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## **Human prosocial preferences are related to slow-wave activity in sleep**

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Human prosocial preferences are related to slow-wave activity in sleep

Deep sleep and prosocial preferences

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32        **Abstract**

33        Prosocial behavior is crucial for the smooth functioning of society. Yet, individuals differ vastly in  
34        the propensity to behave prosocially. Here we try to explain these individual differences under  
35        normal sleep conditions without any experimental modulation of sleep. Using a portable high-  
36        density EEG we measured sleep data in 54 healthy adults (28 females) during a normal night's sleep  
37        at participants' homes. To capture prosocial preferences, participants played an incentivised public  
38        goods game in which they faced real monetary consequences. Whole-brain analyses showed that  
39        higher relative slow-wave activity (SWA, an indicator of sleep depth) in a cluster of electrodes over  
40        the right temporo-parietal junction (TPJ) was associated with increased prosocial preferences.  
41        Source localization and CSD analyses further support these findings. Recent sleep deprivation studies  
42        imply that sleeping enough makes us more prosocial; the present findings suggest that it is not only  
43        sleep duration, but particularly sufficient sleep depth in the TPJ that is positively related to  
44        prosociality. Because the TPJ plays a central role in social cognitive functions, we speculate that  
45        sleep depth in the TPJ, as reflected by relative SWA, might serve as a dispositional indicator of social  
46        cognition ability, which is reflected in prosocial preferences. These findings contribute to the  
47        emerging framework explaining the link between sleep and prosocial behavior by shedding light on  
48        the underlying mechanisms.

49

50

51

53 **Significance Statement**

54 Sleep deprivation reportedly hampers prosocial behavior. Yet, sleep loss is not a regular  
55 occurrence. We studied participants without experimentally manipulating their sleep and conducted  
56 polysomnography along with a prosocial economic task. We found that higher relative slow-wave  
57 activity (an indicator of sleep depth) in the right TPJ – a brain region involved in social cognition – is  
58 associated with increased prosociality. This demonstrates a novel link between deep sleep neural  
59 markers and prosocial preferences. Furthermore, our study provides evidence about a possible  
60 neural mechanism that underlies the behavioral findings of previous studies on sleep deprivation  
61 and prosocial behavior. Our findings highlight the significance of sleep quality in shaping prosociality  
62 and the potential benefits of interventions targeting sleep quality to promote social capital.

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64 **Introduction**

65 Prosocial behavior is of vital importance for holding our society together. Yet, the propensity to  
66 exhibit prosocial behavior is characterized by vast individual differences (e.g., Declerck & Boone,  
67 2018; Fischbacher et al., 2001; Thielmann et al., 2020). However, within a person, prosocial behavior  
68 has been shown to be stable over time and across different situations (Carlsson et al., 2014;  
69 Peysakhovich et al., 2014). Here, we aim at explaining individual differences in prosocial preferences  
70 using a stable neural trait, namely the topographic distribution of slow-wave activity (SWA) during  
71 sleep.

72 Recent evidence shows a striking relationship between the amount of sleep we get and social  
73 functioning (e.g., Ben Simon et al., 2020, 2022; Clark & Dickinson, 2020; Holbein et al., 2019).  
74 Specifically, sleep deprivation has been associated with reduced altruism, trustworthiness, trust and  
75 helping behavior (e.g., Anderson & Dickinson, 2010; Ben Simon et al., 2022; Dickinson & McElroy,  
76 2017).

77 There have been two prevailing attempts to explain why prosocial behavior is negatively  
78 impacted by sleep deprivation (for a review, see Dorrian et al., 2019). One possible reason may be  
79 that sleep deprivation hampers social cognition abilities (Ben Simon et al., 2020, 2022; Ben Simon &  
80 Walker, 2018; Guadagni et al., 2014, 2017). Support for this explanation is provided by Ben Simon et  
81 al. (2022) who reduced activity in key nodes of the social cognition network (TPJ, mPFC, precuneus)  
82 and a decrease in the desire to help others under conditions of sleep loss.

83 A second attempt to explain reduced prosocial behavior after sleep deprivation stems from the  
84 idea that sleep deprivation interferes with self-control abilities, deliberative thinking and executive  
85 functioning (e.g., Anderson & Dickinson, 2010; Dickinson & McElroy, 2017; Holbein et al., 2019).

86 These functions are crucial for forming prosocial behavior (e.g., Wyss & Knoch, 2022 and are

87 associated with prefrontal brain regions (Hare et al., 2009; Knoch & Fehr, 2007) which are  
88 particularly affected by sleep deprivation (Groeger et al., 2014; Harrison et al., 2000; Killgore et al.,  
89 2008; Thomas et al., 2003).

90 The studies reported above nicely demonstrate that artificially limiting sleep affects prosocial  
91 behavior. However, no study has yet examined how electrophysiological measures of sleep under  
92 normal conditions (i.e., without experimental manipulation) are linked to prosocial behavior. In the  
93 present study we hence examine how processes happening in the sleeping brain relate to the vast  
94 individual differences in prosocial preferences. To do so, we look at trait-like characteristics of the  
95 sleeping brain in individuals that habitually sleep between 7 and 8 hours every night. Specifically, we  
96 measured SWA during sleep. SWA is a major EEG hallmark of deep sleep and an objective measure  
97 of sleep depth. We then correlated the topographic distribution of SWA with individual prosocial  
98 preferences.

99 The topographic distribution of SWA shows local differences which are highly stable within but  
100 vary between individuals (Finelli et al., 2001; Lustenberger et al., 2017) and is therefore unique to  
101 each person (Markovic et al., 2018; Rusterholz & Achermann, 2011). Here, we investigated the  
102 association of the relative SWA topography with individual differences in prosocial preferences.

