

# 1 On the complexity of resting state 2 spiking activity in monkey motor 3 cortex

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11 **Abstract** Resting state has been established as a classical paradigm of brain activity studies,  
12 mostly based on large scale measurements such as fMRI or M/EEG. This term typically refers to a  
13 behavioral state characterized by the absence of any task or stimuli. The corresponding neuronal  
14 activity is often called idle or ongoing. Numerous modeling studies on spiking neural networks  
15 claim to mimic such idle states, but compare their results to task- or stimulus-driven experiments,  
16 which might lead to misleading conclusions. To provide a proper basis for comparing physiological  
17 and simulated network dynamics, we characterize simultaneously recorded single neurons' spiking  
18 activity in monkey motor cortex and show the differences from spontaneous and task-induced  
19 movement conditions. The resting state shows a higher dimensionality, reduced firing rates and  
20 less balance between population level excitation and inhibition than behavior-related states.  
21 Additionally, our results stress the importance of distinguishing between rest with eyes open and  
22 closed.

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## 24 Introduction

25 The resting state in behavioral studies is defined operationally as an experimental condition without  
26 imposed stimuli or other behaviorally salient events (*Raichle, 2009; Snyder and Raichle, 2012*). It has  
27 become a classical paradigm for experiments involving large scale measurements of brain activity  
28 like fMRI and M/EEG (*Vincent et al., 2007; Raichle, 2009; Deco et al., 2011; Snyder and Raichle,*  
29 *2012; Baker et al., 2014*). A major conclusion of these studies is that spontaneous brain activity in  
30 human and monkey can be characterized as a sequence of re-occurring spatio-temporal patterns of  
31 activation or deactivation resembling task-evoked activity, but present during rest (*Vincent et al.,*  
32 *2007; Fox and Raichle, 2007; van den Heuvel and Hulshoff Pol, 2010*) Defined on the *whole-brain*  
33 *level*, they are shaped by anatomical connectivity and derived from functional connectivity (*Honey*  
34 *et al., 2009; Bastos and Schoffelen, 2016*).

35 While the exact link between the fMRI signal and neuronal activity is a matter of ongoing research  
36 (*Logothetis and Wandell, 2004; Ekstrom, 2010*), resting state studies have also been carried out on  
37 the *level of single brain areas*. Here, the spontaneous activity is often referred to as ongoing, intrinsic,  
38 baseline, or resting state activity, and can be studied by means of, for example, optical imaging  
39 combined with single electrode recordings (*Arieli et al., 1996; Tsodyks et al., 1999; Kenet et al.,*  
40 *2003*). Such data, collected under anesthesia, were used to investigate the variability in evoked

41 cortical responses (*Arieli et al., 1996*), the switching of cortical states (*Tsodyks et al., 1999*), and the  
42 link of these cortical states to the underlying functional architecture (*Kenet et al., 2003*). In our  
43 study, we aim to characterize the resting state on yet another spatio-temporal scale, namely on the  
44 scale of simultaneous single unit (SU) spiking activity recorded in macaque monkey (pre-)motor cortex.

45 Spiking activity in monkey motor cortex has been studied extensively during arm movements,  
46 which gives rise to an increased average neuronal firing compared to wait (*Nawrot et al., 2008*;  
47 *Rickert et al., 2009*; *Riehle et al., 2018*). On a single unit level, direction-specific neuronal sub-  
48 populations encode the movement direction by firing rate modulations (*Georgopoulos et al., 1986*;  
49 *Rickert et al., 2009*). These and other studies also investigated the spike time irregularity and the  
50 spike count variability in monkey motor cortex during various behavioral epochs: Movements have  
51 been related to a lower spike count variability across trials (*Rickert et al., 2009*; *Churchland et al.,*  
52 *2010*; *Riehle et al., 2018*) and to a higher spike time irregularity (*Davies et al., 2006*; *Riehle et al.,*  
53 *2018*) compared to wait or preparatory behavior without movements. However, the resting state  
54 we analyze in this study is conceptually distinct from waiting or preparatory epochs: there is no  
55 task to prepare for and no signal to be anticipated. It is a state without any particular expectations  
56 or dispositions.

57 Studies on spiking neural network models aim to mimic brain dynamics down to the level of  
58 individual neuron activities. Bottom-up modeling approaches thereby derive the structure and  
59 parameters of network models from anatomy and electrophysiology, trying to reproduce and  
60 understand experimentally observed activity features of increasing complexity. For simplicity and  
61 due to missing knowledge of inputs to local circuits, such studies often focus on the idle state  
62 and intrinsically generated dynamics of networks (*van Vreeswijk and Sompolinsky, 1996, 1998*;  
63 *Brunel, 2000*; *Kumar et al., 2008*; *Voges and Perrinet, 2010*; *Potjans and Diesmann, 2014*; *Dahmen*  
64 *et al., 2019*). This approach provides the prerequisite to study network dynamics and function  
65 in the presence of external stimuli and finally its relation to behavior. There are computational  
66 frameworks that can be used for a quantitative comparison or, ultimately, validation of such spiking  
67 neural network models against experiments (*Gutzen et al., 2018*), but data on single unit activity  
68 in resting-state condition is still lacking. As a consequence, network models are often compared  
69 to data collected in behavioral experiments, where tasks or stimuli lead to transient deviations  
70 from the resting-state statistics such as e.g. the average firing rates (*Georgopoulos et al., 1986*;  
71 *Riehle et al., 1997*; *Kaufman et al., 2013*; *Riehle et al., 2018*). Recently developed biophysical  
72 forward modeling schemes (*Einevoll et al., 2013*) in combination with large-scale network models  
73 (*Potjans and Diesmann, 2014*; *Schmidt et al., 2018a,b*; *Markram et al., 2015*) in principle provide a  
74 possible way to employ existing resting-state fMRI and M/EEG data to benchmark spiking network  
75 models. However, the complexity of the dynamics on the level of individual neurons is lost in these  
76 mesoscopic and macroscopic measures of activity. Therefore, to provide a suitable reference for  
77 the validation of spiking neural network models on the single neuron (microscopic) level, we here  
78 present an analysis of massively parallel spiking activity in macaque monkeys at rest.

79 The aim of this study is a detailed characterization of the spiking activity at rest compared to  
80 task-induced and spontaneous movements. To this end, we recorded the ongoing activity with a  
81 4x4 mm<sup>2</sup> 100 electrode Utah Array (Blackrock Microsystems, Salt Lake City, UT, USA) situated in the  
82 hand-movement area of macaque (pre-)motor cortex. We performed two types of experiments:

- 83 1. During resting state experiments (REST), we recorded the neuronal activity of two monkeys  
84 seated in a chair with no task or stimulation. The spontaneous behavior was then classified  
85 into periods of (sleepy) rest and movements.
- 86 2. Reach-to-grasp experiments (R2G) (*Riehle et al., 2013*; *Torre et al., 2016*; *Brochier et al., 2018*;  
87 *Riehle et al., 2018*) provide well-defined periods of task-related movements and task-imposed  
88 waiting. The latter behavior is similar to rest but contains a mental preparation task.

89 We ask if a distinction between spontaneous (resting and non-resting) and task-evoked (reach-to-  
90 grasp) neuronal dynamics is expressed on the level of single unit (SU) and network spiking activity.

91 More specifically, we also ask if certain features of the neuronal firing during pure resting periods  
92 allow for a differentiation from spontaneous and task-induced movements, preparatory periods,  
93 or sleepiness. Contrary to this expectation, the motor system may show invariants, i.e., statistical  
94 properties of the neuronal spiking that do not change with respect to different behavioral epochs.  
95 While such comparisons have been performed on the level of local field potential (LFP) recordings,  
96 e.g., the investigation of behavior-related frequency modulations (*Engel and Fries, 2010; Kilavik*  
97 *et al., 2013*), to our knowledge this is the first study to perform such comparison on the level of  
98 spiking activity.

99 In the following, we first detail how we performed the segmentation of REST recordings according  
100 to behavior, and then explored the activity of single neurons in different behavioral states. To  
101 investigate if there are comparable neuronal activity states in task-related data, we performed  
102 similar analyses for the R2G data. Apart from the SU dynamics, we also focused on network  
103 properties of the neuronal activities: We evaluated pairwise covariances, dimensionality of rate  
104 activities, and excitatory-inhibitory balance in the different behavioral states of both REST and R2G.  
105 The comparison to the R2G data enabled us to identify systematic network state changes which are  
106 less pronounced in REST.

## 107 Results

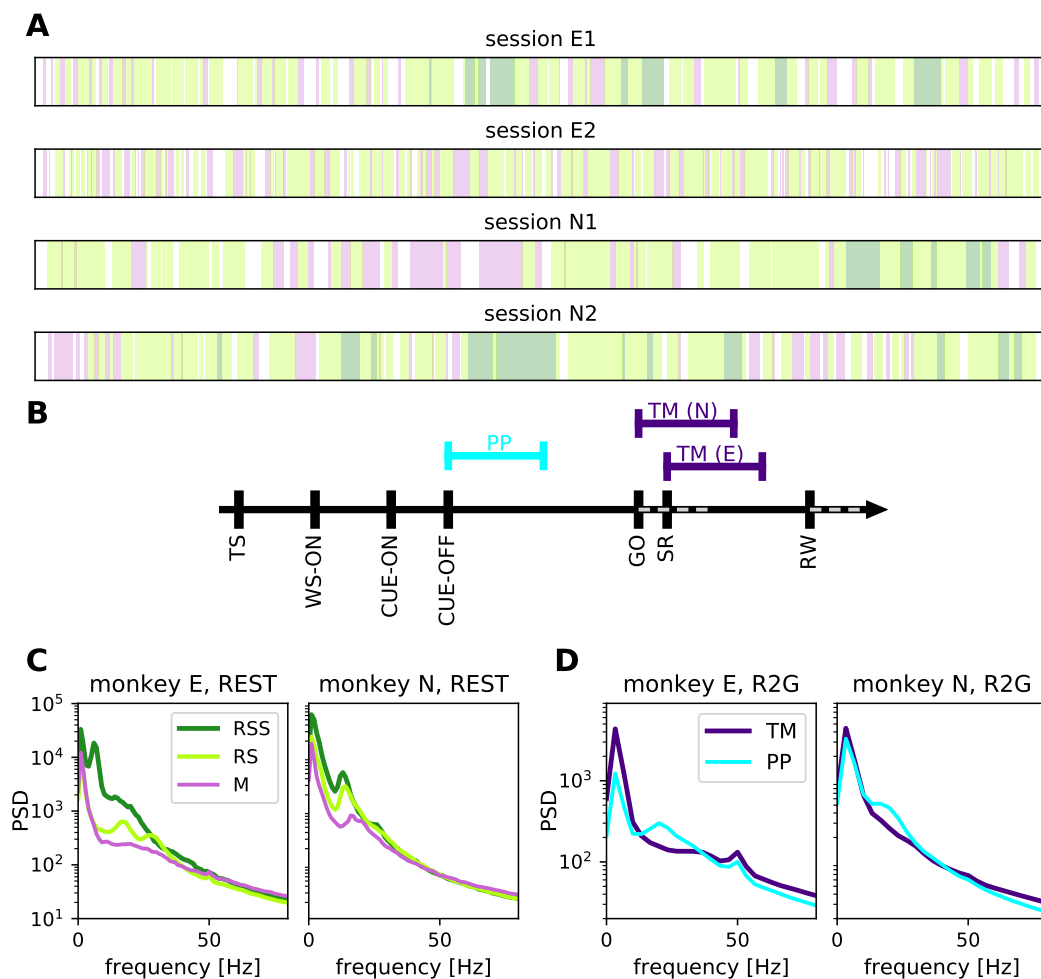
108 We aim to determine in what regards spiking activity during rest is distinct from other behavioral  
109 states like spontaneous movements, sleepiness, movement preparation, or task-induced grasping.  
110 To do so, we first describe the behavioral segmentation of the REST data based on videos of the  
111 monkeys during the experiment, resulting in a sequence of defined behavioral states in REST. The  
112 segmentation of R2G was chosen as in previous studies on these data (*Riehle et al., 2018*). Then,  
113 we show that the behavioral segmentation is meaningful in terms of neuronal activity on two  
114 different scales: On the mesoscopic scale, which incorporates the collective behavior of neurons,  
115 we show that the LFP spectra differ across states. On the microscopic scale, we show that SU firing  
116 is correlated to the monkeys' behavior, and examine the relation between behavior, spiking activity  
117 dimensionality and excitatory-inhibitory balance.

