more local sleep in
224 MW and MB compared to ON reports (comparison between models including or not the
225 information about mind-states to explain slow-wave density: $\chi^2(2)=31.9$, $p=1.2 \times 10^{-7}$; MW vs ON:
226 $\beta=0.048$, CI: [0.023, 0.073]; MB vs ON: $\beta=0.097$, CI: [0.060, 0.133]) as well as steeper waves

227 (model comparison: $\chi^2(2)=79.2$, $p<10^{-16}$; MW vs ON: $\beta=10.7$, CI: [8.3, 13.0]; MB vs ON: $\beta=5.6$,
 228 CI: [2.1, 9.0]). In addition, for MW but not for MB reports, local sleep events had a larger
 229 amplitude compared to ON reports (model comparison: $\chi^2(2)=76.1$, $p<10^{-16}$; MW vs ON: $\beta=0.78$,
 230 CI: [0.60, 0.97]; MB vs ON: $\beta=0.20$, CI: [-0.25, 0.29]).



231

232 **Figure 4. Local sleep impacts behavioral performance and subjective reports in a region-**
 233 **specific fashion**

234 *a*: Single-trial analysis of the effects of local sleep (defined as the presence or absence of local
 235 sleep events during stimulus presentation for a given electrode and at the single-trial level) and
 236 behavioral outcomes. Mixed-Effects Models were used to quantify the impact of local sleep
 237 occurrence on reaction times (left), false alarms (middle) and misses (right) at the single-trial
 238 level. Topographies show the scalp distribution of the associated t-values. *b*: Similar approach as
 239 in *a*, showing the impact of MW vs. ON on local sleep amplitude (left) and slope (middle) and of
 240 MB vs. ON on local sleep slope (right). *a-b*: Red dots denote significant clusters of electrodes
 241 ($p_{cluster} < 0.05$, see Online Methods).

242

243 To further understand the association between local sleep and attentional lapses, we examined the
244 influence of local sleep on participants' behavior at the single-trial level. To do so, for each trial
245 and electrode, we marked the presence or absence of local sleep events between stimulus onset
246 and offset (see Online Methods) and used this as a (binary) predictor of RT, misses and false alarms
247 (Figure 4a). This analysis revealed spatially-specific effects of local sleep on distinct behavioral
248 outcomes. Namely, local sleep in frontal electrodes co-occurred with faster reaction times while
249 local sleep in posterior electrodes co-occurred with slower reaction times ($p_{\text{cluster}} < 0.005$,
250 Bonferroni corrected cluster threshold; see Figure 4a). Likewise, frontal local sleep was associated
251 with more false alarms (a marker of impulsivity) while posterior local sleep with more misses (a
252 marker of sluggishness). We obtained a similar spatial correlation pattern when considering mind
253 states: local sleep amplitude and slope was larger for MW compared to ON reports in frontal
254 electrodes only whereas local sleep amplitude was larger for MB compared to ON reports in
255 posterior channels only ($p_{\text{cluster}} < 0.05$, Bonferroni corrected cluster threshold; Figure 4b).

256 **Decision modeling.** Finally, we implemented an influential model of two-alternative forced-
257 choice (2AFC) decision making: the diffusion decision model (DDM)³⁹. The DDM decomposes
258 full reaction-time distributions and choice proportions into latent cognitive processes that are
259 thought to underlie participants' decisions in 2AFC tasks (see Online and Supplementary Methods
260 and Supplementary Figure 1). We used this modeling approach to examine how local sleep impacts
261 the different cognitive processes leading to participants' responses, with a particular focus being
262 the test of our core hypothesis: frontal local sleep disrupts the cognitive mechanisms underlying
263 executive control leading to impulsivity, while posterior local sleep slows down the integration of
264 sensory inputs leading to sluggishness. A hierarchical Bayesian approach was used to fit the DDM
265 to the reaction times obtained in the Go/NoGo tests⁴⁰ so that each parameter (Supplementary

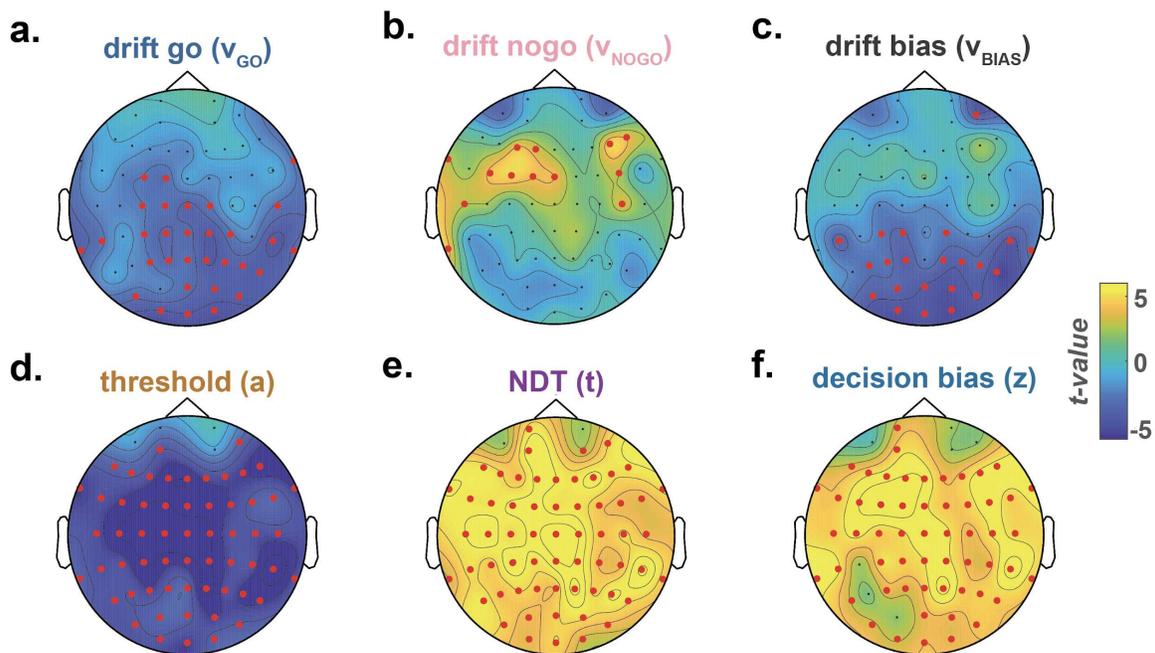
266 Figure 1) was free to vary by participant, task and local sleep occurrence (present vs. absent). The
267 estimated parameters comprised the rate of evidence accumulation for Go and NoGo responses
268 (i.e. drift rate for Go trials v_{Go} and NoGo trials v_{NoGo}), the amount of evidence needed to reach a
269 decision (i.e. the decision threshold a), the decision bias (z) and the non-decision time (t). A drift
270 bias (v_{Bias}) was also computed by taking the difference between the Go and NoGo drift rates (see
271 Online Methods), where greater values indicate stronger dynamic bias toward the Go choice
272 bound. Simulations confirmed this hierarchical DDM can successfully predict the observed data
273 (Supplementary Figure 2). We report here the differences in the parameters' estimates in the
274 presence or absence of local sleep (Figure 5).