103 The present study is designed to scrutinize whether the topographical distribution of relative  
104 SWA under normal sleep conditions explains individual differences in prosocial preferences. To  
105 capture individual differences in prosocial preferences, we employed a Public Goods Game (PGG). To  
106 comprehensively measure prosocial preferences, it is necessary to also measure what people believe  
107 others would contribute (see methods for a detailed explanation). As this is the first study of its kind,  
108 we do not have any a-priori hypotheses. However, based on the sleep-deprivation studies  
109 mentioned above, we may tentatively expect SWA differences in areas involved in impulse control



110 and deliberate thinking, such as the PFC (Dickinson & McElroy, 2017; Holbein et al., 2019) and/or the  
111 social cognition network including the TPJ, mPFC, and precuneus (Ben Simon et al., 2022).

112

## 113 **Material and Methods**

### 114 ***Participants***

115 We calculated the sample size required to achieve 80% power to detect significant correlations ( $\alpha$   
116 = 0.005) using G\*Power 3.1.9.7 (F tests, Linear multiple regression; Faul et al., 2007). Based on our  
117 previous sleep study on neural traits and risk preferences (Studler et al., 2022) and based on  
118 previous studies on neural traits and economic preferences during wakefulness (Baumgartner et al.,  
119 2013; Gianotti et al., 2009; Knoch et al., 2010) we assumed a medium effect size  $f^2 = 0.25$ . The power  
120 analysis yielded a recommended sample size of 58 participants. Since we performed sleep EEG  
121 recordings at participants' homes without the constant supervision of an experimenter, we expected  
122 dropouts because of technical issues. We therefore recruited a total of 62 healthy right-handed  
123 participants.

124 Eight participants were excluded due to non-compliance to the study protocol ( $n = 2$ ), or missing  
125 EEG data ( $n = 6$ ), leaving 54 participants (mean age = 21.5 years old; SD age = 2.0 years; females =  
126 28) for analyses. All participants were informed of their right to discontinue participation at any time  
127 and gave written informed consent. Participants received 155 Swiss francs (CHF 155; CHF 1  $\approx$  \$ 1  
128 U.S.) compensation for participating in the morning after the night of sleep, in addition to money  
129 earned in the behavioral task, which depended on their own and others' behavior (see measurement  
130 of prosocial preferences). The earnings from the behavioral assessment were paid immediately after  
131 completing the PGG. Ethical approval for this experiment was provided by the local ethics committee  
132 and adheres to the principles of the Helsinki Declaration.

133

134 **Procedure**

135 All recruited participants were screened before the experiment to meet the following inclusion  
136 criteria: right-handedness (Chapman & Chapman, 1987), self-reported good sleepers with a habitual  
137 sleep duration of 7-8 hours per night (Pittsburgh Sleep Quality Index < 5; Buysse et al., 1989), normal  
138 sleepiness index (Epworth Sleepiness Scale < 10; Johns, 1991), no extreme chronotype (Munich  
139 Chronotype Questionnaire > 2 & < 7; Roenneberg et al., 2003), no current or past history of  
140 neurological, psychiatric, or sleep disorders, no drug nor alcohol abuse, no regular medication  
141 intake, normal weight, and no traveling across more than two time-zones within the last 30 days  
142 before the experiment. Additionally, participants were asked about their regular caffeine, alcohol,  
143 and nicotine consumption. Because women's sleep quality can be influenced by their menstrual  
144 cycle phase (e.g., Baker & Driver, 2004), we controlled for cycle phase using the forward counting  
145 method. Naturally cycling women were not invited during their estimated fertile days or during the  
146 first 2 days of their menstrual cycle. Women using hormonal contraception were not invited during  
147 pill-free intervals.

148 One week before the experiment, participants were invited to the laboratory where they  
149 received detailed instructions. We asked participants to keep a regular sleep-wake rhythm adjusted  
150 to their habitual bedtimes (sleep duration of 7-8 hours) and to refrain from daytime napping  
151 throughout the week before the experiment (Figure 1). Participants were also asked to limit their  
152 caffeine consumption to two units/day (1 unit = caffeine content of one cup of coffee) and their  
153 alcohol consumption to one standard drink/day (1 standard drink = 1 beer (350ml) = 10g ethanol).  
154 Smokers were told to adhere to their habitual nicotine consumption. Each participant received a tri-  
155 axial accelerometer (GENEActiv, activinsights Ltd., Kimbolton, Huntingdon, UK) to wear on their non-  
156 dominant hand. Actigraphy is a validated objective measure of sleep behavior (e.g., de Souza et al.,

157 2003; Marino et al., 2013), discerning sleep from being awake based on motion. Single-use straps  
158 ensured that participants did not remove the actigraph during the week of actigraphy measurement.  
159 Additionally, we also used sleep diary and consumption diary entries to confirm adherence to the  
160 study protocol. Finally, participants were given a chest harness with a sham amplifier to simulate the  
161 wearing of the portable high-density EEG system. We asked participants to sleep with the chest  
162 harness and the sham amplifier to find the optimal amplifier position for the recording night.

163 On the day of the experiment, participants were asked to refrain from extensive exercise or  
164 visiting the sauna to avoid post sweating. Participants came to the laboratory in groups of three to  
165 play the PGG (Figure 1). To ensure anonymity, participants were invited to three different floors of  
166 the building and were accompanied one after the other to the cubicles they were randomly assigned  
167 to. After this, participants were fitted with the portable high-density EEG system and were sent  
168 home, where they continued with their habitual routine. Shortly before bedtime, experimenters  
169 visited participants at home to check and, if needed, correct the impedances of the electrodes, and  
170 start the recording (Figure 1). Participants also underwent an implicit association task (IAT), but this  
171 task was irrelevant for the present study.