### 118 Behavioral segmentation

119 Based on video recordings, each REST session (two per monkey) was segmented according to  
120 the monkey's behavior, (cf. Materials and Methods: Behavioral Segmentation). Three states were  
121 considered: resting state (RS)—no movements and eyes open; sleepy resting state (RSS)—no  
122 movements and eyes (half-)closed; spontaneous movements (M)—movements of the whole body  
123 and/or limbs (Fig. 1A). For R2G recordings, two behavioral states were defined with respect to trial  
124 events. For these states, interval lengths of 500 ms were used: the first part of the preparatory  
125 period (PP)—500 ms after the first cue, when the monkey waits immobile for the GO; and a task-  
126 related movement period (TM)—an interval containing movement onset and grasping (Fig. 1B).

127 The visual segmentation is substantiated by comparison of the LFP spectra in the above defined  
128 states (Fig. 1C). The relationship between LFP and behavior has been shown in several studies, e.g.  
129 *Pfurtscheller and Aranibar (1979); Fontanini and Katz (2008); Engel and Fries (2010); Takahashi*  
130 *et al. (2011); Kilavik et al. (2013)*. Beta oscillations ( $\approx 13$  to 30 Hz) have been linked to states of  
131 general arousal, movement preparation, or postural maintenance (*Baker et al., 1999; Kilavik et al.,*  
132 *2012*) and are typically suppressed during active movement (*Pfurtscheller and Aranibar, 1979*).

133 In our data, RS and PP show peaks in the range from  $\approx 10$  to  $\approx 30$  Hz (alpha/beta range), the  
134 peak in PP occurs for a higher frequency than in RS. In both monkeys, M and TM contain more  
135 power compared to other states in frequencies above  $\approx 50$  Hz (gamma), while beta power is reduced.  
136 However, the spectrum during RSS differs between monkeys. In monkey E, RSS seems to be a  
137 distinct physiological state: it shows strong slow oscillations, as to be expected (*Gervasoni et al.,*  
138 *2004; Fontanini and Katz, 2008*) for a sleepy version of RS. In monkey N, however, the spectra  
139 during RSS are more similar to RS, but still with more power in the lower frequency bands.



**Figure 1.** Behavioral segmentation in REST and R2G recordings. **(A)** Order and relative duration of the behavioral states defined within each REST session (single second precision): resting state (RS, light green) represents no movements and eyes open, sleepy rest (RSS, dark green) represents no movements and eyes (half-)closed, spontaneous movements (M, pink) represent movements of the whole body and limbs. **(B)** Order and timing of events within a single trial of an R2G session. Colored lines above the time axis indicate time intervals considered for the analysis: preparatory period (PP, cyan) and task-induced movements (TM, purple). SR indicates the switch-release event—beginning of the hand movement. PP was defined as [CUE-OFF, CUE-OFF+500 ms], and TM as [SR, SR+500 ms] for monkey E, and [SR-150 ms, SR+350 ms] for monkey N (different for the two monkeys due to differences in performance speed). **(C and D)** Power spectral density of LFP in different behavioral states. Panels in C pertain to REST, panels in D to R2G, left for monkey E and right for monkey N, respectively. States are defined in A and B. The peak at 50 Hz in the R2G spectra is an artifact (line frequency) and was not considered.

**Table 1.** List of all considered experimental recordings. Session names (first column) starting with "e" refer to monkey E, and with "i" to monkey N. Throughout the manuscript the REST sessions are referred to as E1, E2, N1 and N2. Each R2G trial yields one PP and one TM period, equally long (0.5 s each).

REST session	#slices: 3 s (0.5 s)			#SUs (#bs, #ns)
	RSS	RS	M	
e170103-002 (E1)	40 (232)	196 (1058)	43 (200)	115 (56, 50)
e170131-002 (E2)	0	189 (970)	67 (308)	133 (67, 56)
i140701-004 (N1)	20 (114)	151 (840)	58 (312)	130 (76, 45)
i140615-002 (N2)	45 (258)	156 (836)	36 (180)	154 (78, 62)
R2G session	#trials		#SUs (#bs, #ns)	
e161212-002	108		131 ( 50, 56)	
e161215-001	102		92 ( 41, 37)	
e161220-001	114		98 ( 45, 33)	
e161222-002	102		118 ( 57, 41)	
e170105-002	101		115 ( 60, 45)	
e170106-001	100		116 ( 57, 43)	
i140613-001	93		138 ( 71, 56)	
i140616-001	130		154 ( 75, 61)	
i140617-001	129		154 ( 83, 59)	
i140703-001	142		142 ( 84, 46)	
i140704-001	141		124 ( 70, 43)	

140 Table 1 lists all single recording sessions for both REST and R2G experiments. It provides  
 141 information about the number of SUs (separated into putative excitatory / broad spiking (bs) and  
 142 putative inhibitory / narrow spiking (ns)) and the number of data slices (3 or 0.5 s long in REST) or  
 143 trials (R2G), in the different behavioral states. Thus in total we have 2 sessions of 15-20 min from  
 144 each monkey during REST, and 6/5 sessions (of similar durations) of monkey E/N during R2G. This  
 145 results in 627 R2G trials of monkey E and 635 trials of monkey N. These were compared to the  
 146 following numbers of data segments of 0.5 s during REST: 232, 2028 and 508 segments of RSS, RS  
 147 and M, respectively, for monkey E and 372, 1676 and 492 segments for monkey N. For details on  
 148 cutting the data see Materials and Methods: Behavioral Segmentation.

### 149 Relation between neuronal firing and behavior

150 A prerequisite for the following analyses is to formalize a relationship between neuronal spiking  
 151 activity and the behavioral states of a monkey. Therefore, we quantified the correlation between  
 152 SU firing and behavior. This is by no means to be taken as a decoding approach, but rather as a  
 153 substantiation for the approach taken above to differentiate between behavioral states in REST.

154 Figure 2A shows the time-resolved firing rates (FR) of all recorded SUs in one REST session  
 155 (N1) (Sec. Materials and Methods: Behavioral correlation). They change in time and are variable  
 156 across SUs, which is true for all REST sessions. The firing rates range from 0 up to  $\approx 100$  spikes per  
 157 second. Some SUs exhibit a consistent firing (not visible by eye), e.g., unit 4 in Fig. 2A with a small  
 158 absolute standard deviation,  $FR = 1.23 \pm 1.16$ , and similarly unit 127 (relative standard deviation  
 159  $FR = 25.29 \pm 6.46$ ). The firing of other SUs changes considerably over time, e.g., unit 126 with a  
 160 large absolute standard deviation  $FR = 20.08 \pm 12.15$ , and similarly unit 17 with a relative standard  
 161 deviation  $FR = 1.74 \pm 3.53$ .

162 To examine this variability with respect to the behavior of the monkey, we defined a behavioral  
 163 state vector (cf. bottom panel of Fig. 2A). Its entries represent the behavioral states: the value is set  
 164 to +1 if there are movements (M) and -1 if the monkey is at rest (RS), and for the following analysis

165 all other states are not taken into account. The bottom row of Fig. 2B shows the values of the  
166 behavioral correlation (BC, see Sec. Materials and Methods: Behavioral correlation) between the  
167 state vector and the firing rate (in 1 s bins) of each of the SUs, ordered from minimum to maximum.  
168 The panel above shows the FR of the corresponding SUs in identical order, averaged over the  
169 whole recording period (bars), only over RS periods (green markers) and only over M periods (pink  
170 markers). Most SUs increase their firing rate during M (mostly on the right side of the panel), many  
171 of them significantly ( $BC > 0.17$ ,  $p < 0.001$ ). A much smaller set of SUs increases the firing rate during  
172 RS ( $BC < -0.17$ ), seen mostly on the left side of the panel. This asymmetry between the two states  
173 is reflected by the positive average BC in all 4 REST sessions (Tab. 2 col. 3). The second column  
174 of Tab. 2 lists the percentage of SUs with significant BC, for all sessions (see Sec. Materials and  
175 Methods: Behavioral correlation for the derivation of the BC significance). They range from 40.8  
176 to 66.9%, however, neither the sign nor the amount of the behavioral correlation can be reliably  
177 predicted from the average FR: Both SUs with very high or very low mean FR show negative, positive  
178 and close to zero BC values. This is also indicated by the insignificant correlation between FR and  
179 BC (Tab. 2 col. 4):  $\rho_{BC,FR}$ . Yet, the consistently negative  $\rho_{BC,FR}$  values suggest that SUs with smaller  
180 firing rates tend to be more sensitive to behaviour than highly active ones (the lower the mean FR,  
181 the higher the mean BC).

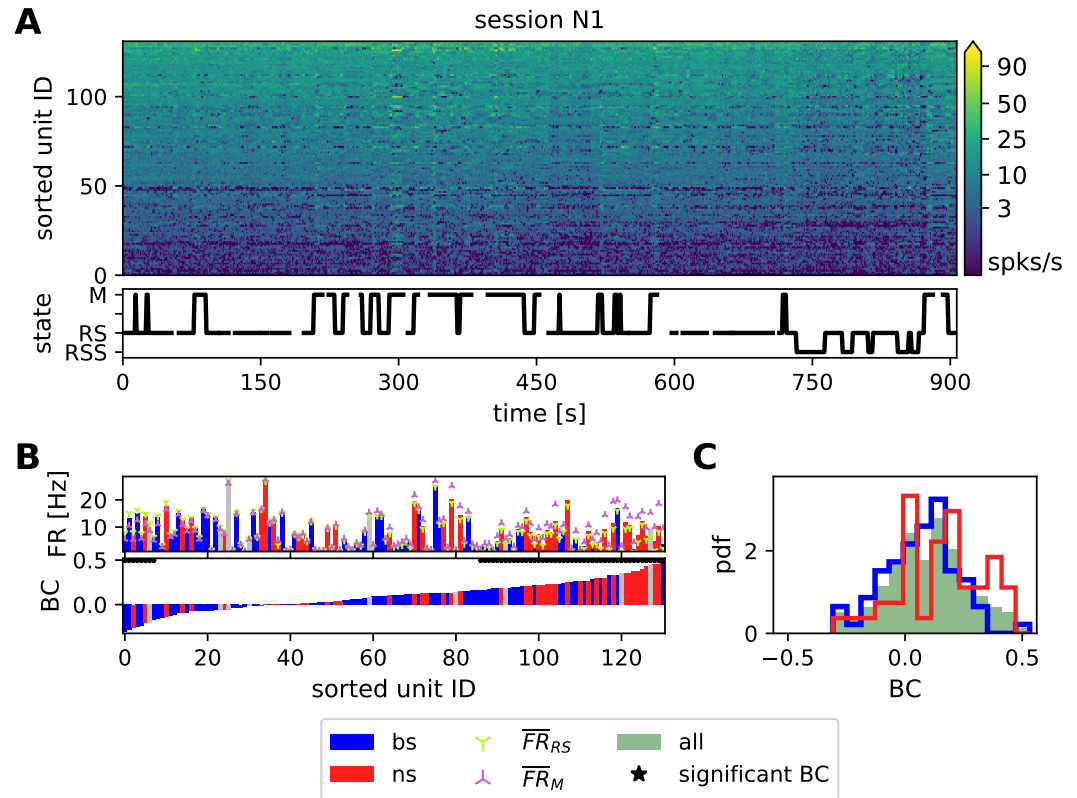
182 In order to include the RSS state (in addition to M & RS) in the correlation of neuronal activity and  
183 behavioral states, we performed a Kruskal-Wallis test (KW) per SU, which provides information about  
184 the significance, but no quantification of the strength of the correlation. The obtained percentage  
185 of significantly correlated SUs ( $p < 0.001$ ) ranges from 55% to 77% in monkey E and from 44% to  
186 48% in monkey N (last column of Tab. 2). Thus, we find a clear inter-relation of the behavioral state  
187 and the neuronal activity.

188 Since firing rates seem to be not indicative of the behavioral state, we further differentiated the  
189 data into putative excitatory and inhibitory neurons (Sec. Materials and Methods: Pre-processing).  
190 Fig. 2C shows the distribution of BC values obtained in session N1 for all SUs (green shaded area),  
191 and for SU separated into putative excitatory / broad spiking SUs (bs) and putative inhibitory /  
192 narrow spiking (ns) SUs (blue and red lines, respectively). In this session we find a significant  
193 difference between the ns and the bs BC distribution. However, this could not be substantiated in  
194 the data from other recording sessions, indicating that the neuron type does not determine the  
195 strength of correlation with behavior. Still, firing of putative inhibitory as compared to excitatory  
196 neurons seems to be more related to behavioral states. This is indicated by higher percentages of  
197 significantly correlated ns than bs SUs (cf. Tab. 2 col. 2&5), particularly in monkey N, see also the  
198 higher mean BC of ns in monkey N (cf. Tab. 2 col. 3).