275 The scalp topographies of the effect of local sleep on DDM parameters indicate both general and
276 electrode-specific effects. As general (electrode-non-specific) effects (Figure 5d-f), we found first
277 that local sleep was associated with a reduction in decision threshold (a ; Figure 5d), consistent
278 with the idea that local sleep facilitates impulsive responses. Second, local sleep was also
279 associated with longer non-decision times (t ; Figure 5e), implying that local sleep can slow down
280 neural processes underlying stimulus encoding and/or motor preparation. Finally, local sleep was
281 correlated with an increase in the starting point of the decision process (prior bias z ; Figure 5f),
282 implying shifts in the decision process towards Go responses.

283 As regional (electrode-specific) effects, we observed contrasting results between posterior and
284 frontal local sleep (Fig 5.a-c). Local sleep within posterior electrodes was associated with a
285 reduction of v_{Go} and v_{Bias} , meaning that evidence accumulation was slower for Go decisions and
286 the dynamic bias of the decision process for Go responses was reduced (Figure 5a,c). Conversely,
287 local sleep within frontal electrodes correlated with a reduction of v_{NoGo} , indicating that evidence
288 accumulation was slower for NoGo Decisions (Figure 5b). This provides an explanation of the

289 region-specific behavioral results reported in Figure 4, whereby posterior local sleep was
 290 associated with sluggish responses and increased misses while frontal local sleep was associated
 291 with faster, impulsive responses and more false alarms. Indeed, slower evidence accumulation in
 292 favor of Go responses would lead to slower reaction times or even misses, whereas slower evidence
 293 accumulation for NoGo responses would lead to faster responses and possibly false alarms.

294



295

296 **Figure 5. Global and local effects of local sleep on sub-components of decision-making**

297 *Reaction Times in the Go/NoGo tasks were modelled according to a Hierarchical Drift Diffusion*
 298 *Model (see Online Methods). a-f: Topographical maps of the effect of local sleep (i.e. whether or*
 299 *not a local sleep event was detected for each trial and for a specific electrode) on the parameters*
 300 *of decision-making: v_{Go} (a), v_{NoGo} (b), v_{Bias} (c), a (d), t (e), z (f). The effect of local sleep was*
 301 *estimated with LMEs (see Online Methods) and topographies show the scalp distribution of the*
 302 *associated t-values. Red dots denote significant clusters of electrodes ($p_{cluster} < 0.05$, Bonferroni-*
 303 *corrected, see Online Methods).*

304 These results suggest that local sleep could represent both a general index of fatigue as well as a
 305 mechanism underlying specific consequences of sleepiness. In a region-nonspecific manner, local

306 sleep could thus reflect the global “sleepiness” of the brain (reflected in t , a and z for global
307 decision parameters) while in a region-specific manner, local sleep could reflect the disruption of
308 specific cognitive processes carried out by the affected brain regions. Taken together, we interpret
309 these as strong evidence to support the idea that local sleep is a compelling physiological
310 phenomenon, which precedes and co-occurs with subjective and behavioral aspects of attentional
311 lapses. In addition, mechanisms of local sleep are spatio-temporally specific enough to explain
312 distinctive components of attentional lapses in a unified and quantitative manner.

313 **Discussion**

314 According to both in-lab and real-life studies, humans spend up to half of their waking lives not
315 paying attention to their environment or the task-at-hand^{34,35}. However, despite the ubiquitousness
316 of attentional lapses, it is unclear why they occur so frequently in the first place. Part of the
317 difficulty in identifying the neural correlates of attentional lapses could be due to their intrinsic
318 diversity as well as the lack of adequate taxonomy for these lapses^{7,8}. Rather than shying away
319 from this diversity, we embraced this difficult challenge to clarify the neural mechanisms
320 underlying attentional lapses by linking three different levels of explanation: behavior,
321 phenomenology and physiology. Based on our results, we argue that a large subset of attentional
322 lapses could be simply explained by “local sleep”. We show that local sleep can reflect global
323 states of the brain (Figure 5d-f) and, like pupil size or subjective ratings of fatigue (Figure 2d-e),
324 index the build-up of a pressure for sleep. However, local sleep is also specific enough in both
325 time and space (Figure 4 & 5a-c) to account for the occurrence of different types of attentional
326 lapses.

327 Indeed, recent findings have revisited the classical view of sleep as an all-or-nothing

328 phenomenon^{22-24,41,42}. Although sleep is orchestrated at the scale of the entire brain, some of the
329 key neural mechanisms underlying sleep are implemented and regulated at the level of local
330 cortical circuits^{24,25}. Consequently, when the pressure for sleep increases, an awake brain can start
331 displaying local sleep-like patterns of activity such as delta or theta waves^{21,22,29,43}. These bouts of
332 local sleep are both time-dependent (i.e. increase with time spent awake) and use-dependent (i.e.
333 depend on the level of activation of a given brain region)^{29,30}. The occurrence of local sleep has
334 been linked to perturbations of information processing and task-related errors or attentional lapses
335 in animal and human intracranial data^{21,22}. A similar relationship between local sleep and
336 behavioral errors has been evidenced when detecting local sleep in non-invasive scalp recordings
337 of sleep-deprived^{29,30} or well-rested³¹ individuals.

338 Our findings expand this previous literature by showing that within the same individual, local sleep
339 temporally precedes (at a single-probe level) different types of attentional lapses. In particular, we
340 observed that sluggish responses (slow responses and misses) defined at the behavioral level
341 tended to be associated with mind-blanking at the phenomenological level (Figure 2b-c) and that
342 both were associated with an increase in local sleep over posterior electrodes (Figure 3-4).
343 Conversely, impulsive responses (fast responses and false alarms) were associated with mind-
344 wandering (Figure 2b-c) and with an increase in local sleep over frontal electrodes (Figure 3-4).
345 These results imply a tight relationship between local sleep and behavioral errors: only local sleep
346 events occurring at the right time (i.e. during stimulus presentation) and in the right place (i.e. in
347 the brain regions involved in the task) would be predictive of distinct behavioral and
348 phenomenological aspects of attentional lapses¹¹.