172

173 ----- Figure 1 -----

174

### 175 ***Measurement of prosocial preferences***

176 In each experimental session, the three participants sat in their cubicles with interconnected  
177 computer terminals where they could make their decision in complete anonymity from the other  
178 two participants. For the measurement of prosocial preferences, we used the PGG. Each participant  
179 was endowed with 20 points (1 point = CHF 0.5) and faced the decision (one-shot) to either keep

180 their endowment or contribute all or part of it to a public good (0–20 points). Each point contributed  
181 was doubled by the experimenter and the resulting sum was divided equally among the three  
182 participants. Hence, each point contributed increased the aggregate group payoff while diminishing  
183 the contributing individual's payoff. Immediately after the contribution decision, participants  
184 reported their belief about the average contribution of the other two participants (0–20 points). This  
185 was done because several studies have shown that the amount people contribute to the public good  
186 is influenced by what they believe the other participants will contribute (Fischbacher & Gächter,  
187 2010; Neugebauer et al., 2009). For example, one participant might contribute half of their  
188 endowment because they assume that the other participants would contribute a comparable  
189 amount. In contrast, a different participant might also contribute half of the endowment because  
190 they simply find this the fairest decision. In the latter case, the participant contributes according to  
191 their prosocial inclination without strategically considering the decisions of the other players while in  
192 the first case the contribution is conditional on what other players are expected to contribute. So,  
193 even though in both cases the two exemplified participants contributed the same amount, this does  
194 not reflect the same level of prosocial preferences. To accommodate differences in prosocial  
195 preferences, we hence asked our participants after their contribution decisions what they believed  
196 the other players had contributed. To get a measure that comprehensively measures prosocial  
197 preferences, we generated a difference score by subtracting the value of participants' beliefs from  
198 their own contributions (contribution-minus-belief score).

199 The participants' final payoff in the PGG consisted of the earnings they gained from the public  
200 good and the points they had kept for themselves. Participants received detailed written instructions  
201 before the task, including information about the calculation of the final payoff. Comprehension trials  
202 ensured their understanding by asking participants to calculate payoff distributions in different  
203 scenarios.

204

205 ***Sleep EEG recording***

206 High-density portable EEG (LiveAmp64, Brain Products) with 64 electrodes (actiCAP, EASYCAP),  
207 including three electrooculogram, and two submental electromyogram were continuously recorded  
208 during the nighttime sleep episode. Two additional electrodes were used as recording reference (Cz)  
209 and as ground (AFz) The electrical signals were recorded with a sampling rate of 500Hz (third order  
210 low pass filter at 131Hz). Impedances were kept below 25k $\Omega$ . For each participant, lights-off and  
211 wake-up times were determined according to his or her habitual sleep time.

212

213 ***Sleep EEG pre-processing***

214 Data were offline bandpass filtered between 0.5-40 Hz. Sleep was visually scored according to  
215 standard criteria (Berry et al., 2018). Data from seven channels required for sleep scoring only (two  
216 electromyogram, three electrooculogram, and two mastoids) were then excluded, leaving a total of  
217 59 electrodes for further analyses. The following sleep parameters were extracted from sleep stage  
218 scoring: total sleep time (i.e., the objective sleep quantity), sleep efficiency (proportion of total time  
219 in bed spent asleep), wake after sleep onset (length of periods of wakefulness occurring after sleep  
220 onset), percentage of total sleep time spent in each sleep stage (N1, N2, N3 and REM).

221 Bad channels were individually identified by visual inspection of time frequency plots and  
222 spectrograms of the whole night. On average, 5.75% of channels were deemed bad and were  
223 excluded, if problematic at any time of the night. The remaining signals were then re-referenced to  
224 the average of all good channels. Power density spectra were then calculated for 30-s epochs using  
225 Fast Fourier Transformation (5-s subepochs, Hanning window, no overlap). Artifacts were excluded

226 semi-automatically, whenever power exceeded a threshold based on a moving average over epochs  
227 for the frequency bands 0.8-4.6 and 20-40 Hz (Buckelmüller et al., 2006).

228

### 229 ***SWA distribution maps and source localization***

230 SWA in the range between 0.8-4.6 Hz in sleep stages N2 and N3 was computed for further  
231 analyses. SWA values from excluded channels were interpolated using spherical linear interpolation  
232 (Delorme & Makeig, 2004). Individual SWA distribution maps were normalized to the mean values  
233 across all electrodes, yielding relative SWA distribution maps (e.g., Finelli et al., 2001). Relative SWA  
234 was log-transformed before statistical analyses in order to approach normal distribution.

235 Source localization analysis was performed using the standardized low-resolution electromagnetic  
236 tomography method (sLORETA; Pascual-Marqui, 2002). The sLORETA algorithm has been used in  
237 many sleep EEG studies (e.g., Bersagliere et al., 2017; Castelnovo et al., 2022; Moffet et al., 2020)  
238 and has been applied to estimate the cortical localization of NREM sleep sources (e.g., Fernandez  
239 Guerrero & Achermann, 2019; Siclari et al., 2018; Stephan et al., 2021). Using the manual  
240 regularization method in the sLORETA software, we selected the transformation matrix with the  
241 signal-to-noise ratio set to 10. sLORETA images were then log-transformed before statistical  
242 analyses. Additionally, we calculated Current Source Density (CSD) maps. The CSD maps were  
243 computed from artifact-free EEG data using the Laplacian transformation. CSD maps are effectively  
244 reference-free (Kayser & Tenke, 2015). CSD power in the range between 0.8-4.6 Hz (CSD SWA) was  
245 then calculated in sleep stages N2 and N3 using Fast Fourier Transformation. Individual CSD SWA  
246 distribution maps were normalized to the mean values across all electrodes, yielding relative CSD  
247 SWA distribution maps. Relative CSD SWA was log-transformed before statistical analyses in order to  
248 approach normal distribution. An electrode-wise Pearson correlation approach was taken to identify

249 scalp regions whose relative CSD SWA during an entire night of sleep under normal condition  
250 correlate with the contribution-minus-belief score.