199 In order to include also the RSS state (in addition to M & RS) in the correlation of neuronal  
200 activity and behavioral states, we performed a Kruskal-Wallis test (KW) per SU, which provides  
201 information about the significance, but no quantification of the strength of the correlation. The  
202 obtained percentage of significantly correlated SUs ( $p < 0.001$ ) ranges from 55% to 77% in monkey E  
203 and from 44% to 48% in monkey N (last column of Tab. 2). Thus, we find a clear inter-relation of the  
204 behavioral state and the neuronal activity of the observed population.

205 To examine in more detail behavior-related modulations of average FR, we performed a set of  
206 pairwise comparisons between behavioral states per SU (using 3 s slices, see Sec. Materials and  
207 Methods: Behavioral correlation). Table 3 summarizes the results by listing the percentages of SUs  
208 that significantly change their FR with respect to behavior. We observe that  $\approx 34$  to 67% of the SUs  
209 show significantly higher FR during M as compared to RS, but still, 5 to 11% of SUs show significantly  
210 higher FR during RS (second and fifth column in Tab.3). Correspondingly, the percentages for RSS  
211 versus M show a similar tendency ( $\approx 25$  to 48% and 2 to 8%, respectively, col. 3&6). This confirms  
212 the results obtained so far, i.e., that there are mostly lower firing rates during rest (RS and RSS) than  
213 during movement (M).

214 The properties of M in relation to RS are consistent in the two monkeys, but the RSS state  
215 differs between them. Only 3 to 4% of SUs show significantly lower firing in RS than in RSS in



**Figure 2.** The correlation between SU firing and behavior for one REST session of monkey N. **(A)** Time- and population-resolved firing (spikes/s). SUs are sorted according to average firing rates in increasing order from bottom to top. The state vector describing the monkey's behavior is shown below. The time resolution is 1 s. Empty spaces denote periods of unclassified behavior, vertical lines indicate transitions between identified states. **(B)** Comparison of average firing rates and behavioral correlation (only M and RS are taken into account). The SUs in both diagrams are sorted according to increasing values of BC. Red bars indicate broad-spiking (bs, putative excitatory) and blue narrow-spiking (ns, putative inhibitory) SUs, grey indicates unclassified units. Green and pink triangles on top of the FR bars indicate the average firing rate of the corresponding SU during RS and M, respectively. Black stars above the BC bars indicate significant correlations. **(C)** Distributions of BC values. In this recording session the difference between the ns (red) and the bs (blue) distribution is significant.

**Table 2.** Behavioral correlation for all REST sessions. The second column gives the percentage of SUs that show a significant behavioral correlation (BC,  $p < 0.001$ ), the third column gives BC averages, and the fourth column the Spearman rank correlation between average SU firing rate and BC ( $\rho_{BC,FR}$ ). Column five lists the percentages of SUs that change their firing significantly ( $p < 0.001$ ) with the behavioral state, obtained with a Kruskal-Wallis test on M, RS, and RSS. The numbers in brackets indicate the values obtained when separating between bs (first entry) and ns (second entry) SUs. 1 s resolution.

Session	% SUs <sub>BC</sub> (bs, ns)	mean BC (bs, ns)	$\rho_{BC,FR}$	% SUs <sub>KW</sub> (bs, ns)
E1	53.9 (50, 60)	0.13 (0.14, 0.13)	-0.19, $p=0.03$	54.7 (51.7, 58)
E2	66.9 (64.2, 71.4)	0.14 (0.14, 0.15)	-0.09, $p=0.3$	76.9 (79.1, 76.8)
N1	40.8 (32.9, 53.3)	0.10 (0.07, 0.15)	-0.13, $p=0.2$	48.1 (39, 62.2)
N2	46.8 (39.7, 54.8)	0.12 (0.09, 0.14)	-0.04, $p=0.7$	43.5 (39.7, 50)

**Table 3.** Pairwise comparisons of SU firing rates in different states. Percentage of SUs that exhibit significantly lower (first three columns) or higher (last three columns) firing rates in the first of the two states indicated in the column header (RS vs M, RSS vs M, and RS vs RSS) for all REST sessions (in 3 s slices).

Session	RS < M	RSS < M	RS < RSS	RS > M	RSS > M	RS > RSS
E1	37.6	24.8	18.8	7.7	7.7	3.8
E2	67			11		
N1	33.6	30.5	3.8	6.1	1.5	19.8
N2	42.9	48.1	2.6	4.5	1.9	30.5

216 monkey N, but in monkey E the percentage is  $\approx 20\%$  (Tab. 3 col. 4). Vice versa, only 3.8% of SUs show  
217 significantly higher firing in RS than in RSS in monkey E, while it is  $\approx 20$  to 30% in monkey N (last  
218 column). Moreover, the percentages of SUs showing lower firing during RS and RSS as compared  
219 to M (second and third column in Tab.3) are rather similar in monkey N. However, in monkey E  
220 only 25% of SUs show higher firing during M than during RSS while 38% of the SUs show a higher  
221 firing during M as compared to RS. Thus, in agreement with our observations of the LFP spectra  
222 (cf. Sec. Results: Behavioral segmentation), rest and sleepy rest in monkey E express rather different  
223 features while they are quite similar for monkey N.

224 Above we show that the firing of approximately half of the SUs is significantly correlated to the  
225 behavior and that RS is, on average, associated with lower FRs than movements. However, the  
226 absolute value of the FR alone is not predictive of the response of a SU to different behavioral states.  
227 In the following section, we aim to investigate other aspects than mere SU spiking in different  
228 behavioral states.

### 229 Further single unit firing properties and their relation to behavior

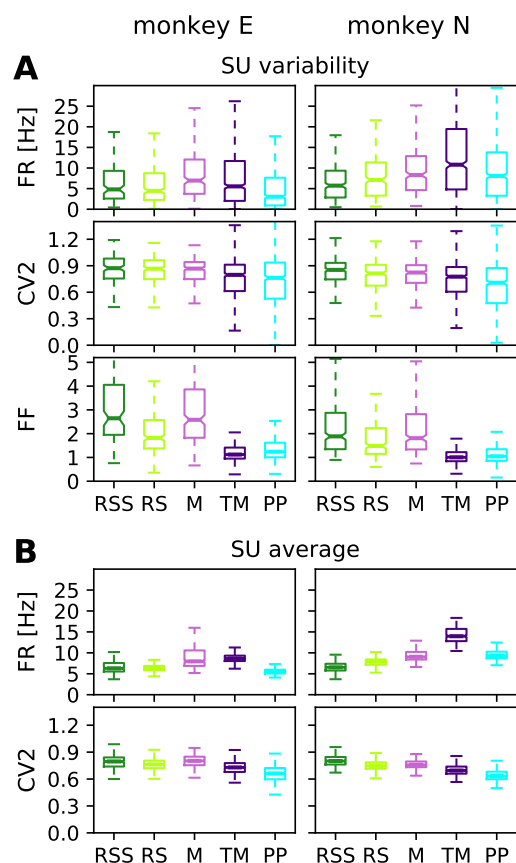
230 Given the relation between behavior and SU firing rate modulations, we now ask if other features  
231 of SU activity can be directly linked to particular behavioral states. From now on, we include R2G  
232 data to additionally look for differences on the level of spontaneous versus task-related behaviors.  
233 The box plots in Fig. 3 and the values listed in Tab. 5 describe averaged firing rates (FR), local  
234 coefficients of variation (CV2) and the Fano factor (FF), calculated for 0.5 s time slices of all REST  
235 and R2G sessions, per SU and time slice (see Sec. Materials and Methods: Data analysis). The CV2  
236 characterizes the (ir-)regularity of neuronal firing across time. A value closer to zero ( $CV2 \lesssim 0.5$ )  
237 indicates regular spiking, Poissonian firing is characterized by  $CV2=1$  (*Shinomoto et al., 2003; Voges  
238 and Perrinet, 2010*), and values higher than one indicate more irregular spiking. The FF describes  
239 the variability of SU spike counts across trials (R2G) or time slices (REST) (*Nawrot et al., 2008;  
240 Nawrot, 2010; Riehle et al., 2018*). It equals one for a Poisson process and decreases for more  
241 reliable spiking.

242 Averaged across time slices (Fig. 3A), FR shows the highest median in movement states (M & TM),  
243 while it is lower in RS(S) and PP (the differences being mostly significant, see below). Inferred from  
244 CV2, the firing is less regular in REST as compared to R2G states, and slightly less regular during TM  
245 than during PP, both showing a larger spread of values than the REST states. These differences are  
246 minor compared to the differences in the spike count variability: R2G states exhibit a much smaller  
247 and less variable FF, i.e., a higher reliability. M and RSS show the highest spread of FF, i.e. highest  
248 SU variability. The RS state exhibits a medium mean and spread of FF values.

249 Kruskal-Wallis tests on all 5 behavioral conditions yield highly significant differences between  
250 states for each measure ( $p \ll 0.0001$ ) for both monkeys. The results of all pairwise comparisons  
251 are listed in Tab. 4. For both monkeys, most differences are significant, though CV2 differentiates  
252 primarily between REST and R2G recordings, thus between spontaneous and task-related behaviors.

253 Averaging across SUs (Fig. 3B), we examine the variability in time. Note that even though  
254 the number of RS time slices highly exceeds that of SUs (cf. Tab. 1), the observed spread of the





**Figure 3.** Comparison of firing properties in REST & R2G states calculated for 0.5 s data slices. **(A)** Box plots showing the variability across SUs: firing rate, spiking regularity, and spike count variability characterized by FR, CV2, and FF, here averaged over time slices. **(B)** Box plots showing the variability over time: distributions of time-resolved FR and CV2 averaged over SUs. Data pooled over REST sessions, two for each monkey (states RSS, RS, and M), and over R2G sessions, six of monkey E and five of monkey N (states TM and PP).

FR	RSS	RS	M	TM	PP
RSS		-	-	-	*
RS	-		*	-	*
M	*	-		-	*
TM	*	*	*		*
PP	*	-	-	*	

CV2	RSS	RS	M	TM	PP
RSS		-	-	*	*
RS	-		-	*	*
M	-	-		*	*
TM	*	-	-		-
PP	*	*	*	*	

FF	RSS	RS	M	TM	PP
RSS		*	-	*	*
RS	*		*	*	*
M	-	*		*	*
TM	*	*	*		*
PP	*	*	*	-	

**Table 4.** Significance of pairwise comparisons of firing rate (FR), local coefficient of variance (CV2) and Fano factor (FF) results shown in Fig. 3A. Upper triangle of each table: monkey E; lower: monkey N. Stars indicate significant differences (\*:  $p < 0.001$ ) and minuses insignificant differences after Bonferroni correction with  $\alpha = 0.001$ . Grey background highlights significant results.

**Table 5.** Quantification of average firing rate (FR, top row), regularity in spiking (CV2, middle row), and spike count variability (FF, bottom row). Given are mean values (averaged across time slices and SUs) and corresponding standard deviations with respect to SUs. All values are obtained from 0.5 s slices, for different behavioral states in REST (RSS, RS, M) and R2G (TM, PP), pooled across all recordings of the respective type.