349 Our results are largely consistent with previous findings on the neural correlates of attentional
350 lapses. Most of these studies focused on mind wandering, although often defined as any mental

351 state that is not on task (i.e. MW+MB here). fMRI studies showed that mind wandering in this
352 sense was associated with the activation of the Default Mode Network (DMN)^{44,45}. Interestingly,
353 a phasic activation of the DMN in a resting state fMRI paradigm has been suggested to reflect a
354 state of low alertness and possibly local sleep⁴⁶. EEG correlates of mind wandering are less clear.
355 A seminal study reported a reduction of alpha and/or beta oscillations during mind wandering⁴⁷
356 whereas others have reported an increase⁴⁸⁻⁵⁰. However, alpha oscillations are not an unambiguous
357 marker of sleepiness, as they only transiently increase with sleepiness. Alpha power is low when
358 participants are both fully alert or, on the contrary, approaching sleep onset^{51,52}. Thus, the divergent
359 results obtained regarding mind wandering and alpha oscillations could be explained by a shift in
360 participants' baseline level of fatigue. Importantly, these results are not contradictory to our work
361 (and others¹⁵) which shows the association between mind wandering and sleepiness.

362 Previous results on attentional lapses obtained with pupillometry are similarly inconclusive. While
363 most studies found a dampening of stimulus-locked increases in pupil size during mind wandering
364 (e.g. ^{45,53,54}), results diverge for baseline pupil size, which has either been reported as increasing
365 (e.g. ^{55,56}) or decreasing (e.g. ^{45,57}). When distinguished from mind wandering, mind blanking has
366 also been associated with a reduced pupil size compared to task-focused states^{10,53}. Our results
367 largely align with the latter results, with both mind wandering and mind blanking being
368 characterized by a decrease in pre-probe pupil size (Figure 2e) which goes together with low
369 vigilance ratings (Figure 2d) and local sleep (Figure 3-4). The complex pattern of results reported
370 in the literature regarding pupil size and mind-wandering could be explained by the fact that pupil
371 size does not index only arousal but it also correlates with motivation⁵⁸, cognitive load⁵⁹, etc. In
372 contrast, the sleep-like nature of local sleep (Figure 3) makes it an unambiguous marker of
373 sleepiness. Furthermore, local sleep is a multivariate variable, defined across space and can

374 therefore indicate how brain regions respond differently to sleep pressure. In this study, we
375 scratched only the surface of this rich source of information by showing a fronto-posterior contrast
376 (Figure 4 and 5). Further investigations, including source localization or simultaneous recording
377 of EEG and fMRI^{60,61}, promise a deeper understanding of the mechanisms underlying attentional
378 lapses.

379 Beyond attentional lapses, our results could inform how different brain regions participate in
380 shaping the stream of consciousness. Local sleep, considered as a spontaneous perturbation of
381 local cortical networks, could indicate the functions fulfilled by these networks. For example, we
382 observed that local sleep in frontal regions was associated with false alarms (Figure 4a), which
383 aligns well with the role of frontal cortices in executive functions and response inhibition⁶².
384 Conversely, local sleep in the back of the brain was associated with misses (Fig 4a), which is
385 consistent with the involvement of parietal cortices in sensorimotor integration⁶³. At the
386 phenomenological level, frontal local sleep was associated with mind wandering, whereas
387 posterior local sleep was associated with mind blanking. Thus our results could speak to the debate
388 on the respective involvement of frontal and posterior cortices in supporting different conscious
389 states^{64,65}. Our results suggest that a perturbation of frontal cortices leads to unconstrained thoughts
390 (mind wandering) rather than the loss of awareness, but that awareness decreases when posterior
391 regions go momentarily offline, a pattern similar to the neural correlates of dreaming during sleep
392 or spontaneous thoughts during wakeful rest^{60,66}. However, frontal and posterior local sleep do not
393 only differ by their location but also in terms of spatial expanse: local sleep in frontal electrodes
394 appears more focal, whereas local sleep in posterior electrodes is more widespread (Supplementary
395 Figure 3). Thus, the loss of awareness reported during mind blanking and associated with posterior
396 local sleep could be due to the fact that posterior local sleep might actually involve a broader

397 fronto-parietal network. This is in line with theories attributing an essential role of fronto-parietal
398 connections in the emergence of conscious representations⁶⁷⁻⁶⁹.

399 In conclusion, we show here that attentional lapses occurring in the context of an undemanding
400 task are accompanied by local sleep, even when participants are well-rested. Furthermore, the
401 location of local sleep events is predictive of certain behavioral and phenomenological properties
402 of these lapses. Thus, we propose local sleep as a more mechanistic and proximate cause to explain
403 attentional lapses. When our minds go somewhere else or nowhere, it is possible that it is because
404 part of our brain is already snoozing.

405 **Online Methods**

406 ***Participants.*** Thirty-two (N=32) healthy adults were recruited and participated in this study. Six
407 individuals were not included in our analyses because of technical issues during recordings or an
408 abnormal quality of physiological recordings assessed through a post-hoc visual inspection of the
409 data. The remaining 26 participants (age: 29.8 ± 4.1 years, mean \pm standard-deviation; 10 females)
410 were included in all analyses except for one individual for whom we do not have eye-tracking data.

411 ***Experimental Design and Stimuli.*** Participants were seated in a dim-light room with their chin
412 resting on a support at approximately 60cm from a computer screen. All task instructions and
413 stimuli were displayed and button responses were collected via the Psychtoolbox toolbox
414 extension⁷⁰ for Matlab (Mathworks, Natick, MA, USA).

415 The experimental design consisted of two modified Sustained Attention to Response Tasks
416 (SARTs)³² in which participants were instructed to pay attention to a series of pictures of human
417 faces in the Face SART blocks or digits in the Digit SART blocks. The order of Face or Digit

418 blocks was pseudo-randomized for each participant. Each block lasted approximately 12 to 15
419 minutes. Participants were allowed to rest between blocks. Participants performed 3 Face SART
420 blocks and 3 Digit SART blocks for a total duration of 103 ± 19.7 minutes (mean \pm standard-
421 deviation) from beginning to end. Each type of the Face and Digit SART was preceded by a brief
422 training session (27 trials) on each SART. During this SART training session, feedback on the
423 proportion of correct trials and average reaction times was provided to participants. Participants
424 were encouraged to prioritize accuracy over speed.

425 Each face or digit was presented for a duration of 750 to 1250ms (random uniform jitter). Face
426 stimuli were extracted from the Radboud Face Database⁷¹ and consisted of 8 faces (4 females)
427 with a neutral facial expression and one smiling female face. Digits from 1 to 9 were displayed
428 with a fixed font size. For the Face SART, participants were instructed to press a button for all
429 neutral faces (Go trials) but to avoid pressing the response button for the smiling face (NoGo
430 trials). The order of faces was pseudo-randomized throughout the entire task (i.e. we permuted the
431 presentation order every 9 stimuli and we did not present twice the same stimuli in a row). For the
432 Digit SART, participants were instructed to press a button for all digits except the digit “3” (NoGo
433 trials), with the order of the digits pseudo-randomized as well.