251

### 252 ***Statistical analyses***

253 In the main analyses, as a first step, an electrode-wise Pearson correlation approach was taken to  
254 identify scalp regions whose relative SWA during an entire night of sleep under normal condition  
255 correlate with the contribution-minus-belief score. To correct for multiple comparisons, statistical  
256 non-parametric mapping (SnPM) using a suprathreshold cluster analysis was applied (Huber et al.,  
257 2004; Nichols & Holmes, 2001). For each permutation, the maximal cluster size of neighboring  
258 electrodes reaching an  $r$  value above the critical value was counted and used to build a cluster size  
259 distribution. The 95th percentile was defined as the critical cluster size threshold. To better describe  
260 and visualize the result of this analysis, for each participant, relative SWA was then averaged in the  
261 significant cluster. As a second step, we estimated the intracerebral sources that gave rise to the  
262 significant cluster. For our voxel-by-voxel Pearson correlation analyses, we created a 15-mm sphere  
263 centered on MNI coordinates of the right temporoparietal junction (right TPJ:  $x = 54$ ,  $y = -52$ ,  $z = 32$ ,  
264 Krall et al., 2015). We corrected for multiple testing in all of 59 voxels via a non-parametric  
265 randomization approach (Nichols & Holmes, 2001).

266 As additional analyses, we repeated the electrode-wise Pearson correlation approach between  
267 SWA and the contribution-minus-belief score for individual sleep cycles. Sleep cycles were defined  
268 according to an adaptation of Feinberg and Floyd's criteria (Feinberg & Floyd, 1979; Jenni &  
269 Carskadon, 2004; Kurth et al., 2010). For the calculation of relative SWA in individual sleep cycles, we  
270 normalized SWA values to the mean values across all electrodes within each cycle.

271

272 **Results**

273 ***Behavioral results and sleep parameters***

274 As illustrated in Figure 2, we observed large inter-individual differences in prosocial preferences.

275 The contribution-minus-belief score varied from -10 to 10 ( $M = 1.56$ ,  $SD = 4.03$ ). Sleep parameters

276 were within the expected range for this age group (see Table 1).

277

278 ----- Figure 2 -----

279

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280 **Table 1.** Mean with 95% CIs for total sleep time, sleep efficiency, wake after sleep onset, and  
 281 duration of sleep stages for total sample (N = 54).

282

	Total sleep time [min]	Sleep efficiency [%]	Wake after sleep onset [min]	Duration of sleep stages (% of total sleep time)			
				N1	N2	N3	REM
Mean	431.6	93.1	21.5	7.7	46.3	24.7	21.3
95% CIs	422.6-441.0	92.2-93.9	18.2-24.9	6.7-8.7	44.8-47.9	23.2-26.3	20.2-22.3

283

284 **Brain results**

285 In the main analysis, we checked whether individual differences in the topographical distribution  
 286 of relative SWA in N2 and N3 (see Figure 3A) during an entire night of sleep explain individual  
 287 differences in prosocial preferences. We found robust and significant positive associations in a  
 288 cluster of six electrodes placed over the right TPJ (C6, CP4, CP6, FT8, P4, P6,  $p < 0.05$ , corrected for  
 289 multiple testing, see Figure 3B). The correlation between mean relative SWA in the significant cluster  
 290 and prosocial preferences resulted in a correlation coefficient of 0.49 ( $df = 52$ ),  $p = 0.00019$ ,  $R^2 = 0.24$   
 291 (see Figure 3C). Crucially, partialling out participants' total sleep time or time spent in deep sleep  
 292 (i.e. sleep stages N2 and N3) did not affect the relation between relative SWA over the right TPJ and  
 293 prosocial behavior ( $r(51) = 0.49$ ,  $p = 0.00019$ ,  $R^2 = 0.24$ ;  $r(51) = 0.50$ ,  $p = 0.00016$ ,  $R^2 = 0.25$ ). Thus,  
 294 the positive correlation between relative SWA over the right TPJ and prosocial preferences was  
 295 independent of the quantity of sleep. Moreover, partialling out participants' age and gender also did  
 296 not affect the relationship between relative SWA over the right TPJ and prosocial preferences ( $r(50)$   
 297  $= 0.49$ ,  $p < 0.00001$ ,  $R^2 = 0.24$ ).

298

299 ----- Figure 3 -----

300

301 Since scalp-based correlation maps provide only a rough estimate of regional characteristics, we  
302 used sLORETA to estimate the regional specificity of the previous findings. We found 3 voxels in the  
303 right TPJ showing significant positive correlations between SWA current density and prosocial  
304 preferences ( $p < 0.05$ , small volume corrected for multiple testing, MNI coordinates of peak voxel:  $x$   
305  $= 55$ ,  $y = -55$ ,  $z = 45$ , inferior parietal lobule, BA 40; see Figure 3D and for the CSD results, see Figure  
306 4).