Monkey	RSS	RS	M	TM	PP
Firing rate FR [Hz]					
E	6.60 ± 5.34	6.43 ± 5.74	8.79 ± 6.57	8.74 ± 9.69	5.65 ± 6.92
N	6.64 ± 4.66	7.81 ± 5.51	9.44 ± 6.32	14.34 ± 12.90	9.58 ± 7.74
Local coefficient of variation CV2					
E	0.86 ± 0.16	0.83 ± 0.17	0.83 ± 0.15	0.78 ± 0.31	0.76 ± 0.36
N	0.83 ± 0.15	0.79 ± 0.15	0.80 ± 0.16	0.74 ± 0.24	0.69 ± 0.29
Fano factor FF					
E	3.14 ± 1.53	2.06 ± 0.88	3.05 ± 1.72	1.32 ± 0.82	1.41 ± 0.64
N	2.31 ± 1.30	1.86 ± 1.07	2.29 ± 1.42	1.12 ± 0.64	1.21 ± 0.78

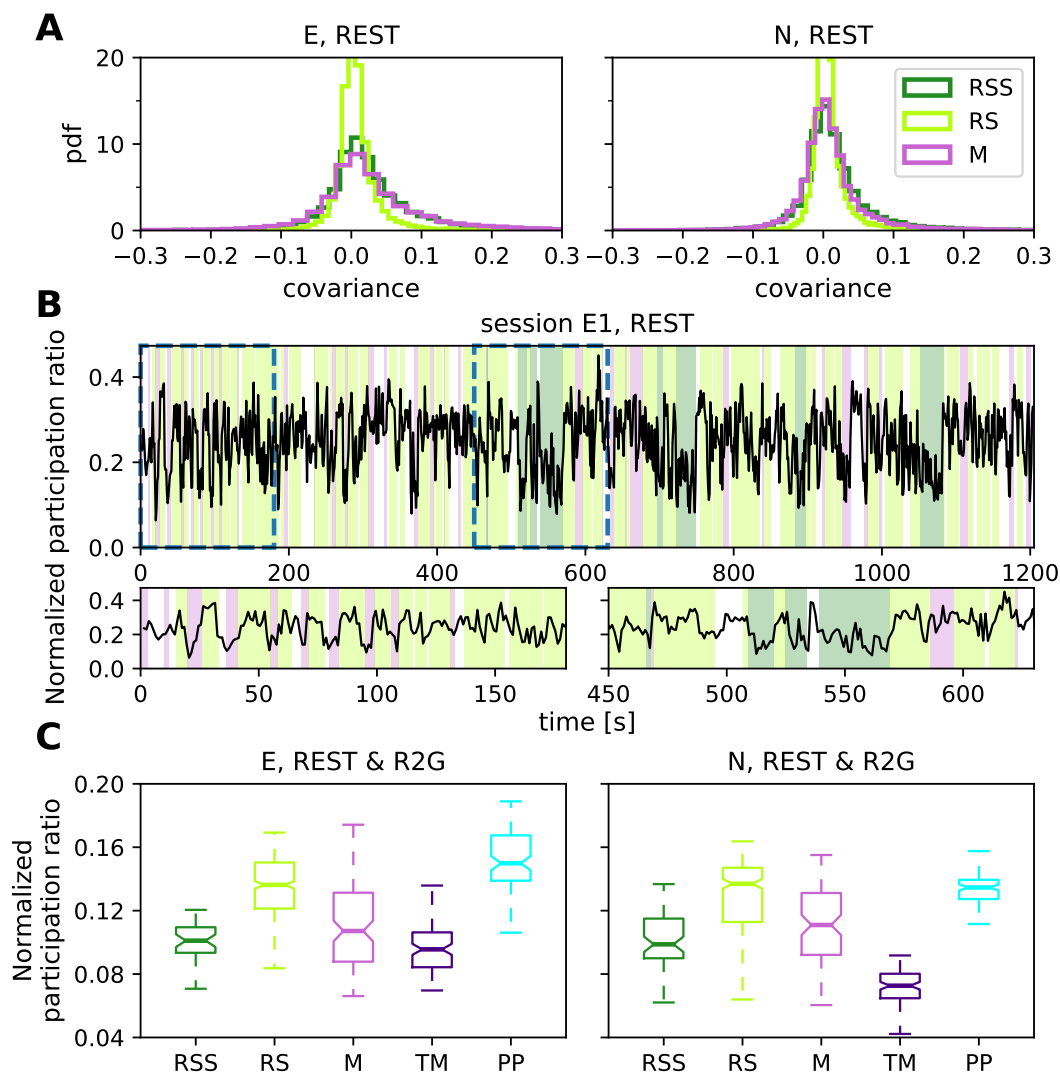
255 corresponding values is much smaller. This holds for all behavioral states. Since the variability  
 256 across time slices (panel B) is much smaller than the variability across SUs (panel A), we later on  
 257 averaged over time and considered only the variability with respect to SUs.

258 In summary, we find high SU variability in most of the measures for most of the states and the  
 259 observed differences between states are mostly significant. Resting periods are characterized by  
 260 rather low firing rates as compared to movements in agreement with the results in Sec. Results: Re-  
 261 lation between neuronal firing and behavior. The RS in particular shows a higher reliability (lower  
 262 FF) than M and RSS, but all REST states show a clearly higher FF as compared to R2G states.

### 263 Network firing properties

264 We now turn towards the analysis of coordinated firing as opposed to single unit dynamics. Co-  
 265 ordination between neurons can be measured at various time scales and quantified with various  
 266 methods. We here consider spike-count covariances calculated for 3 s slices with a bin size of  
 267 100 ms, see Sec. Materials and Methods: Covariances and dimensionality. To this end, we first  
 268 show the covariance (COV) distributions, averaged over slices of the REST data (Fig. 4A). While  
 269 the average value during all REST behaviors is close to zero, the spread of the COV distributions  
 270 differs between states, leading to highly significant differences ( $p \ll 0.0001$ ). In monkey E, the  
 271 standard deviation of the covariances is considerably lower during RS ( $\overline{\text{COV}}_{\text{RS}} = 0.007 \pm \mathbf{0.033}$ ) than  
 272 during RSS ( $\overline{\text{COV}}_{\text{RSS}} = 0.014 \pm \mathbf{0.069}$ ) and M ( $\overline{\text{COV}}_{\text{M}} = 0.033 \pm \mathbf{0.11}$ ). The same is true for monkey N:  
 273  $\overline{\text{COV}}_{\text{RS}} = 0.008 \pm \mathbf{0.028}$  compared to  $\overline{\text{COV}}_{\text{RSS}} = 0.017 \pm \mathbf{0.062}$  and  $\overline{\text{COV}}_{\text{M}} = 0.012 \pm \mathbf{0.062}$ . Statistical  
 274 comparison of the shape of the distributions with two-sample Kolmogorov-Smirnov tests reveals  
 275 significant differences for all pairs in both monkeys. In summary, we find that neuronal firing is less  
 276 correlated during rest as compared to movements and we again observe distinct RSS properties in  
 277 the two monkeys.

278 The differences in the COV distributions motivate a more detailed investigation of the coord-  
 279 ination of all recorded neurons. Apart from mean and variance of the covariance distribution,  
 280 another summarizing measure for the covariance structure has been established and discussed  
 281 in the recent years: the participation ratio (PR) (Abbott et al., 2011; Mazzucato and La Camera,  
 282 2016; Gao et al., 2017). The PR depends on all covariances in the network as it is derived from the  
 283 eigenvalues of the covariance matrix using a principle component analysis. One can show that  
 284 it depends on a combination of first and second order moments of auto- and cross-covariances  
 285 (Mazzucato and La Camera, 2016). The physical interpretation of the PR is the dimensionality of  
 286 the manifold spanned by the neuronal activity (see Sec. Materials and Methods: Covariances and



**Figure 4.** Network firing properties. **(A)** Distributions of pairwise covariances (COV) for the REST recordings of monkey E (left) and monkey N (right), calculated in 3 s slices with 100 ms bins, averaged over slices per SU pair and pooled over sessions. **(B)** Time-resolved participation ratio in session E1, calculated in 3 s long sliding windows with an overlap of 2 s. Each value on the plot corresponds to the center of the respective window. Colors in the background indicate behavioral states (cf. legend in the right panel of A). Two bottom panels show close-up view at periods marked by dashed lines in the top panel. **(C)** Dimensionality: Box plots show the normalized participation ratio of REST (RSS, RS, M) and R2G (TM, PP) states for monkey E (left) and monkey N (right), each single value of the distributions corresponds to a single 3 s data slice. Pooled over sessions.

287 dimensionality). The higher the PR, the more eigenvectors (principle components) are needed to  
288 capture most of the variance of the dynamics. We performed an analysis for the REST and also for  
289 the R2G states (0.5 s slices were concatenated to 3 s slices). To make the PR of different experiments  
290 and recordings comparable, we normalized to the total number of SU obtained in each session.

291 Figure 4B shows that the dimensionality varies over time (shown for monkey E during REST  
292 experiment). It changes with relation to behavior consistently across monkeys (as shown in Fig. 4C).  
293 This is true for all sessions (see also Tab. 6). The PR is highest during RS and PP and lowest during  
294 TM. The RSS state in both monkeys is clearly distinct from RS, its PR being more similar to the one  
295 obtained for M, as seen in the covariance distributions. The spread of the values is notably higher  
296 in REST than in R2G states, especially in monkey N.

297 Kruskal-Wallis tests on all behavioral conditions yield highly significant differences ( $p \ll 0.0001$ )  
298 for both monkeys. Pairwise comparisons yield mostly significant results except for RS vs PP, RSS vs  
299 M & TM and M vs TM in monkey E, as well as RS vs PP and RSS vs M in monkey N. These results hold  
300 for different bin sizes (shown in Sec. Materials and Methods: Covariances and dimensionality).

301 The higher dimensionality of RS as compared to movement states and sleepy rest is a clear  
302 evidence for the complexity of this state. Moreover, the large difference between the PR of RS  
303 and RSS emphasizes the necessity to distinguish between rest with eyes open and closed. In the  
304 following, we will support this claim by analyzing the balance between putative excitatory and  
305 inhibitory population activity.

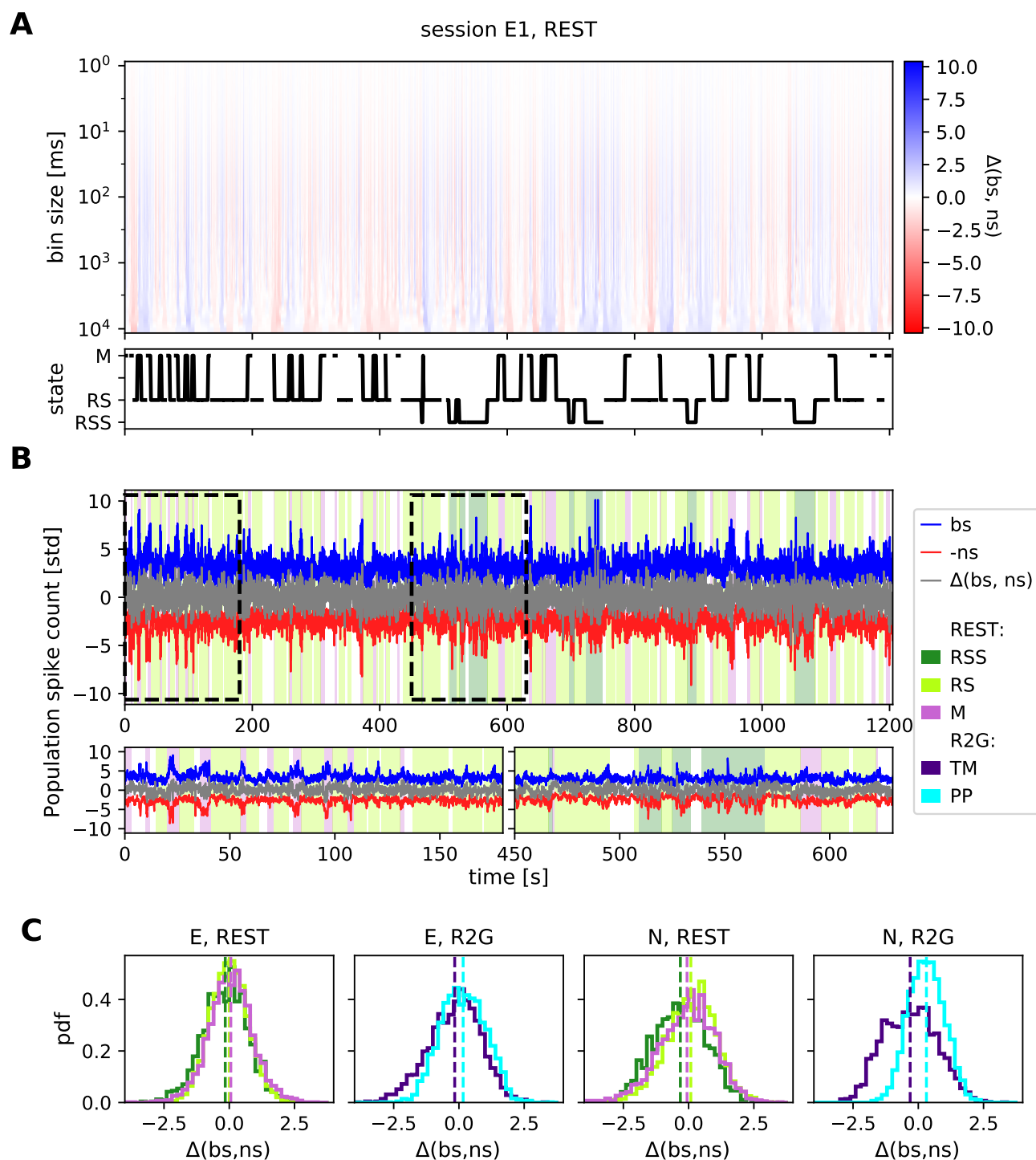
### 306 **Balance in population activity**

307 Population activities are the most straight forward and well studied low-dimensional projections  
308 of neuronal spiking data. Based on summed SU activities, they provide a global view on the  
309 network activity, disregarding single neuron-specific fluctuations. Due to the population-averaging,  
310 fluctuations on the population level are only determined by the average single-neuron covariances  
311 (*Kriener et al., 2008*) and are insensitive to the large variability across single neurons (Fig. 4A).  
312 The latter, in contrast, affects the participation ratio (*Mazzucato and La Camera, 2016*). Studying  
313 population-level coordination is therefore complementary to the analysis of dimensionality.