434 During the SART, we stopped the presentation of stimuli at random times (every 30 to 70s, random
435 uniform jitter) with a sound and the word “STOP” displayed on the screen. These interruptions
436 allowed to probe the mental state of the participants with a series of 8 questions (including 1
437 conditional question; see Supplementary Methods). In particular, we instructed participants to
438 report their attentional focus “just before the interruption”. Participants had to select one of the
439 four following options: (1) “task-focused” (i.e. focusing on the task, ON), (2) “off-task” (i.e.
440 focusing on something other than the task, which we define here as mind wandering MW), (3)

441 “mind blanking” (i.e. focusing on nothing), (4) “don’t remember”. As the 4th option accounted for
442 only 1.1% of all probes and since previous studies do not always distinguish between these options
443 (e.g. ⁷²), we collapsed the 3rd and 4th options as mind-blanking (MB) in all analyses. We also
444 instructed participants to rate their level of vigilance, reflecting “over the past few trials”, with a
445 4-point scale (Figure 2d; from 1=“Extremely Sleepy” to 4=“Extremely Alert”). Each of the 12-15
446 min SART blocks included 10 interruptions (in total, 30 interruptions for each SART task).
447 Participants were informed of the presence of interruptions and the nature of each question before
448 starting the experiment. The mind-state categories (ON, MW and MB) were also explained to
449 participants orally and in writing.

450 ***Physiological Recordings and Preprocessing.*** High-density scalp electroencephalography (EEG)
451 was recorded using an EasyCap (63 active electrodes) connected to a BrainAmp system (Brain
452 Products GmbH). A ground electrode was placed frontally (Fpz in the 10-20 system). Electrodes
453 were referenced online to a frontal electrode (AFz). Additional electrodes were placed above and
454 below the left and right canthi respectively to record ocular movements (electrooculogram, EOG).
455 Two electrodes were placed over the deltoid muscles to record electrocardiographic (ECG)
456 activity. EEG, EOG and EMG were sampled at 500Hz. Eye-movements and pupil size on one eye
457 were recorded with an EyeLink 1000 system (SR Research) with a sampling frequency of 1000Hz.
458 The eye-tracker was calibrated at the start of each recording using the EyeLink acquisition
459 software.

460 The EEG signal was analyzed in Matlab with a combination of the SPM12, EEGLab⁷³ and
461 Fieldtrip⁷⁴ toolboxes. The raw EEG signal was first high-pass filtered above 0.1 Hz using a two-
462 pass 5th-order Butterworth filter. A notch filter was then applied (stop-band: [45, 55] Hz, 4th-order
463 Butterworth filter) to remove line noise. Electrodes that were visually identified as noisy

464 throughout the recording were interpolated using neighboring electrodes. Finally, the continuous
465 EEG data was segmented according to probe onsets on a 64s window ([-32, 32] s relative to the
466 probe onset); the average voltage over the entire window (64s) was then removed for each
467 electrode and probe.

468 Pupil size was analyzed with custom functions in Matlab and corrected for the occurrence of blinks
469 (see ³³ and Supplementary Methods). Pupil size was averaged over the stimulus presentation
470 window for each trial (window length: 0.75 to 1.25s). Pupil size values in Figure 2e were computed
471 by averaging the pupil size in all trials within 20s preceding the probe onset and then by
472 discretizing them into 5 bins across all probes for each participant and task to normalize pupil size
473 across participants³³.

474 **Behavioral Analyses.** Go trials were considered incorrect (Miss) if no response was recorded
475 between stimulus onset and the next stimulus onset. Conversely, NoGo trials were considered
476 incorrect (false alarm) if a response was recorded between stimulus onset and the next stimulus
477 onset. Reaction times were computed from the onset of the stimulus presentation. Trials with
478 reaction times shorter than 300ms were excluded from all analyses (so not considered correct or
479 incorrect). For analyses of behavior prior to probes, we analyzed only the trials within 20s from
480 probes' onset (Figure 2). For analyses of behavior at the trial level (Figure 4-5), we examined trials
481 within 30s of probes' onset (minimum inter-probe interval).

482 **Local sleep.** The detection of local sleep events was based on previous algorithms devised to
483 automatically detect slow waves during NREM sleep^{30,37}. First, the preprocessed EEG signal was
484 re-referenced to the average of the left and right mastoid electrodes (TP9 and TP10) to match the
485 established guidelines for sleep recordings⁷⁵. Then, the signal was down-sampled to 128Hz and

486 band-pass filtered within the delta band. A type-2 Chebyshev filter was used to reach an attenuation
487 of at least 25 dB in the stop-band ([0.05, 7.5] Hz) but less than 3 dB in the pass-band ([0.5, 5] Hz).
488 All waves were detected by locating the negative peaks in the filtered signal. For each wave, the
489 following parameters were extracted: start and end point (defined as zero-crossing respectively
490 prior the negative peak of the wave and following its positive peak), negative peak amplitude and
491 position in time, positive peak amplitude and position in time, peak-to-peak amplitude, downward
492 (from start to negative peak) and upward (from negative to positive peak) slopes.

493 Slow waves in sleep typically have a larger negative peak compared to their positive peak (Figure
494 3a) and are predominantly observed over fronto-central channels^{37,38}. This contrasts with artefacts
495 in the EEG signal caused by blinks, which typically have a large positive component and are more
496 frontally distributed. Thus, to reduce the false detection of these artefacts as candidate slow waves,
497 we excluded waves with a positive peak above 75 μ V. We also excluded waves within 1s of large-
498 amplitude events (>150 μ V of absolute amplitude). Finally, we discarded all waves that were
499 shorter than 143ms in duration (corresponding to a frequency > 7Hz). We then selected the waves
500 with the highest absolute peak-to-peak amplitude (top 10% computed for each electrode
501 independently) as local sleep slow waves.