307

308 ----- Figure 4 -----

309

310 SWA levels typically decline across a night of sleep (Achermann et al., 1993). As the rate of the  
311 decline varies at different cortical areas, averaging SWA over an entire night of sleep might lead to a  
312 loss of information. Therefore, we performed additional analyses where we correlated relative SWA  
313 over the right TPJ cluster with prosocial preferences separately for all sleep cycles. Not all  
314 participants had a fifth sleep cycle, hence we present analyses from four cycles. Results, presented in  
315 Figure 5 demonstrated a highly similar pattern for each of the four cycles compared to the whole  
316 night (see Figure 3B).

317

318 ----- Figure 5 -----

319

320 To ensure that the main result was not driven by SWA in the first sleep cycle, when SWA levels  
321 are typically highest, we excluded this cycle in a further analysis and correlated relative SWA of the  
322 second, third and fourth sleep cycles pooled together with prosocial preferences. The result once  
323 again shows a significant positive correlation between relative SWA over the TPJ and prosocial  
324 preferences ( $r(52) = 0.48$ ,  $p = 0.00021$ ,  $R^2 = 0.23$ ).

325

### 326 *Additional Analysis*

327 Our study aimed to investigate how human prosocial preferences are related to slow-wave activity  
328 during sleep. As mentioned in the methods section, ample evidence demonstrates that individuals  
329 adjust their contributions based on their beliefs about other's contributions (e.g., Fischbacher &  
330 Gächter, 2010; Neugebauer et al., 2009). Therefore, in the main analyses, we focused on the  
331 contribution-minus-belief score, because this measure more accurately reflects prosocial  
332 preferences rather than contribution or belief alone (see methods section for a detailed  
333 explanation). However, for the sake of completeness, we present additional results separately for  
334 the contribution and the belief scores (see Figure 6).

335

336 ----- Figure 6 -----

337

### 338 **Discussion**

339

340 Recent research emphasizes the importance of sleep for prosocial behavior (e.g., Ben Simon et  
341 al., 2020, 2022; Clark & Dickinson, 2020; Holbein et al., 2019). While this research demonstrates that  
342 adverse sleep conditions have negative consequences on people's social behaviors, these studies

343 offer no conclusions on the underlying mechanisms of how sleep impacts prosocial behavior and  
344 how individual differences in prosocial inclinations come about. We attempted to better understand  
345 the connection between sleep and prosociality by directly looking at the sleeping brain. Rather than  
346 experimentally preventing people from sleeping and then looking at their prosocial behavior, we  
347 used a portable high-density EEG system to record SWA in self-reported good sleepers during a  
348 normal night's sleep. Our results demonstrate an intriguing association between a trait-like sleep  
349 characteristic, relative SWA, in the TPJ and prosocial preferences.

350 Different attempts have been made to explain why prosocial behavior is negatively impacted by  
351 sleep deprivation. One suggested possibility for why sleep deprivation may lead to reduced prosocial  
352 behavior is that sleep deprivation hampers self-control, deliberative thinking and executive  
353 functioning (e.g., Anderson & Dickinson, 2010; Dickinson & McElroy, 2017; Holbein et al., 2019). A  
354 second explanation assumes the involvement of the social cognition network (Ben Simon et al.,  
355 2020, 2022; Ben Simon & Walker, 2018). For example, it has been found that the desire to socially  
356 interact with others decreases upon sleep loss while the desire to be alone increases (Axelsson et al.,  
357 2020; Ben Simon & Walker, 2018). Other studies have found that sleep loss negatively impacts  
358 empathy. For example, Guadagni et al. (2014) demonstrated that one night of total sleep deprivation  
359 leads to reduced emotional empathy. Of special interest in the context of the present study is the  
360 finding of Ben Simon et al. (2022), who used functional MRI analyses to examine the underlying  
361 neural changes in order to explain the association between inadequate sleep and reduced  
362 prosociality. They found that, relative to the rested condition, sleep loss was associated with a  
363 significant reduction in task-evoked activity within the social cognition network, namely in the TPJ,  
364 the mPFC, mid and superior temporal sulcus, and the precuneus. So, these authors could nicely  
365 demonstrate that the social cognition network functions differently *after* adverse sleep conditions.  
366 In the present study, we go a step further by looking at activity in the sleeping brain during habitual

367 sleep. We found that more relative SWA in the TPJ is associated with increased prosocial  
368 preferences. Our finding hence offers further support for the idea that sleep influences the social  
369 cognition network (cf., Ben Simon et al., 2020, 2022; Ben Simon & Walker, 2018).

370 A large body of evidence looking at the waking brain has consistently linked task-dependent  
371 activation of the TPJ with aspects of social cognition such as mentalizing, perspective-taking or  
372 “theory-of-mind” (ToM), self-other distinction, and empathy (e.g., Decety & Lamm, 2007; Carter &  
373 Huettel, 2013; Saxe, 2006). These aspects of social cognition include understanding and monitoring  
374 the mental states of others such as their intentions, beliefs, desires, emotions and actions and are  
375 crucial for prosocial behavior (Frith & Frith, 2007). Various studies have linked activation in the TPJ  
376 with generous choices (Hutcherson et al., 2015; Park et al., 2017; Strombach et al., 2015) and  
377 donation behavior (e.g., Hare et al., 2010; Van Hoorn et al., 2016). Support for the causal  
378 involvement of the TPJ in prosocial behavior and perspective-taking stems from neuro-modulation  
379 studies (e.g., Hao et al., 2021; Langenbach et al., 2022; Li et al., 2020). Li et al. (2022) for example  
380 demonstrated that increasing the cortical excitability using anodal tDCS over the TPJ increased  
381 participants’ charitable giving.