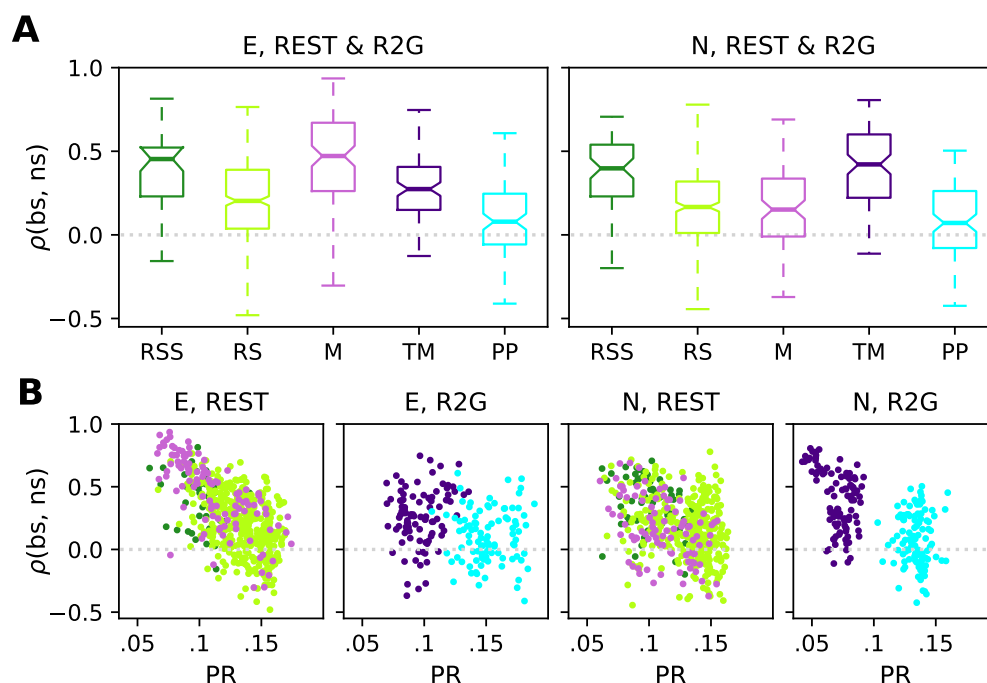
314 Balance between excitation and inhibition is considered an attribute of a physiological network  
315 state in contrast to non-physiological states like, e.g., epilepsy (*Zhang and Sun, 2011; Deghani et al.,*  
316 *2016*). Theoretical studies simulating cortical network dynamics mostly assume a balanced resting  
317 state (*van Vreeswijk and Sompolinsky, 1996, 1998; Brunel, 2000*) and relate this to low average  
318 covariances between neurons (*Renart et al., 2010; Tetzlaff et al., 2012*). We here investigate the  
319 balance between putative excitatory (bs) and inhibitory (ns) population activities, first globally,  
320 similar to *Deghani et al. (2016)*, and then relating the balance levels to different behavioral states.

321 Figure 5A shows the deviations from balance at different time scales (bin width) in session E1.  
322 White color indicates values close to zero, i.e., well-balanced activity, prevalent on smaller time  
323 scales. On time scales larger than  $\approx 30$  ms, blue and red vertical stripes indicate transient deviations  
324 from perfect balance, i.e., an instantaneous dominance of excitation or inhibition, respectively. Such  
325 brief fluctuations were also observed during physiological activity by *Deghani et al. (2016)*.

326 Fig. 5B presents a detailed view on one single time scale: the spike counts in 100 ms bins of  
327 bs (blue) and ns (red) population and the difference between z-scored population spike counts in  
328 grey, representing a horizontal slice of Fig. 5A. Putative excitatory and inhibitory activities seem  
329 to fluctuate simultaneously, indicating balance, although the considered bin size is much larger  
330 than 30 ms: Pronounced deviations from average spike counts can be seen in both populations,  
331 especially during RSS (dark green background color) and M (pink background). Considering the  
332 distributions of mean population spike counts (Appendix 1 Fig. 1), the standard deviations during M  
333 and RSS ( $9.56 \pm 2.49$  and  $7.81 \pm 2.75$ , respectively, ns population, session E1) are much higher than  
334 during RS ( $7.56 \pm 1.54$ ). They are even larger (approximately factor 1.7) than expected from the  
335 larger means (approximately factor 1.1) which indicates distributions with more extreme values, i.e.,  
336 potential transient increases in the population spike count.



**Figure 5.** Balance between putative excitatory and inhibitory population activity. **(A)** Multiscale balance during a single REST session of monkey E. The x-axis (shared with B) indicates time, the y-axis indicates the temporal resolution (bin size), the color marks the difference between z-scored putative excitatory and inhibitory population activities. The black trace below indicates behavioral states (cf. Fig. 2A). **(B)** Close-up view on a 100 ms scale. Population activities and the difference (grey) between z-scored putative excitatory and inhibitory firing from the same session as in A. Colors in the background denote behavioral states (cf. Fig. 1A). For a better visualization, spike counts of bs (blue) and ns (red) populations, calculated in 100 ms bins, are normalized by their standard deviation instead of z-scoring. Additionally, ns time series is multiplied by (-1). **(C)** Histograms of the difference between globally z-scored population activities of putative excitatory (bs) and inhibitory (ns) SUs of all REST (left) and R2G sessions (right) for monkey E (first two panels) and monkey N (last two panels), calculated in 100 ms bins. Results are pooled across all recordings of the respective type.



**Figure 6.** Instantaneous balance and its relation to dimensionality. **(A)** Box plots of the correlation between putative excitatory and inhibitory population activity calculated in 3 s slices, which quantifies the instantaneous (100 ms) balance for monkey E (left) and N (right). **(B)** Scatter plots showing the relationship between the instantaneous balance  $\rho(\text{bs, ns})$  and dimensionality PR, for monkey E (panels on the left) and N (panels on the right). Each dot represents the PR and  $\rho(\text{bs, ns})$  values of one 3 s slice during REST or R2G recording. Results are pooled across all recordings of the respective type.

337 We performed a quantitative analysis of how the balance between bs and ns SUs relates to the  
338 behavioral states, on the time scale of 100 ms, for our REST and R2G data.

339 Firstly, we asked if there was a state-specific prevalence of ns or bs activity. Fig. 5C shows the  
340 results of subtracting z-scored ns from z-scored bs population activity. The histograms show the  
341 distributions of values obtained in all 100 ms bins in the pooled REST and R2G sessions of monkey  
342 E and N, and Tab. 6 (top row) lists the values of mean and standard deviation.

343 We find a clear shift between PP and TM distributions in the R2G data of both monkeys: TM  
344 distributions are shifted towards negative and PP towards positive difference values (mean $\pm$ std:  
345  $\bar{\Delta}_{\text{TM}} = -0.16 \pm 1.01$ ,  $\bar{\Delta}_{\text{PP}} = 0.16 \pm 0.85$  for monkey E and  $\bar{\Delta}_{\text{TM}} = -0.31 \pm 1$ ,  $\bar{\Delta}_{\text{PP}} = 0.31 \pm 0.68$  for monkey N),  
346 pointing out a prevalence of ns or bs activity, respectively. This indicates that the balance between  
347 the excitatory and inhibitory activity dynamically changes depending on the behavioral state of the  
348 monkey during task performance.

349 In the REST data of both monkeys, the RSS state is dominated by inhibition ( $\bar{\Delta}_{\text{RSS}} = -0.15 \pm 0.86$  for  
350 monkey E and  $\bar{\Delta}_{\text{RSS}} = -0.32 \pm 1$  for monkey N). Concerning RS and M, however, the general tendencies  
351 are less pronounced and inconsistent: For monkey E, we find  $\bar{\Delta}_{\text{RS}} = 0 \pm 0.72$  and  $\bar{\Delta}_{\text{M}} = 0.06 \pm 0.85$ , thus  
352 no particular dominance. For monkey N, we find a slight tendency of movements being dominated  
353 by putative inhibitory firing similarly to TM ( $\bar{\Delta}_{\text{M}} = -0.06 \pm 0.11$ ), while resting periods are again not  
354 significantly dominated by any population ( $\bar{\Delta}_{\text{RS}} = 0.09 \pm 0.98$ ).

355 Secondly, we quantified the level of instantaneous balance by computing the Spearman rank  
356 correlation  $\rho(\text{bs, ns})$  between bs and ns population activity in 3 s data slices (cf. *Renart et al. (2010)*;  
357 *Tetzlaff et al. (2012)*). A higher correlation value indicates a more strict instantaneous balancing  
358 between the excitatory and inhibitory activity. Fig. 6A and B show box plots of the correlation  
359 measure  $\rho(\text{bs, ns})$  for the different behavioral states of the two monkeys, and the corresponding

**Table 6.** Quantification and correlation of balance and dimensionality. Top rows: quantification of balance between putative excitatory and inhibitory population activities ( $\Delta$ (bs, ns) and  $\rho$ (bs, ns)). Middle row: quantification of dimensionality as measured by the participation ratio (PR). Bottom row: Spearman rank correlation between  $\rho$ (bs, ns) and PR; only  $p$ -values smaller than 0.05 are listed. All values were obtained from 3 s slices, for different behavioral states in REST (RSS, RS, M) and R2G (TM, PP), pooled across all recordings of the respective type.

Monkey	RSS	RS	M	TM	PP
Putative excitatory/inhibitory prevalence $\Delta$ (bs, ns)					
E	$-0.15 \pm 0.86$	$0.00 \pm 0.72$	$0.06 \pm 0.85$	$-0.16 \pm 1.04$	$0.16 \pm 0.89$
N	$-0.32 \pm 1.00$	$0.09 \pm 0.98$	$-0.06 \pm 1.07$	$-0.28 \pm 0.97$	$0.28 \pm 0.68$
Instantaneous balance $\rho$ (bs, ns)					
E	$0.39 \pm 0.22$	$0.2 \pm 0.23$	$0.44 \pm 0.29$	$0.26 \pm 0.22$	$0.1 \pm 0.21$
N	$0.36 \pm 0.21$	$0.17 \pm 0.24$	$0.16 \pm 0.24$	$0.39 \pm 0.24$	$0.08 \pm 0.21$
Participation ratio PR					
E	$0.100 \pm 0.015$	$0.135 \pm 0.019$	$0.111 \pm 0.028$	$0.097 \pm 0.015$	$0.152 \pm 0.018$
N	$0.101 \pm 0.018$	$0.130 \pm 0.023$	$0.111 \pm 0.023$	$0.071 \pm 0.012$	$0.134 \pm 0.010$
Spearman rank correlation between $\rho$ (bs, ns) and PR					
E	-0.31	$-0.44 (p \ll 0.001)$	$-0.77 (p \ll 0.001)$	0.14	0.04
N	$-0.32 (p < 0.01)$	$-0.21 (p < 0.001)$	$-0.42 (p < 0.0001)$	$-0.33 (p < 0.001)$	-0.08

360 means and standard deviations are listed in Tab. 6. For monkey E, the correlation between bs and  
 361 ns activity is highest during M ( $\bar{\rho}_M = 0.47 \pm 0.25$ ), meaning that the balance was kept best during  
 362 M state, closely followed by RSS ( $\bar{\rho}_{RSS} = 0.4 \pm 0.2$ ), see Fig. 6A, left. RS shows the lowest correlation  
 363 ( $\bar{\rho}_{RS} = 0.26 \pm 0.17$ ), it is thus the least balanced state during REST. Pairwise comparisons confirm  
 364 significantly different results for RS vs M, but not for RSS vs M & RS. In monkey N, RS and M exhibit  
 365 nearly identical correlations ( $\bar{\rho}_{RS} = 0.23 \pm 0.17$ ,  $\bar{\rho}_M = 0.24 \pm 0.17$ ), see Fig. 6B, both are less balanced  
 366 than RSS ( $\bar{\rho}_{RSS} = 0.38 \pm 0.18$ ) which is significantly more balanced than M.

367 In the R2G data of both monkeys (right panels of Fig. 6A and B, respectively), PP ( $\bar{\rho}_{PP} = 0.18 \pm 0.13$   
 368 for monkey E and  $\bar{\rho}_{PP} = 0.19 \pm 0.14$  for monkey N) is less balanced than TM ( $\bar{\rho}_{TM} = 0.3 \pm 0.16$  for  
 369 monkey E and  $\bar{\rho}_{TM} = 0.38 \pm 0.23$  for monkey N); PP shows a significantly ( $p < 0.001$ ) lower correlation  
 370 between ns and bs activities. We thus conclude that behavioral states without movements (RS, PP)  
 371 are less balanced than movement states when considering a timescale of 100 ms.