502 ***Hierarchical Drift Diffusion Modeling.*** Hierarchical Bayesian Drift Diffusion Modeling
503 (HDDM) was used to extend our analysis beyond simple behavioral metrics and examine the
504 impact of local sleep on the sub-processes of decision making. The DDM is a sequential-sampling
505 model of 2AFC decision making that can be considered an extension of signal detection theory
506 into the time-domain, accounting for full reaction time distributions as well as choice behavior³⁹.
507 The HDDM package⁴⁰ in Python 2.8 was used to fit the drift-diffusion model to the SART data.
508 DDM parameters were estimated using a hierarchical Bayesian method that uses Markov-chain

509 Monte Carlo (MCMC) sampling to generate full posterior distributions of model parameters. The
510 following DDM parameters were estimated: the drift rate for Go trials (v_{Go}), the drift rate for NoGo
511 trials (v_{NoGo}), the decision threshold (a), the decision bias (z) and the non-decision time (t). Drift
512 bias (v_{Bias}) was computed by taking the difference between the absolute values of v_{Go} (positive)
513 and v_{NoGo} (negative), where greater values indicate stronger v_{Go} drift bias (Supplementary Figure
514 1). To examine whether the model could reproduce key patterns in the SART data, posterior
515 predictive checks were undertaken by simulating 100 datasets from the joint posteriors of model
516 parameters and comparing these to the observed data⁷⁶ (Supplementary Figure 3).

517 To estimate HDDM parameters 8,000 samples from the posterior were generated with MCMC
518 methods and the initial 2,000 were discarded as burn-in to reduce autocorrelation. HDDM models
519 were fit to the data so as to examine the influence of local sleep (event present vs. absent; Figure
520 5). To do so we considered each EEG electrode separately. For a given electrode, a trial was
521 flagged as being associated with local sleep if the onset of a local sleep event (slow wave) was
522 detected for this electrode during stimulus presentation (i.e. between stimulus onset and offset).
523 Parameters were also free to vary by task (Digit vs. Face). We included trials within 30s of probe
524 onset to maximize the number of available trials for trial-by-trial analysis. From the estimated
525 models, we extracted the subject-level point-estimates of parameters as the mean of each
526 individual's posterior distribution for a given task (Face and Digit) and mind-state (ON, MW or
527 MB) or local sleep (present or absent) combination.

528 **Statistical Analyses.** Statistics were performed using Linear Mixed-Effects modeling (LMEs). In
529 all models, subject identity was coded as a categorical random effect. The task type (Digit or Face
530 SART) was used as a categorical fixed effect in all analyses. Several fixed effects were
531 independently tested in our different analyses: mind-states (categorical variable: ON, MW and

532 MB; Figure 2-4) or local sleep (binary variable: present/absent, Figure 4). LMEs were run to
533 predict different variables of interest: behavioral variables (misses, false alarms, reaction times) or
534 physiological variables (pupil size, presence or properties of local sleep slow waves). We also used
535 LMEs to estimate the effect of mind states or local sleep on the point-estimates derived from the
536 HDDM models (Figure 5). Model comparisons were performed using a Likelihood Ratio Test to
537 estimate the influence of multi-level categorical variables such as mind states. In practice, we
538 compared a model including mind-states (along possibly other random and fixed effects) with a
539 model not including mind-states as a predictor. All models and model comparisons are described
540 in Supplementary Table 1. In the Results section, we report the Likelihood Ratio Test as $\chi^2(df)$,
541 where χ^2 is the Likelihood Ratio Test statistic and df the degrees of freedom^{77,78}. When several
542 model comparisons were performed for the same analysis using the Likelihood Ratio Test, a
543 Bonferroni correction was applied to the statistical threshold. To indicate the magnitude and
544 direction of the effects, we report the estimates (β) and confidence interval (CI) for the contrasts
545 of interest (MW vs. ON, MB vs ON, MB vs MW). All models performed are described in
546 Supplementary Table 1. For topographical maps, clusters were identified using a cluster-
547 permutation approach (cluster alpha: 0.01; Monte-Carlo p-value threshold: 0,05 with a Bonferroni
548 correction in the case of multiple comparisons; see Supplementary Methods for details).

549

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557

558

559 **Author Contributions**

560 Design: TA, TM, JW & NT. Data collection: TA & TM. Analyses: TA & AB. Manuscript: TA,
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Figures