382 Previous research using a neural trait approach during wakefulness also report a link between  
383 individual differences in prosociality and the TPJ (Baumgartner et al., 2019; Gianotti et al., 2018,  
384 2019; Morishima et al., 2012). For example, a resting-state EEG study found that task-independent  
385 baseline activation in the TPJ is related to interindividual variation in prosocial behavior (Gianotti et  
386 al., 2019). Similarly, gray matter volume in the TPJ was positively associated with altruistic choices in  
387 a structural MRI study (Morishima et al., 2012). Interestingly, recent studies showed that increased  
388 SW density is linked to higher cortical thickness (e.g., Dubé et al., 2015).

389 In the present study, we found a positive correlation between relative SWA in the TPJ and  
390 prosocial preferences. SWA is an ideal candidate for capturing individual differences in prosocial

391 preferences. We have several reasons to believe that the SWA measured in our study indeed reflects  
392 trait-like differences. During the seven days before the experiment, sleep and consumption diaries  
393 as well as actigraphy were used to confirm adherence to the study protocol (i.e., regular sleep-wake  
394 rhythm, sleep duration of 7-8 hours, no daytime napping). This procedure was introduced to  
395 minimize possible state effects. In addition, we divided SWA power at every single electrode by the  
396 average SWA over all electrodes, resulting in individual topographical distributions indicating relative  
397 SWA. Absolute SWA levels (i.e. without normalization) are subject to day-to-day variations and to a  
398 decline across the sleep period (state-dependent) and therefore reflect the prevailing sleep-wake  
399 history. On the contrary, topographical maps of relative SWA have been shown to be very stable and  
400 thus trait-like (Finelli et al., 2001; Rusterholz & Achermann, 2011). Consequently, the fingerprint-like  
401 SWA topography has been suggested to reflect neural differences across individuals (Finelli et al.,  
402 2001). Also, we ran separate analyses for the individual sleep cycles and in every sleep cycle relative  
403 SWA over the right TPJ correlated significantly with prosocial preferences. So, the relationship  
404 between relative SWA and prosocial preferences was not only present in the first sleep cycle, when  
405 the need for sleep and absolute SWA levels are highest, but was similar in all sleep cycles. If the  
406 relationship was mainly driven by the sleep need of the brain region, we would have expected a  
407 critical role of SWA mainly during the first sleep cycle, which is influenced the most by sleep pressure  
408 that accumulated during previous wakefulness, and thus by state effects (Borbély 1982; Dijk et al.,  
409 1987). Finally, prosocial preferences were measured on the day before the sleep EEG measurements  
410 took place. This ensured that - should the EEG recording lead to deteriorated sleep efficiency - this  
411 would not influence the behavior in the PGG. As it turned out, the objective sleep efficiency (as  
412 measured by actigraphy) in the nights before the EEG measurement was not significantly different  
413 from the sleep efficiency in the EEG night (92.1% vs 93.2%). While we have no absolute proof that  
414 relative SWA represents a trait-like characteristic, the above-mentioned efforts aimed at minimizing

415 state effects. Ultimately, further studies measuring prosociality and sleep physiology longitudinally  
416 will be necessary to support our conclusions.

417 SWA is seen as a physiological marker of sleep depth. We found a correlation between relative  
418 SWA values in the TPJ and individual differences in prosocial preferences, suggesting that local sleep  
419 depth specifically in the TPJ may have a crucial impact on prosocial behavior, irrespective of the  
420 absolute level of sleep pressure. CSD maps and sLORETA images gave further support for the  
421 regional specificity of the association between relative SWA and prosocial preferences in the TPJ.  
422 Because SWA is believed to reflect a restorative function (Borbély et al., 2016; Tononi & Cirelli,  
423 2006), we speculate that higher SWA in the right TPJ is indicative of an individual's propensity for  
424 prosocial behavior because of local restorative processes. More SWA in the right TPJ might lead to a  
425 better restoration of TPJ functions, resulting in a higher capacity of mentalizing and/or perspective-  
426 taking, which in turn might lead people to be more prosocially inclined.

427 Social decision-making is known to be influenced by chronotype or by (sub)optimal time-of-day  
428 (e.g., Francis et al., 2021; Gunia et al., 2014). Evening chronotypes for example have been shown to  
429 be less likely to act prosocially, regardless of whether they have been tested during their matched  
430 time (in the evening) or in the morning (Francis et al., 2021). To avoid a confounding factor of  
431 chronotype and circadian (mis)timing of our decision-making task, we excluded extreme  
432 chronotypes from the present study.

433 To conclude, we demonstrate that not only sleep duration (as shown by Ben Simon et al., 2020;  
434 Ben Simon et al., 2022; Clark & Dickinson, 2020; Holbein et al., 2019), but also sleep depth has an  
435 impact on prosocial decisions. Importantly, it depends on where in the brain this happens. Our study  
436 offers a first step towards a neural explanation for how sleep patterns explain prosociality by  
437 highlighting the crucial role of sleep depth in the right TPJ in prosocial decisions. Our approach  
438 therefore improves our understanding of neurobiological mechanisms underlying prosocial

439 preferences and may have implications for future approaches to improve poor perspective-taking  
440 and low prosociality. Recent evidence shows that brain stimulation techniques, such as transcranial  
441 magnetic stimulation, transcranial direct current stimulation, and auditory closed-loop stimulation  
442 enable the modulation of SWA (e.g., Bellesi et al., 2014; Lustenberger et al., 2022; Ngo et al., 2013;  
443 Sousouri et al., 2021). Thus, these techniques might be promising tools for boosting SWA in specific  
444 areas to potentially remedy dysfunctions and impairments of perspective-taking capacities and  
445 other-regarding behavior through targeted interventions.