372 Participation ratio and balance measure different aspects of correlations in the underlying  
 373 network. We now ask if and how these measures relate to each other. To this end, we analyzed the  
 374 relation of PR and  $\rho$ (bs, ns) using scatter plots (Fig. 8C & D)—each 3s slice is represented by a single  
 375 data point. The points are colored according to the behavioral state they are computed from; RSS,  
 376 RS & M for REST, and TM & PP during R2G. For the REST data, we observe a negative correlation  
 377 between PR and  $\rho$ (bs, ns) (see Tab.6): The higher the complexity, the lower the balance. Data points  
 378 from different behavioral states overlap strongly and are thus not clearly separable. In contrast, TM  
 379 and PP of the R2G data separate into two different clouds according to their PR, but there is no  
 380 clear correlation to  $\rho$ (bs, ns).

## 381 Discussion

382 Experiments without any imposed stimuli or task have been investigated in numerous studies and  
 383 referred to with multiple names: (a) ongoing, intrinsic or baseline activity of single brain areas  
 384 (Arieli et al., 1996; Tsodyks et al., 1999), (b) spontaneous or resting state activity on the whole  
 385 brain level (Vincent et al., 2007; Raichle, 2009; Deco et al., 2011), as well as (c) idle state of point-

386 neuron network simulations (*Brunel, 2000; Potjans and Diesmann, 2014; Dahmen et al., 2019*). Yet,  
387 a thorough characterization of spiking activity in the resting condition on the level of single neurons  
388 was still missing.

389 Here, we investigate the properties of spiking activity in macaque motor cortex during five  
390 behavioral states: resting state (no movements, RS), sleepy rest (no movements with eyes closed,  
391 RSS), spontaneous movement (M), task-related movement (TM) and task-imposed waiting without  
392 movements (PP), with a particular focus on RS. Our main findings are: (a) we demonstrate a  
393 considerable correlation between neuronal firing and behavior, (b) we find that RS single unit  
394 activity is characterized by relatively low average firing rates and a high variability of interspike  
395 intervals and spike counts across data slices, (c) we identify a high dimensionality of the joint  
396 activity during RS, which is (d) correlated with a low level of balance between putative excitatory  
397 and inhibitory population spiking.

### 398 **Single unit activity and LFP during different behaviors**

399 Many studies investigate the link between neuronal activity in the motor cortex and behavior using  
400 LFP data (e.g. *Pfurtscheller and Aranibar (1979); Fontanini and Katz (2008); Engel and Fries (2010);*  
401 *Kilavik et al. (2013)*). Low frequency oscillations (<15 Hz) are often linked to sleep (*Gervasoni et al.,*  
402 *2004; Fontanini and Katz, 2008*), beta oscillations ( $\approx$ 13-30 Hz) typically appear during movement  
403 preparation or postural maintenance (*Baker et al., 1999; Kilavik et al., 2012*), while faster oscillations  
404 mostly reflect attention and neuronal processing during movements (*Fontanini and Katz,*  
405 *2008; Liu and Newsome, 2006*). Our visual classification of the behavior is in good agreement with  
406 the LFP characteristics shown in the above studies.

407 Firstly, all states without movements (RSS, RS & PP) show pronounced beta oscillations which  
408 are shifted towards higher frequencies during task-imposed rest (PP) compared to spontaneous  
409 rest (RS). Secondly, both spontaneous and task-related movements (M & TM) show stronger fast  
410 oscillations than non-movement states. The spectra obtained during RSS (eyes closed) indicate  
411 distinct physiological states in the two monkeys: the peak frequency during RSS of monkey E occurs  
412 at a much lower frequency compared to monkey N. This suggests that closing the eyes indicates  
413 drowsiness in monkey E but not necessarily in monkey N.

414 Furthermore, in agreement with previous studies on behaving monkeys (*Nawrot et al., 2008;*  
415 *Nawrot, 2010; Rickert et al., 2009; Churchland et al., 2010; Riehle et al., 2018*), we find that the  
416 spiking activity is highly variable across SUs, and that the average firing rate is increased during  
417 movements as compared to waiting for the cue at rest. In REST data, in  $\approx$ 50% of all SUs, we find  
418 a significant correlation between SU firing and the monkey's behavior. This indicates that the  
419 analysis of spiking activity is another valid approach next to LFP and large scale recordings to  
420 investigate behavioral states, including resting state. Analogously to activations and deactivations  
421 of specific brain areas reported in fMRI studies (*Biswal et al., 1995; Raichle, 2009; Deco et al., 2011*),  
422 we observe systematic in- and decreases in firing rates in numerous SUs. Also in agreement with  
423 *Nawrot et al. (2008); Nawrot (2010); Rickert et al. (2009); Churchland et al. (2010); Riehle et al.*  
424 *(2018)*, we find a (slightly) lower spike count variability during task related movements (TM) than  
425 during movement preparation (PP) and vice versa for the spike time irregularity<sup>1</sup>.

426 A new finding of our study is a pronounced difference in variability between REST and R2G  
427 states, i.e., between spontaneous and task-related behavior. All REST states show a significantly  
428 higher spike count variability and a higher firing irregularity than the R2G states. These differences  
429 are probably due to the behavioral constraints present in the R2G but not in the REST experiments.  
430 During R2G task, the monkey received visual input to control periods of waiting or arm movements,  
431 resulting in well-defined behavioral states and partially constrained mental states with a more  
432 regular and reliable firing. In contrast, during REST experiments, the monkey itself decided what to  
433 do (e.g. movement preparation or onset), resulting in a less well-defined behavior and its timing.

<sup>1</sup> Our results are less significant than those presented in *Riehle et al. (2018)*; we analyze only a subset of the R2G data and use partially different methods.



434 The above findings are consistent for the two monkeys, but there are differences concerning  
435 the sleepy resting state: For monkey E, firing rates during RSS are higher than during RS, thus closer  
436 to the values measured during M, while this is not the case for monkey N. Thus, similar to what  
437 we find for the LFP spectra, the distinction between RS and RSS (eyes open vs eyes closed) is more  
438 pronounced in monkey E than in monkey N.

### 439 **Network activity**

440 During all behavioral states, the network activity of groups of neurons in the motor cortex is  
441 characterized by a dimensionality much lower than the maximal possible dimension, i.e., the total  
442 number of recorded single neurons. Task-related movements show the lowest dimensionality,  
443 expressed by a small normalized participation ratio, while non-movement states show a higher  
444 dimensionality. Accordingly, neuronal firing during rest is less coordinated than during other states,  
445 as indicated already by the narrower covariance distribution centered at zero. These findings agree  
446 well with *Mazzucato and La Camera (2016)*; *Gao et al. (2017)* who compare stimulus-evoked and  
447 ongoing neuronal activity, assuming M and TM to represent the evoked activity, and RS and PP the  
448 ongoing activity. The low normalized participation ratio of less than 0.1 during TM (Figure 4) shows  
449 that the neural state space dynamics of the reach-to-grasp movement can be reconstructed from  
450 only a few principal components. Given the number of observed SUs (see Table 1), this corresponds  
451 to a neural state space dimensionality of approximately 7-13. In contrast, the ongoing activity  
452 during RS and PP is of significantly higher dimensionality ( $\approx 12-17$  and  $\approx 12-22$ , respectively) and  
453 thus more complex.

454 In accordance with *Csicsvari et al. (1999)*; *Peyrache et al. (2012)*; *Dehghani et al. (2016)*, we  
455 also find that putative excitatory and inhibitory population spiking are primarily well balanced.  
456 However, our detailed time-resolved analysis, i.e., calculating the balance in 100 ms bins, uncovers  
457 the following particularities. During R2G experiments, the activity alternates between excitation-  
458 dominated movement preparation (PP) and inhibition-dominated movement execution (TM). During  
459 non-movement states (PP and RS), we find a reduced correlation between putative excitation  
460 and inhibition, i.e., a reduced instantaneous balance of non-movement states. In addition, the  
461 instantaneous balance is anti-correlated to the dimensionality, particularly strongly in REST.

462 We suspect that the relatively high instantaneous balance during movements and sleepy rest  
463 is partially an effect of an enhanced number of transient changes in population spiking in these  
464 states as compared to the other states (Fig. 5B). A prominent increase in firing as observed during  
465 movements is an unambiguous type of activity change and is thus easy to capture by correlation  
466 measures. Such transient increases correlated in time between two neuronal populations could  
467 result from the recurrent coupling between excitatory and inhibitory neurons (see Appendix 1). In  
468 addition to the transients in population activity, we find hints of a prevalence of non-stationarities  
469 (e.g. transients) in the SU firing during movements and sleepiness, but not during rest (Appendix 1  
470 Fig. 2). Strong transient comodulations of spiking activities amplify correlations between neurons,  
471 which in turn decrease the dimensionality of network activity. Therefore, transient changes in  
472 firing rates might also be partially responsible for the reduced dimensionality during task-related  
473 movements.

### 474 **Influence of pre-processing and critical assumptions**

475 Specificities of extracellular recordings and the following pre-processing steps impose particular  
476 biases on the resulting statistics and their interpretation. Firstly, the spike sorting procedure,  
477 necessary to identify single cells recorded on the same electrode, is well-known to be problematic  
478 (*Lewicki, 1998*; *Quiari Quiroga, 2012*). Additional limitations on minimal SNR and firing rate of a  
479 sorted unit to be considered for statistical evaluation contributes to the undersampling of sparsely  
480 firing neurons and thus biases results towards highly active neurons. This is often referred to as the  
481 problem of "dark matter" of the brain (*Shoham et al., 2006*).

482 Secondly, the separation between putative excitatory and inhibitory neurons based on the widths

483 of their spike waveforms is also known to have several limitations (*Bartho et al., 2004; Kaufman*  
484 *et al., 2010, 2013; Peyrache et al., 2012; Dehghani et al., 2016; Peyrache and Destexhe, 2019*). Some  
485 pyramidal neurons, in particular when recorded close to the axon, exhibit narrow waveforms. Still,  
486 it was shown that over 10% of M1 interneurons have intermediate or broad waveforms (*Kaufman*  
487 *et al., 2010; Vigneswaran et al., 2011; Kaufman et al., 2013*). When discussing the differences  
488 between the two populations, it should be kept in mind that not all narrow-spiking units are  
489 inhibitory and only a part (majority) of broad-spiking SUs are excitatory (*Peyrache and Destexhe,*  
490 *2019*). Nevertheless, our separation yields higher average firing rates for putative inhibitory neurons  
491 which agrees well with what is known from the literature (*Peyrache et al., 2012; Dehghani et al.,*  
492 *2016; Kaufman et al., 2010*).

493 Thirdly, our study relies on the behavioral segmentation of REST recordings which is highly  
494 subjective and has rather poor temporal resolution (~1 s) in comparison to the recorded neuronal  
495 activity (~1 ms). Nevertheless, our behavioral classification seems to be accurate in terms of  
496 separating sets of dissimilar neurophysiological network states, as reflected by differences in state-  
497 resolved LFP spectra, see above. Still, our definitions of the behavioral states are based on visual  
498 inspection and may not be as precise. For example, the identification of "whole body and limb  
499 movements" in the video recording does not account for the fact that, due to the exact placement of  
500 the Utah array, our recordings are particularly sensitive to contra-lateral arm movements. Likewise,  
501 the RS classification is simply based on the exclusion of movements with the additional criterion  
502 of "eyes open". Compared to the very precise behavioral classification in R2G recordings<sup>2</sup>, the  
503 behavioral segmentation of REST recordings is vague and allows for a much broader range of actual  
504 behaviors.

505 Finally, reliable covariance estimation necessitates very long data slices (*Cohen and Kohn, 2011*).  
506 To satisfy this requirement, in R2G data we had to concatenate slices from 6 consecutive trials  
507 into 3 s slices for the analysis of covariance and participation ratio. Thus, a single PR value results  
508 from averaging over six independent recording periods in contrast to the continuous REST data.  
509 However, this approach can be justified by our observation of a low inter-trial variability obtained  
510 for 0.5 s slices of the R2G data.

### 511 **Towards experimental data for spiking model validation**

512 Modeling studies focusing on spiking-neuron networks often claim to model an "idle" state, i.e.  
513 without any relation to functional aspects, characterized by sparse asynchronous irregular spiking  
514 and balanced input statistics (*van Vreeswijk and Sompolinsky, 1996; Amit and Brunel, 1997; van*  
515 *Vreeswijk and Sompolinsky, 1998; Brunel, 2000; Kumar et al., 2008; Voges and Perrinet, 2010, 2012;*  
516 *Potjans and Diesmann, 2014*). To isolate the ongoing and recurrently generated activity, many of  
517 these studies consider stationary states without any transient network activation due to external  
518 inputs. In this case single-neuron and population firing rates fluctuate around some mean activity.  
519 However, data collected in behavioral experiments often contain transient firing rate fluctuations  
520 on the level of both single units and whole populations. For motor cortex recordings, such firing  
521 rate changes typically occur during movements, which has been shown here and in many other  
522 studies (*Nawrot et al., 2008; Rickert et al., 2009; Churchland et al., 2010; Riehle et al., 2013, 2018*).  
523 We find that this disagreement can (mostly) be avoided by considering resting periods (RS) in REST  
524 recordings only. Using non-movement epochs (PP) during behavioral tasks yields results that are  
525 more similar to RS in terms of network firing properties, but the SU variability is still different  
526 (higher for CV2, and lower for FF). A comparison to inappropriate data sets could lead to erroneous  
527 conclusions on model parameters and the mechanisms that shape the network dynamics. Hence,  
528 network models that claim to mimic an idle state in terms of SU and network activity should ideally  
529 be validated against resting state data.