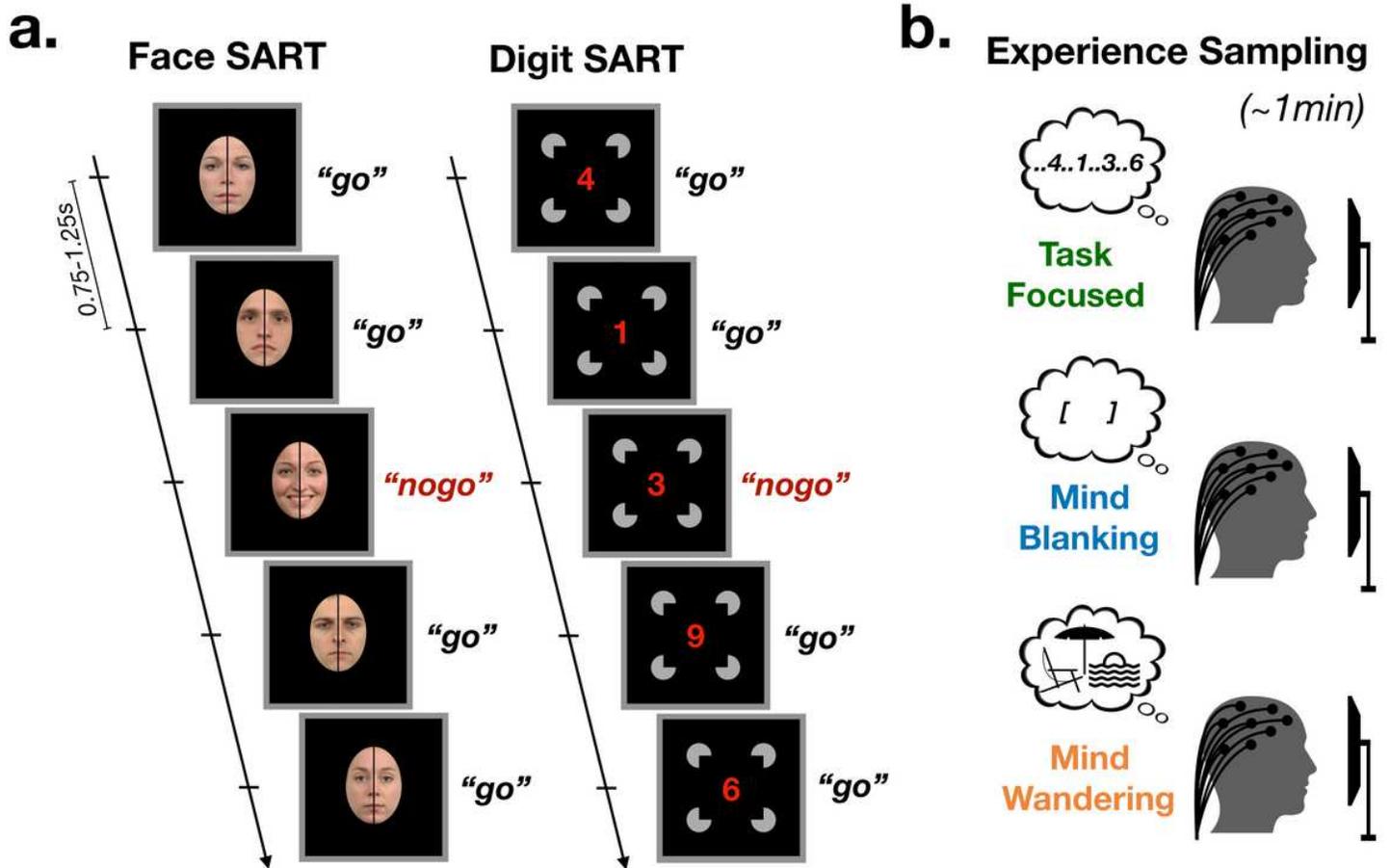


Figure 1

Experimental design and hypotheses. a: Participants performed both a SART on faces stimuli (NoGo trials: smiling faces) and a SART on digits (NoGo trials: “3”). Face/Digit presentation was continuous (new face/digit every 0.75- 1.25s). b: Every 30 to 70s, participants were interrupted and instructed to report their state of mind (see Online and Supplementary Methods). Most importantly, they were asked to indicate whether they were focusing on the task (task-focused: ON), thinking about nothing (mind blanking: MB) or thinking about something other than the task (mind-wandering: MW). High density EEG and pupil size were continuously recorded throughout the task.

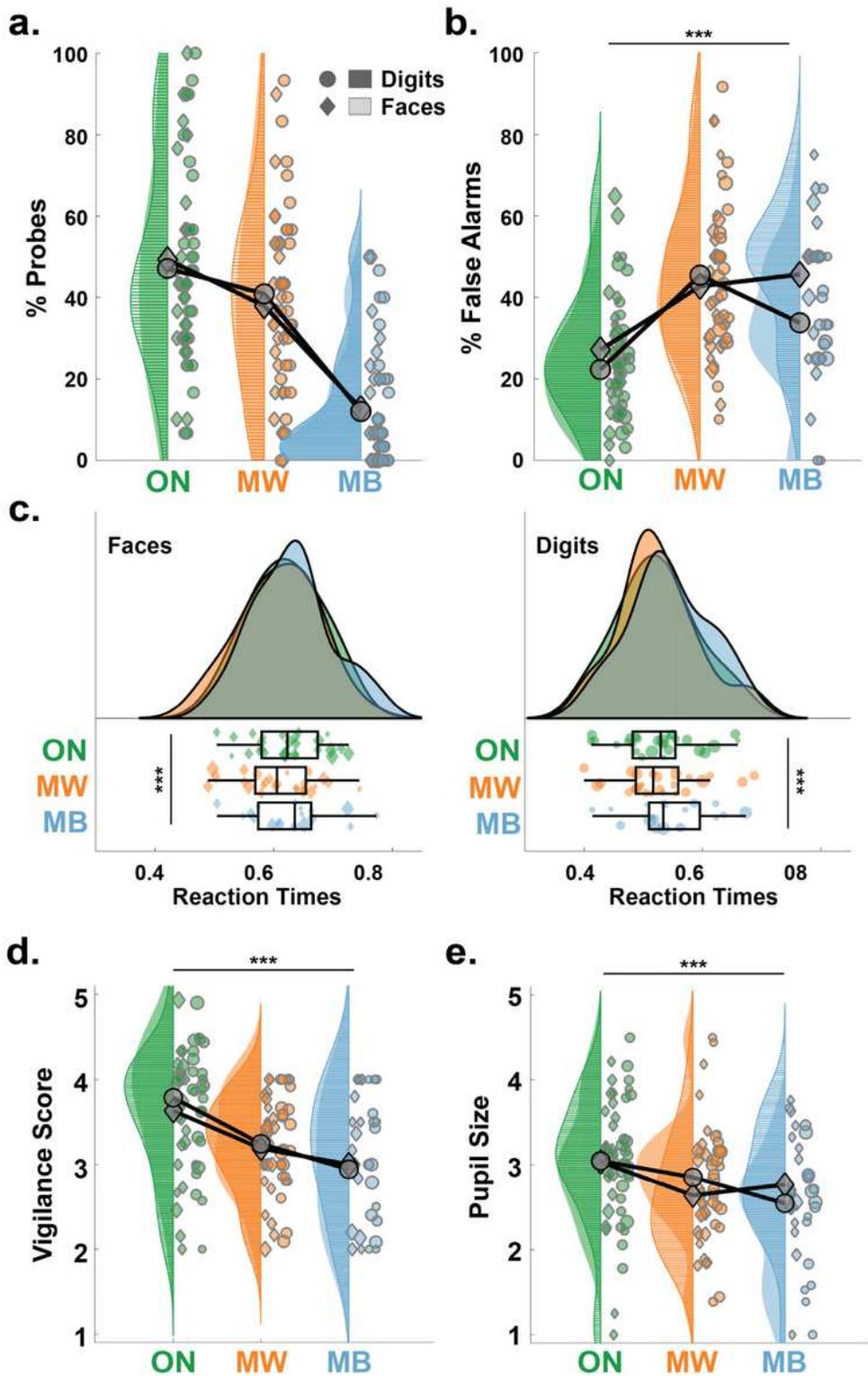


Figure 2

Low arousal is associated with attentional lapses characterized by different behavioral outcomes a: Proportion of mental states reported during probes categorized as task-focused (ON, green), mind-wandering (MW, orange) and mind-blanking (MB, blue) during the tasks with Faces (diamonds for each individual participant; filled surfaces for smoothed density plot) and Digits (circles and surfaces with horizontal lines). Grey diamonds and circles show the average across participants. b: Proportion of false

alarms in the 20s preceding ON, MW and MB reports. The markers' size is proportional to the number of reports for each participant (same for c-e). Grey diamonds and circles show the average across participants, weighted by the number of reports (same for d and e). c: Distribution of reaction times (RT) for Go Trials (left: Face; right: Digit) in the 20s preceding ON, MW and MB reports. d: Vigilance scores (subjective ratings provided during probes) associated with ON, MW and MB reports. e: Discretized pupil size (see Online Methods) in the 20s preceding ON, MW and MB reports. In b-e, stars show the level of significance of the effect of mind-states (Likelihood Ratio Test, see Online Methods; ***: $p < 0.005$).