446

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449

#### 450 **Data and code availability**

451 Relevant data and code are available:

452 <https://github.com/lorenarrgianotti/ProsocialityAndSWA> upon publication.

453



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718

719 **Figure Legends**

720

721 Figure 1. Study design. One week before the experiment, participants were instructed to maintain a  
722 regular sleep-wake rhythm. They were given an actigraph to objectively monitor their sleep-wake  
723 rhythm. During this week, participants completed sleep and consumption diaries to ensure  
724 adherence to the study protocol. On the experiment day, participants came to the laboratory in  
725 groups of three to play the Public Goods Game (PGG). Afterward, they were fitted with a high-  
726 density portable EEG system and sent home where the sleep EEG was recorded during the following  
727 night.

728

729 Figure 2. Histogram depicting the distribution of the contribution-minus-belief score among all  
730 participants.

731

732 Figure 3. Topographical distribution of relative SWA (0.8–4.6 Hz) and its correlation with prosocial  
733 preferences. (A) Topographical distribution of relative SWA (average over all participants). SWA  
734 values at every electrode were normalized in relation to average SWA over all electrodes of a  
735 participant. Dark blue to dark red colors indicate minimal (45%) to maximal (173%) SWA. (B)  
736 Statistical scalp distribution of r-coefficients between relative SWA and prosocial preferences. Blue  
737 areas indicate negative correlations, red areas indicate positive correlations. White dots indicate  
738 electrodes with significant correlations ( $p < 0.05$ , corrected for multiple testing with a  
739 suprathreshold cluster analysis). Black dots indicate the position of the 59 electrodes. (C) Scatterplot  
740 of the positive correlation between mean relative SWA in the significant cluster over the right TPJ  
741 and prosocial preferences (including regression line and confidence interval 95%). (D) Relationship  
742 between SWA current density in the right TPJ and prosocial preferences. Locations of the voxels that

743 showed significant correlations are indicated in red ( $p < 0.05$ , corrected) and yellow ( $p < 0.10$ ,  
744 corrected).

745

746 Figure 4. Topographical distribution of relative CSD SWA (0.8-4.6 Hz) and its correlation with  
747 prosocial preferences. (A) Topographical distribution of relative CSD SWA (averaged over all  
748 participants). Dark blue to dark red colors indicate minimal (58%) to maximal (195%) CSD SWA. (B)  
749 Statistical scalp distribution of r-coefficients between log-transformed relative CSD SWA and  
750 prosocial preferences. Blue areas indicate negative correlations, red areas indicate positive  
751 correlations. White dots indicate electrodes with significant correlations ( $p < 0.05$ ). Black dots  
752 indicate the position of the 59 electrodes.

753

754 Figure 5. Relationship between relative SWA and prosocial preferences for sleep cycle 1 (A), sleep  
755 cycle 2 (B), sleep cycle 3 (C), and sleep cycle 4 (D). Left panels show statistical topographical  
756 distributions of correlation coefficients between relative SWA and prosocial preferences. Blue areas  
757 indicate negative correlations, red areas indicate positive correlations. White dots indicate  
758 electrodes with significant correlations ( $p < 0.05$ ) in the cluster of six electrodes identified in the  
759 main analysis (see Figure 3B). Right panels show scatterplots of the positive correlations between  
760 mean relative SWA in the significant cluster over the right TPJ and prosocial preferences (including  
761 regression line and confidence intervals 95%).

762

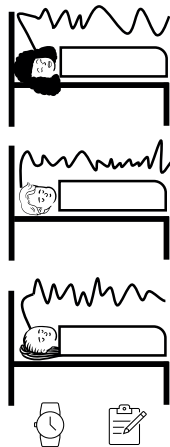
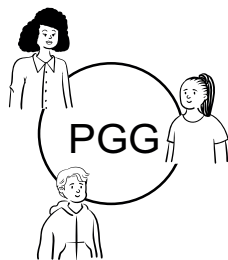
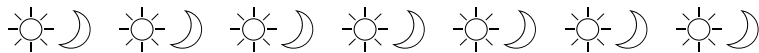
763 Figure 6. Contribution decisions, beliefs and correlations with relative SWA. (A) Contribution  
764 decisions and participants' beliefs about the average contribution of the other participants.  
765 Contribution decision (left) and the belief about others contribution (right) are depicted for each

766 participant. Contribution decisions and corresponding beliefs per participants are joined by a line. (B)  
767 Topographical distribution of r-coefficients between relative SWA and contribution decisions and (C)  
768 participants' beliefs. Blue areas indicate negative correlations, red areas indicate positive  
769 correlations. White dots indicate electrodes with uncorrected significant correlations ( $p < 0.05$ ).  
770 Black dots indicate the position of the 59 electrodes.