<sup>2</sup>For example, PP is defined as 500 ms after CUO-OFF when the monkey is forbidden to move, and constraining the analyzed data to only successful trials ensures that the monkey was focused on the upcoming cue to perform the task.

### 530 Balance and correlations

531 Another typical claim of network simulations is the assumption of a balanced state, see above.  
532 The modeling literature discusses different types of balance (*Deneve and Machens, 2016*). Many  
533 studies assume a cancellation of excitation and inhibition in the *input* to neurons based on a balance  
534 between the strength and number of excitatory and inhibitory afferent connections (*Poil et al., 2012*).  
535 Perfect balance in this context corresponds to a critical point, where network dynamics exhibits  
536 avalanche-like behavior (*Beggs and Plenz, 2003*). This static notion of balance purely relies on the  
537 network structure. In contrast, other studies describe a more or less tight "dynamical balance"  
538 (*van Vreeswijk and Sompolinsky, 1996; Amit and Brunel, 1997; van Vreeswijk and Sompolinsky,*  
539 *1998; Brunel, 2000*), where excitatory and inhibitory inputs cancel each other at each point in time  
540 (*Renart et al., 2010*). The latter cancellation is caused by excess inhibitory feedback (*Tetzlaff et al.,*  
541 *2012*) and, in excitatory-inhibitory networks, is accompanied by correlations between excitatory  
542 and inhibitory spiking (*Renart et al., 2010*). These correlations can be quantified on the level of  
543 neuronal *output*. Therefore, we here study balance based on the correlation between population  
544 activities.

545 Our observation of a reduced instantaneous balance during resting state compared to other  
546 states at first sight seems to argue against model validation with RS data. However, the balanced  
547 state does not necessarily rely on instant tracking between excitatory and inhibitory population  
548 activities. What it demands instead is a cancellation in the input to each single neuron, which  
549 does not uniquely define a correlation structure between outputs (*Helias et al., 2014*). Deviations  
550 between population activities can indeed be organized such that their net effect to the summed  
551 input to single neurons cancels out (*Tetzlaff et al., 2012; Baker et al., 2019*). Furthermore, one  
552 should keep in mind that we investigate a rather large time scale, and the apparent reduction of  
553 balance could be an effect of fewer transient activities contributing to the correlation between  
554 excitatory and inhibitory population activities during rest. Nevertheless, we find principally well-  
555 balanced population firing in all behavioral states and we show that spiking during rest is neither  
556 dominated by excitation nor by inhibition which indicates that RS periods are in agreement with  
557 balanced network models.

558 Related to balance, modelers often assume uncorrelated or weakly correlated external inputs  
559 to local networks, but it is impossible to determine the amount of correlations in the neuronal  
560 input with extracellular recordings. Strongly correlated inputs, attributed to sensory (*Decharms and*  
561 *Merzenich, 1996*) or movement processing (*Murphy et al., 1985*), may boost the modulation of firing  
562 rates on the population level. This could lead to higher pairwise covariances and subsequently lower  
563 dimensionalities than expected in artificial networks with a well controlled input structure. We find  
564 that such a decrease in dimensionality, is, for example, particularly pronounced during task-induced  
565 movements. This again points out the necessity to separate between rest and movements in order  
566 to avoid potential unrealistic mismatch between input and output statistics of spiking models.

### 567 Heterogeneity of neuronal networks

568 Another point is the remarkable heterogeneity of neuronal activities in experimental recordings:  
569 SUs show a broad range of firing rate profiles and spiking (ir-)regularities, as well as distinct activity  
570 modulation related to behavioral state changes. Neuronal network studies mostly are able to  
571 reproduce this heterogeneity. Single-neuron properties (e.g. time constants, synaptic weights)  
572 and connectivities are typically given as parameter ranges described by certain distributions de-  
573 rived from experimental measurements (*Kumar et al., 2008; Voges and Perrinet, 2012; Potjans*  
574 *and Diesmann, 2014*). Depending on the widths of these distributions (and other features) the  
575 resulting activities can and should be adapted to the heterogeneity in experimental data (*Dahmen*  
576 *et al., 2019*). An advantage of heterogeneous network activity is that it enhances the stability  
577 of the "idle" state (*Denker et al., 2004*) which is essential for real-world neuronal networks that  
578 need to be able to operate under various conditions. For example, the different behavioral states  
579 analyzed here demonstrate that the motor cortex operates in similar dynamical regimes for various

580 kinds of behaviors, including movements and sleepiness. The stability range of network models  
581 can be further increased by including more real-world features like homeostatic mechanisms (e.g.  
582 adaptation, short term plasticity) which also support a high (temporal) heterogeneity.

583

584 In summary, we encourage modelers to (continue to) incorporate the heterogeneity of real-world  
585 neuronal activities and we conclude that the validation of network models that claim to simulate idle  
586 states should be based on resting state data. Still, even when considering REST recordings without  
587 any task or stimulus, it is necessary to separate out the "pure" resting state periods because they  
588 show distinct statistical properties: lower firing rates, fewer transient activities, smaller covariances  
589 and thus a higher dimensionality.

### 590 **Definition of behavioral states**

591 The rather vague classification of behavioral states in REST recordings is based on observing the  
592 monkey in contrast to the precise classification in R2G experiments which relies on external cues.  
593 The consequence of this difference in precision is clearly visible on the level of the spiking activity  
594 statistics: In addition to the higher spike time irregularity and the higher (broadly distributed)  
595 spike count variability in REST compared to R2G, REST states also show a less clear state-specific  
596 difference in the dimensionality results.

597 In addition, there is the problem of different time scales (i.e., slice lengths): 0.5 s as forced by  
598 the R2G settings versus the heuristically chosen 3 s in REST. Thus, some comparisons between  
599 single behavioral states of these two data types might be unfair, but we still observe the expected  
600 commonalities in the states with (TM, M) versus without movements (PP, RS): Non-movement states  
601 show generally lower firing rates, a higher dimensionality, and a lower instantaneous balance.

### 602 **Eyes open vs closed**

603 The sleepy resting state RSS, however, turns out to be a special case. As already mentioned,  
604 the LFP spectra during RSS and the firing statistics of RSS are monkey-specific: in monkey E, the  
605 distinction between RS and RSS is more pronounced than in monkey N. However, concerning both  
606 dimensionality and instantaneous balance, the RSS distributions of the monkeys are similar. In  
607 addition, mean dimensionalities are closer to the ones obtained for M than for RS, even though RSS  
608 is a non-moving state. In accordance with observations that the motor cortex can show distinct  
609 reactions to visual stimuli (*Wannier et al., 1989; Riehle, 1991*), we conclude that the distinction  
610 between eyes-open and eyes-closed is important even in the motor cortex, since there is an impact  
611 on the neuronal activity. RS and RSS can be distinct physiological states in a given monkey: monkey  
612 E seems to be really drowsy when its eyes are closed while monkey N might be simply bored. This  
613 example also shows the importance of verifying the result of the visual behavioral segmentation  
614 with the LFP spectra of the resulting states.

### 615 **Alternative classification methods**

616 There are other possibilities for the behavioral segmentation of REST recordings. One idea would  
617 be an automatic decoding of behavioral state purely based on SU firing properties by means of  
618 machine learning methods, e.g., *Pandarínath et al. (2018)*. Given that approximately 50% of all  
619 SUs exhibit a strong correlation between firing rate modulations and behavior, such an approach  
620 would probably be possible but not necessarily straight-forward. If there were enough data to  
621 define an appropriate learn set, a machine learning algorithm could, for example, identify SUs that  
622 consistently increase or decrease their firing rate with specific state changes. Such an approach,  
623 however, is beyond the scope of this study. Another idea would be to increase the temporal  
624 precision of the visual segmentation by means of an automated detection of transient neuronal  
625 activities. Yet, the detection of transient activities in itself is not trivial (*Ito et al., 2019*), it does not  
626 allow to distinguish between RSS and M, and particularly in our data a 3 s long movement epoch  
627 contains several such transients in an unknown frequency. We do not pursue this approach, as it is

628 again beyond the scope of this study.

### 629 Resting state as superposition of sub-network activities

630 An interesting hypothesis emerges from the comparison of our study to resting state studies  
631 based on large-scale measurements. Similar to the observation of activations and deactivations  
632 of specific brain areas in fMRI studies (*Biswal et al., 1995; Fox and Raichle, 2007; Raichle, 2009;*  
633 *van den Heuvel and Hulshoff Pol, 2010; Deco et al., 2011*), we observe systematic in- and decreases  
634 in the spiking activity of numerous SUs. Large-scale studies conclude that spontaneous brain  
635 activity emerges from a set of resting state networks (*Fox and Raichle, 2007; Raichle, 2009; van den*  
636 *Heuvel and Hulshoff Pol, 2010; Deco et al., 2011*), i.e., from a sequence of consistently re-occurring  
637 spatio-temporal activity patterns that resemble task-evoked activity, but are present during rest  
638 (*Vincent et al., 2007; Fox and Raichle, 2007; van den Heuvel and Hulshoff Pol, 2010*). One could  
639 thus hypothesize a similar phenomenon on the microscopic level of spiking activity: a resting state  
640 composed of the activities of several sub-networks of single neurons in the motor cortex. During  
641 movements, one could imagine a convergence of the neuronal activity into specific networks (cf.  
642 (*Fox and Raichle, 2007; Mazzucato and La Camera, 2016*)). The larger spatial spread of the activity  
643 observed during RS compared to M (see Appendix 2) would be in line with the above hypothesis,  
644 assuming that a superposition of many spatially embedded networks yields an enlarged spatial  
645 extent than a single such network (cf. Fig. 1 in Appendix 2). Likewise, the high dimensionality  
646 observed during RS agrees well with the hypothesis of a superposition of several sub-networks.

647  
648 Yet another question concerns the definition of "rest" in general: how to define it in other cortical  
649 areas than motor cortex, e.g., in sensory systems? For the auditory system one would intuitively  
650 assume that silence or white noise as auditory input represents the resting condition. Similarly,  
651 for the visual system one could use a uniform or noise background as visual input. The choice of  
652 "eyes-closed" as rest condition would, however, represent a different behavioral state compared to  
653 our assumption of sleepy rest being a qualitatively different condition.

654 Given all the issues concerning the definition of "rest" and the behavioral segmentation, together  
655 with the superposition of RSNs on the scale of brain areas, one could claim that it is futile to attempt  
656 to characterize the spiking activity during an assumed resting state. However, our results clearly  
657 demonstrate a set of significant differences between the spiking activity in motor cortex during  
658 "rest" as compared to other behavioral conditions.

### 659 Conclusions

660 We demonstrate that spiking activity in monkey motor cortex during rest differs significantly from  
661 other spontaneous and task-related behavioral states, for example sleepiness and movements.  
662 The main characteristics of the resting state activity are low average firing rates combined with a  
663 high variability of single-unit spiking statistics, and a pronounced complexity as indicated by a less  
664 coordinated firing which results in a higher dimensionality of the network activity. We show that  
665 and explain why neuronal network models should be validated against resting state data, aiming to  
666 enhance the trend towards realistic network models that account for the heterogeneity in neuronal  
667 data. We hope that our study is just the beginning of the characterization of "rest" on the level of  
668 spiking neurons. More specific analysis is needed to quantify transient activities, their relation to  
669 the balance between excitatory and inhibitory population activities, and to provide an automated  
670 algorithm for the behavioral segmentation of REST recordings.

### 671 Materials and Methods

672 We first describe the two types of experimental recordings analyzed in this paper: resting state  
673 (REST) and reach-to-grasp (R2G) data, the latter obtained during a behavioral task. Then, we explain  
674 the experimental procedure and the pre-processing of all data types with a particular focus on the

675 REST recordings and their behavioral classification. Finally, the measures calculated to characterize  
676 different behavioral states are listed and explained.