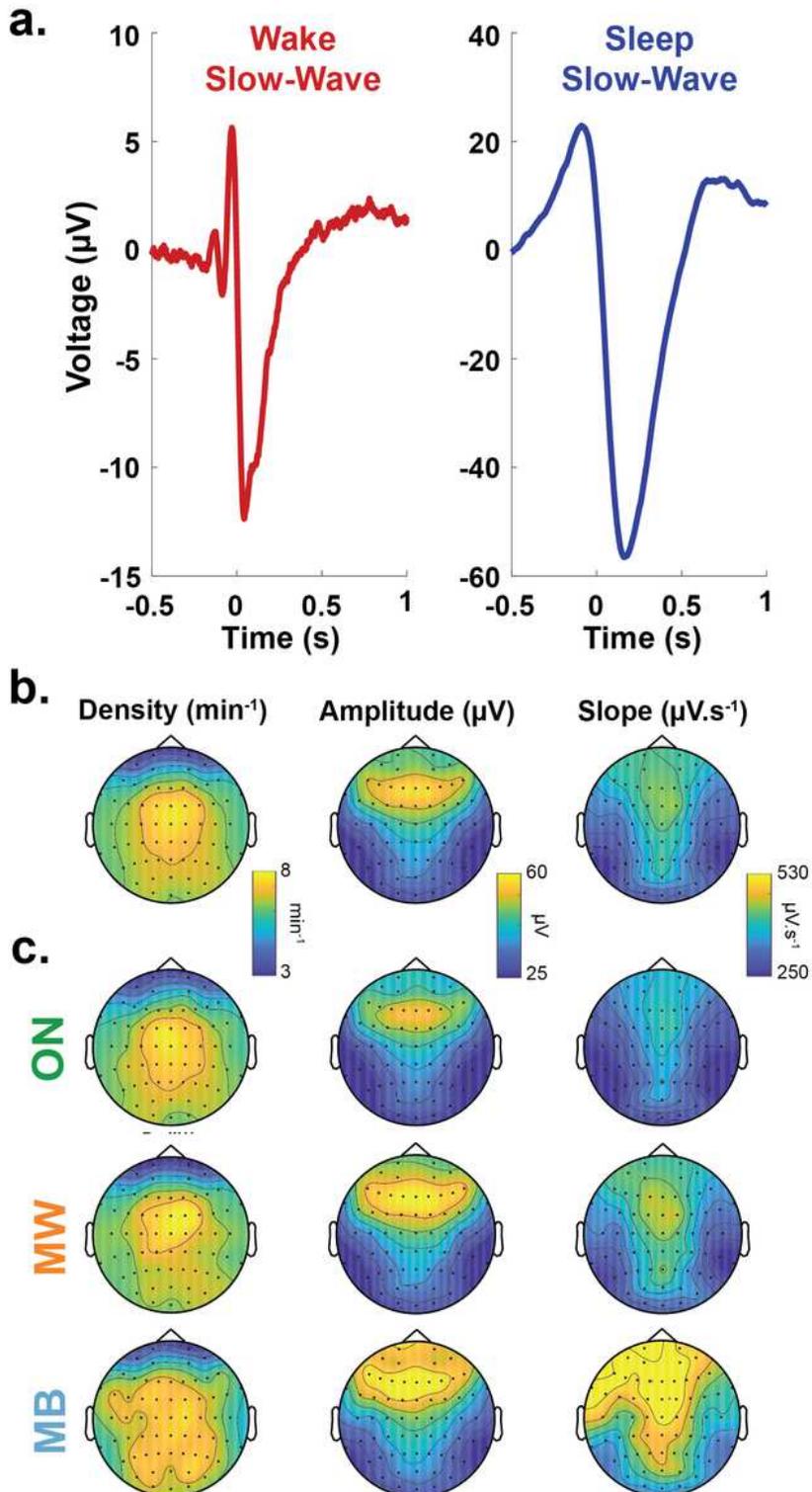


Figure 3

Mind-Wandering, Mind-Blanking and Local Sleep a: Average waveform of the slow-waves detected over electrode Cz during the behavioral tasks (red, left; N=26 participants). The average waveform of slow waves detected during sleep (blue, right) extracted from another dataset (see Supplementary Methods) is shown for comparison. b: Scalp topographies of wake slow-waves properties (left: temporal density; middle: peak-to-peak amplitude; right: downward slope; see Online Methods) averaged across participants (N=26). c: Scalp topographies for slow-waves Density (left), Amplitude (middle) and Slope (right) for the different mind-states (ON, MW and MB).