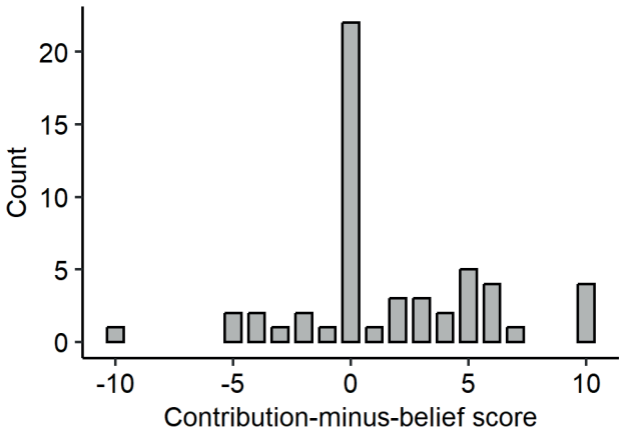
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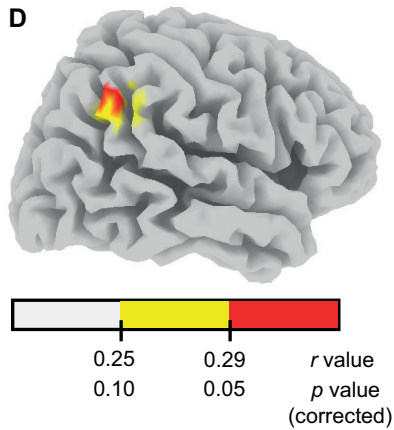
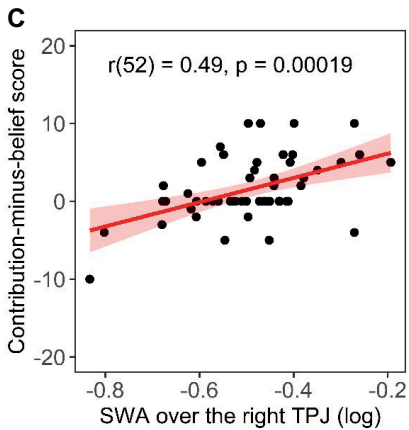
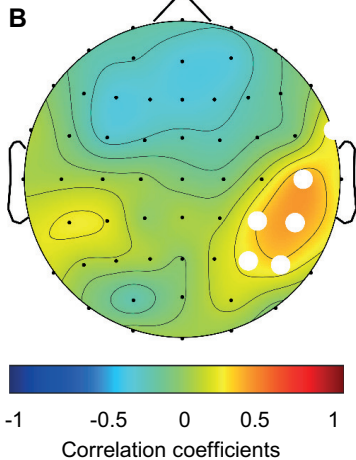
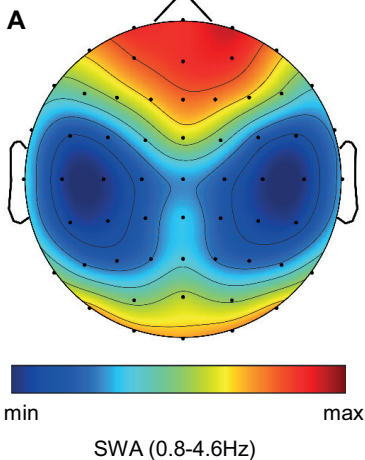
## Week before the experiment

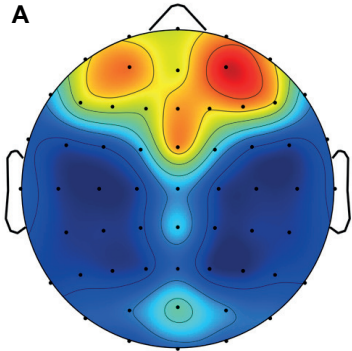
## Day of experiment







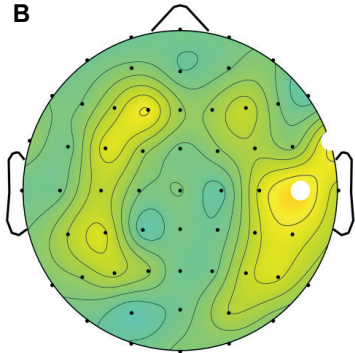


**A**

min

max

CSD SWA (0.8-4.6Hz)

**B**

-1

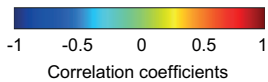
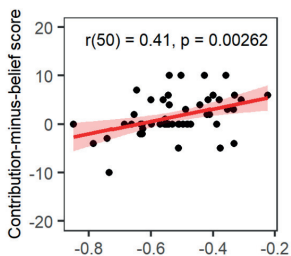
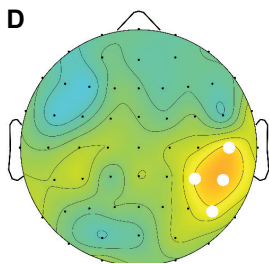
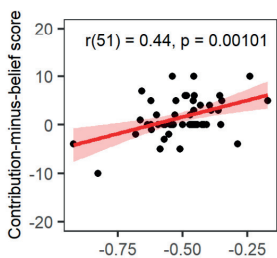
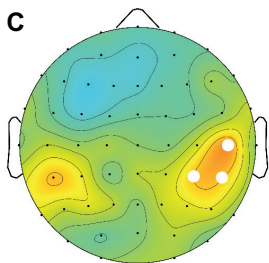
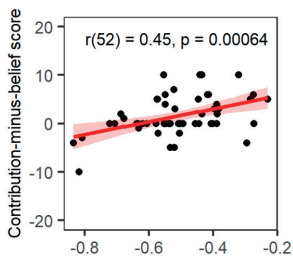
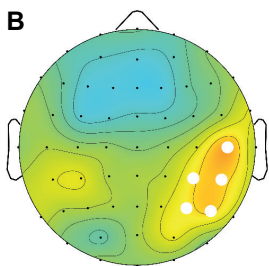
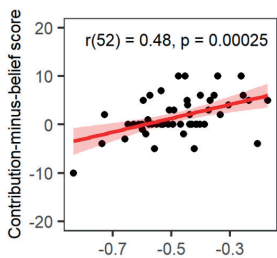
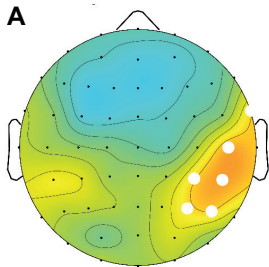
-0.5

0

0.5

1

Coefficients of the correlations between  
CSD SWA and prosocial preferences



SWA over the right TPJ (log)