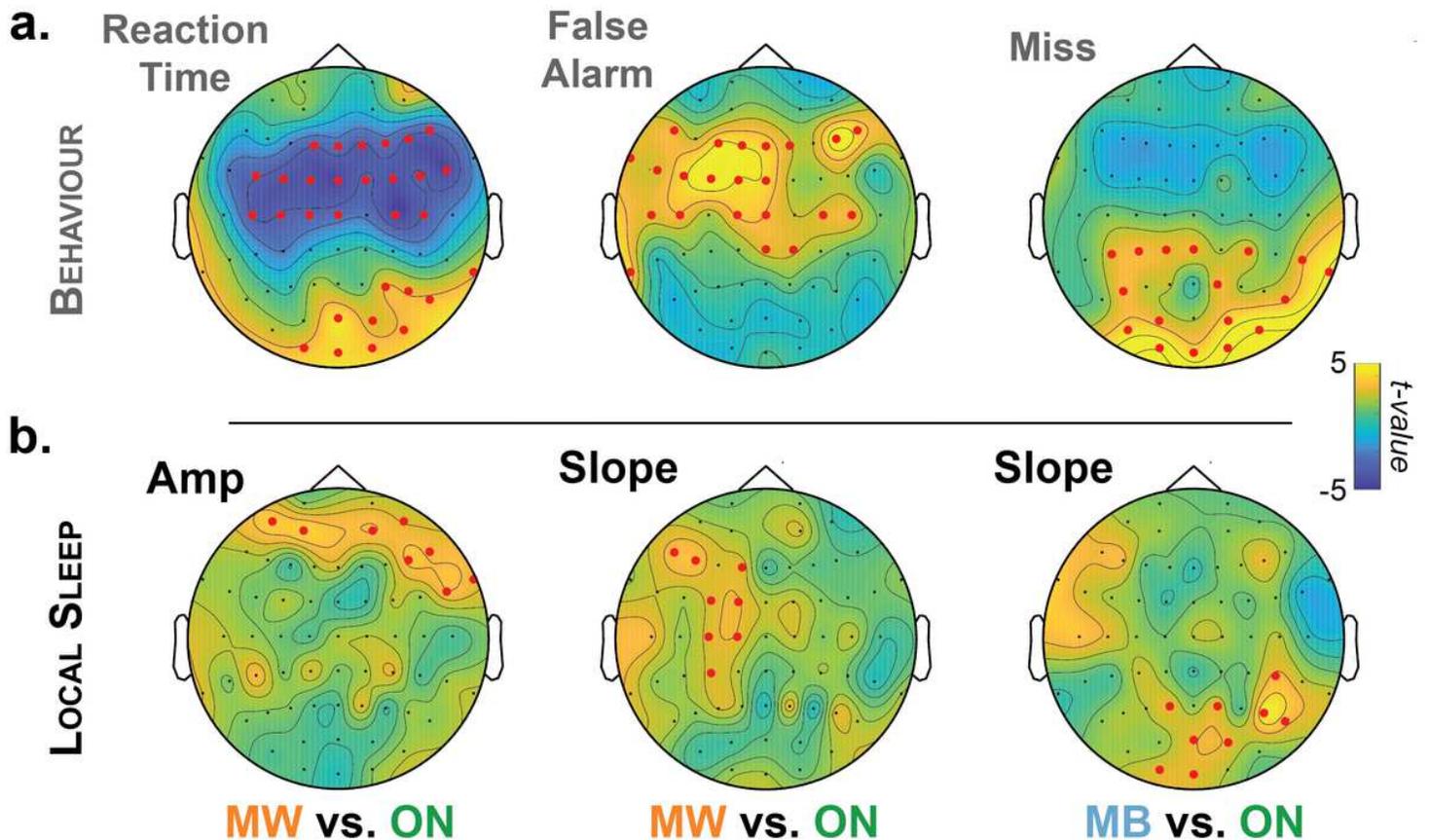


Figure 4

Local sleep impacts behavioral performance and subjective reports in a region specific fashion a: Single-trial analysis of the effects of local sleep (defined as the presence or absence of local sleep events during stimulus presentation for a given electrode and at the single-trial level) and behavioral outcomes. Mixed-Effects Models were used to quantify the impact of local sleep occurrence on reaction times (left), false alarms (middle) and misses (right) at the single-trial level. Topographies show the scalp distribution of the associated t-values. b: Similar approach as in a, showing the impact of MW vs. ON on local sleep amplitude (left) and slope (middle) and of MB vs. ON on local sleep slope (right). a-b: Red dots denote significant clusters of electrodes (pcluster < 0.05, see Online Methods).

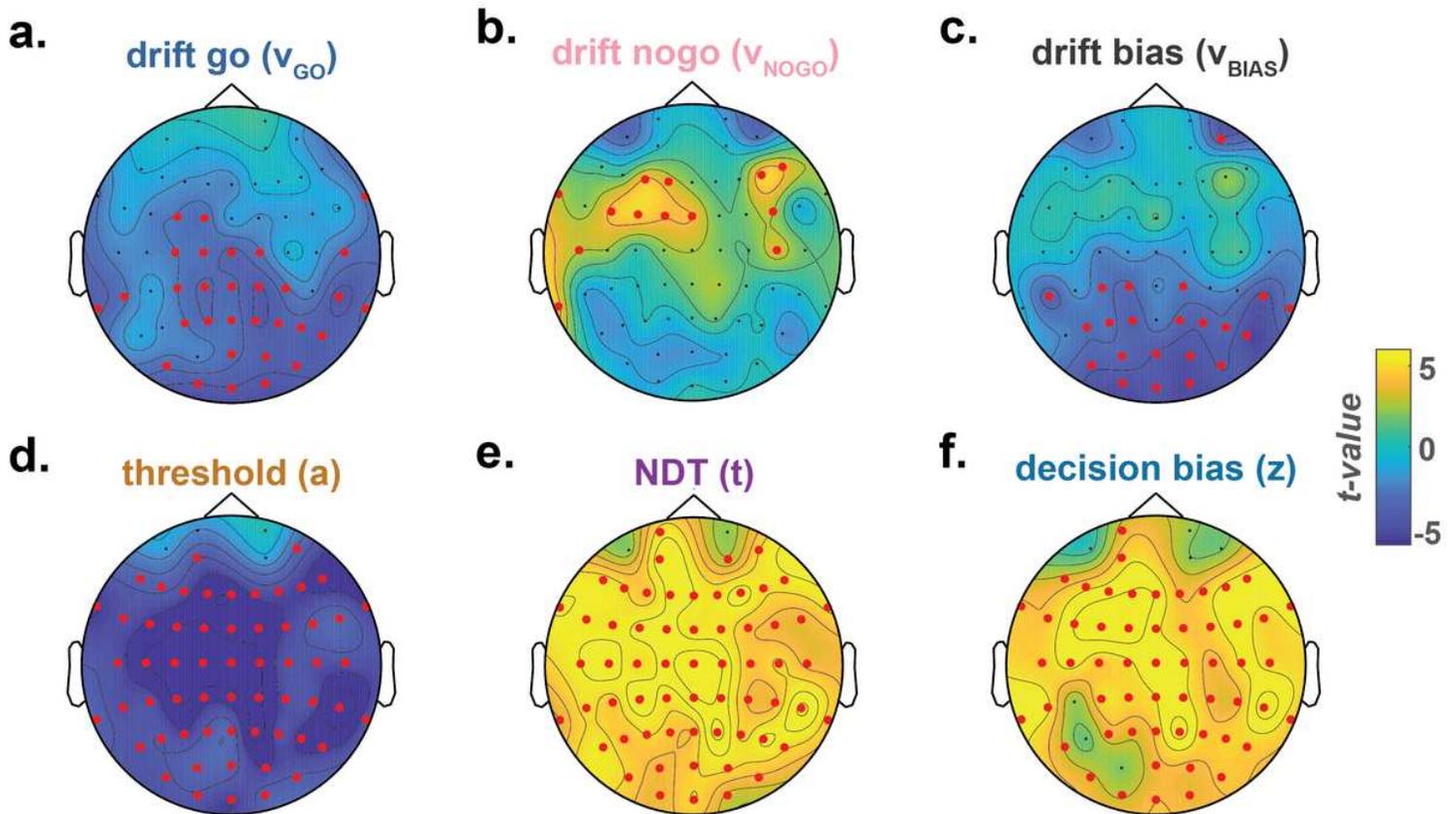


Figure 5

Global and local effects of local sleep on sub-components of decision-making Reaction Times in the Go/NoGo tasks were modelled according to a Hierarchical Drift Diffusion Model (see Online Methods). a-f: Topographical maps of the effect of local sleep (i.e. whether or not a local sleep event was detected for each trial and for a specific electrode) on the parameters of decision-making: v_{Go} (a), v_{NoGo} (b), v_{Bias} (c), a (d), t (e), z (f). The effect of local sleep was estimated with LMEs (see Online Methods) and topographies show the scalp distribution of the associated t-values. Red dots denote significant clusters of electrodes ($p_{cluster} < 0.05$, Bonferroni corrected, see Online Methods).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [AndrillonMWMBLocalSleepNatNeurSISubmission.pdf](#)