### 677 **Experimental paradigm and recordings**

678 Two adult macaque monkeys (*Macaca mulatta*), female (monkey E) and male (monkey N), partici-  
679 pated in two distinct behavioral experiments: resting state (REST) and reach-to-grasp (R2G). Monkeys  
680 were chronically implanted with a 4x4 mm<sup>2</sup> 100 electrode Utah Array (Blackrock Microsystems, Salt  
681 Lake City, UT, USA) situated in the hand-movement area of (pre-)motor cortex. Spiking activity and  
682 LFP were recorded continuously during an experimental session, with sampling frequency of 30 kHz.  
683 Details on surgery, recordings and spike sorting, as well as on the R2G settings are described in  
684 *Riehle et al. (2013, 2018)*; *Brochier et al. (2018)*

685 During a resting state session, the monkey was seated (but not fixated) in a primate chair. The  
686 chair was positioned so as to prohibit the animal from reaching any objects. There was neither a  
687 particular stimulus nor any task, the monkey was free to look around and move spontaneously.  
688 In addition to the registration of brain activity, the monkey's behavior was video recorded and  
689 synchronized with the electrophysiology. For each monkey two such sessions were recorded and  
690 lasted approximately 15 min for monkey N and 20 min for monkey E.

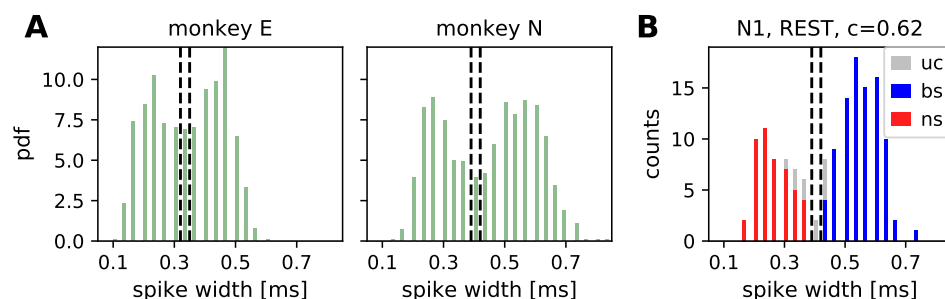
691 In the R2G experiments, monkeys were trained to perform an instructed delayed reach-to-grasp  
692 task to obtain a reward, see Fig. 1B. The monkey had to self-initiate a trial by closing a switch (TS).  
693 After 800 ms a CUE-ON signal provided some task-related information. 300 ms later, the CUE signal  
694 was switched off which defined the start of the preparatory period, during which the monkey was  
695 supposed to sit still. One second after the CUE-OFF, a GO signal provided the complementary  
696 task-related information and indicated the monkey to start moving. The monkey had to release the  
697 switch (SR) and reach to the target. After grasping the object, the monkey had to pull and hold it  
698 for 500 ms to obtain the reward (RW). Brain activity was recorded together with time stamps of all  
699 events within a trial.

700 Table 1 lists all single recording sessions for both REST and R2G experiments. Typically, a  
701 REST recording was performed subsequent to an R2G recording session. Only the E2 session was  
702 recorded directly before an R2G session which is probably the reason for the missing RSS intervals.  
703 The monkey was rather twitchy, impatiently waiting for the R2G tasks, because R2G experiments  
704 include a reward while there was no reward during REST recordings.

### 705 **Pre-processing**

706 The waveforms of potential spikes were sorted into the SUs offline and separately on each electrode  
707 using the Plexon Offline Spike Sorter (version 3.3, Plexon Inc., Dallas, TX, USA), see *Riehle et al.*  
708 *(2018)*. Synchronofacts, i.e., spike-like synchronous events across multiple electrodes at the sampling  
709 resolution of the recording system (1/30 ms) (*Torre et al., 2016*), were then removed. Sorted units  
710 were separated into broad- and narrow-spiking SUs representing putative excitatory and inhibitory  
711 neurons, respectively. The separation was achieved by thresholding the spike-widths distribution  
712 (*Bartho et al., 2004*; *Kaufman et al., 2010, 2013*; *Peyrache et al., 2012*; *Dehghani et al., 2016*) in the  
713 following way. For a given monkey, average waveforms from all SUs recorded in all considered  
714 sessions (REST and R2G) were collected. Based on the distribution of spike-widths (time interval  
715 between trough and peak of a waveform), thresholds for "broadness" and "narrowness" were  
716 chosen such that the values in the middle of the distribution stayed unclassified (Fig. 7). For monkey  
717 N, spikes with a width shorter than 0.4 ms were considered to be narrow (ns—narrow-spiking SUs,  
718 putative inhibitory neurons), whereas spikes longer than 0.41 ms were considered to be broad  
719 (bs—broad-spiking, putative excitatory neurons). For monkey E, spikes narrower than 0.33 ms were  
720 considered as ns SUs and spikes broader than 0.34 ms were considered as bs SUs. The difference  
721 between monkeys was due to different filter settings during the recordings.

722 Next, a two step classification was performed. For a given session, the thresholds were applied  
723 to the *averaged* SU waveforms (first preliminary classification). Secondly, the *single* waveforms of all



**Figure 7.** Separation between broad-spiking (bs) and narrow-spiking (ns) single units (SUs). **(A)** Spike-width distributions calculated from the average spike widths of all REST and R2G recording sessions for monkey E and monkey N. The two vertical lines indicate the thresholds for ns (0.33 ms and 0.4 ms for monkeys E and N, respectively) and bs units (0.34 ms and 0.41 ms for monkeys E and N, respectively). **(B)** Exemplary separation between ns (red) and bs (blue) units for the first REST recording of monkey N (N1). SUs between the thresholds are left unclassified (grey), as well as all SUs with a consistency smaller than 62%.

724 SUs were thresholded and a consistency measure  $c$  was calculated per SU: the percentage of SU  
725 single waveforms preliminarily classified as broad. If  $c > 0.5$ , a SU was classified as bs; if  $c < 0.5$ , a SU  
726 was classified as ns (second preliminary classification). Typically, these two classifications yielded  
727 inconsistent results for some single units, e.g., a SU with majority of spikes slightly narrower than  
728 0.4 ms has been classified (based on its *average* waveform) as bs SU. During an iterative procedure  
729 we increased the minimal required consistency until there were no more contradictions in the  
730 results of both preliminary classifications. SUs with high enough consistency were then declared  
731 classified as putative excitatory or inhibitory. SUs whose mean waveform's widths fell between two  
732 thresholds or whose consistency was too low were declared unclassified.

733 Only SUs with signal-to-noise ratio (SNR, see *Hatsopoulos et al. (2004)*) of at least 2.5 and a  
734 minimal average firing rate of 1 Hz were considered for the analysis to ensure enough and clean  
735 data for valid statistics.

### 736 Behavioral Segmentation

737 Based on video recordings, each REST session was segmented according to monkey's behavior.  
738 Three states were defined with single-second precision as follows: resting state (RS)—no movements  
739 and eyes open; sleepy resting state (RSS)—no movements and eyes (half-)closed; and spontaneous  
740 movements (M)—accounting for movements of the whole body and limbs (Fig. 1A). If a movement  
741 or a RSS interval began during a particular second, this whole second was classified as M or RSS,  
742 respectively. Eye movements and minor head movements were allowed during RS. All other types  
743 of behaviour (e.g., strong isolated head movements) and periods for which it was not possible to  
744 clearly classify the monkey's behavior (e.g., due to a lack of visibility) were considered as unclassified  
745 and excluded from analyses. To increase the reliability of classification, behavioral scoring for each  
746 session was performed by two independent observers, and the results were merged later.

747 Behavior classification in R2G recordings was based on the events registered throughout the  
748 experiment, see Sec. Materials and Methods: Experimental paradigm and recordings. Two periods  
749 within a trial (see Fig. 1B) were considered: preparatory period (PP), defined as 500 ms after the  
750 CUE-OFF (first half of the preparatory delay, no movements), and task-related movement (TM)—  
751 500 ms after SR-ON, including grasping. Due to differences in performance speed of each monkey,  
752 this period was defined as: [SR-ON, SR+500 ms] for monkey E, and [SR-150 ms, SR+350 ms] for  
753 monkey N. All successful trials were used.

754 Since the amount of data strongly differs between behavioral states in REST, we used data slices  
755 of equal length, mostly 3 s slices, to have comparable statistics. The choice of slice length represents  
756 a compromise between different factors: a) the slice length cannot exceed the typical duration of  
757 each behavior (shortest for movement), b) the slice length should be as long as possible for reliable

758 estimation of covariances within each slice, c) to average across slices, we need as many slices as  
759 possible. Following these arguments, each behavioral segment was cut into as many continuous  
760 slices as possible. For example, if a REST segment was 7 s long, it was separated into two slices  
761 of 3 s and the remaining 1 s was not considered for the analysis. In the R2G data, the slice length  
762 for the 2 behavioral states was 0.5 s by definition, see above. When directly comparing REST and  
763 R2G data, we either considered 0.5 s slices for the REST data (comparison of firing statistics) or we  
764 concatenated six 0.5 s slices of the R2G data to 3 s slices (analysis of covariances and balance).

### 765 LFP Spectra

766 The spectral density of the LFP (sampling frequency of 1000 Hz) in different behavioral states in REST  
767 and R2G data was estimated with Welch's method provided by Elephant (<https://python-elephant.org>). We considered 3 s slices for the REST and 0.5 s slices for the R2G data. The spectra shown  
768 in Fig. 1 were obtained by averaging over single spectra from state-specific slices of all respective  
769 recordings. We used a Hanning window of 1 s and an overlap of 50% for the REST data while the  
770 R2G spectra were estimated with a Hanning window of 0.3 s with an overlap of 50%. Additionally, an  
771 artifact in session N1—high-amplitude synchronous peak on all recording channels—was removed:  
772 it was replaced by the average of the remaining signal.  
773

### 774 Data analysis

775 To characterize and compare different behavioral states, we employed a set of analysis tools. We  
776 quantified the correlation between neuronal firing and behaviour and characterized firing properties  
777 of SUs, as well as the coordinated firing of pairs of SUs. We also calculated the dimensionality  
778 of spiking and the balance between time-resolved putative excitatory and inhibitory population  
779 counts.

780 Pre-processing and data analyses were performed in Python, version 2.7, with the Elephant pack-  
781 age (<https://python-elephant.org>). Since our distributions were typically non-Gaussian, significance  
782 of differences between them was assessed via Kruskal-Wallis tests for multivariate comparisons  
783 (KW, non-parametric alternative to a one-way ANOVA), with significance level  $\alpha = 0.001$ . Multiple  
784 comparisons were corrected for with a Bonferroni-Holm correction.

785 For visualizations of distributions obtained for different behavioral states, we used notched  
786 boxplots. The line in the center of each box represents the median, box's area represents the  
787 interquartile range, and the whiskers indicate minimum and maximum of the distribution (outliers  
788 excluded).

### 789 Behavioral correlation

790 For each REST session, we defined a state vector based on the behavioral segmentation, see  
791 Sec. Materials and Methods: Behavioral Segmentation. Each entry represented 1 s of the recording  
792 and was set to -1 for RS, to -2 for RSS and to 1 for M. To assess the relation between SU activity  
793 and monkey's behavior, the FR (in 1 s bins, no overlap) of each SU was correlated (Spearman  
794 rank correlation) with the modified state vector of a given session: entries for RSS were zeroed.  
795 Only pairs of entries in which the modified state vector was different from zero were considered.  
796 This procedure resulted in a value which we called behavioral correlation:  $BC \in [-1, 1]$ , and the  
797 corresponding  $p$  value (indicating statistical significance if  $p < 0.001$ , with correction) for each SU,  
798 see Fig. 2B. Positive BC indicated that the FR increased during movements or decreased during rest,  
799 and vice versa. We investigated the distributions of BC values separated between ns and bs SUs,  
800 see Fig. 2C.

801 For a substantiation of these results, we additionally performed Kruskal-Wallis tests on all three  
802 behavioral states defined in REST (M, RS, and RSS), separately for each SU, to check for significant  
803 changes in the SU firing rates. Note that this method does not provide any quantification of  
804 amplitude of the correlation similar to BC.



805 For both tests described above, we calculated the percentage of SUs that changed their FR  
806 significantly (after correction) with changes in the behavioral states, see Tab. 2. This procedure was  
807 performed for all SUs and separately for ns and bs neurons.

808 Next, we again applied Kruskal-Wallis tests for pairwise comparisons between three behavioral  
809 states per SU, asking for a significant in- and decreases in firing. This analysis was performed on  
810 3 s long data slices. Tab. 3 lists the percentages of all SUs which either significantly increased or  
811 decreased their FR in one state with respect to another.

## 812 Neuronal firing in REST and R2G states

813 To compare the SU firing properties in behavioral states from different experiments, we used 0.5 s-  
814 long slices of both REST and R2G recordings. In REST, the single seconds at the transitions from one  
815 state to another were excluded. For each time slice of each SU, we estimated the average firing rate  
816 FR and the local coefficient of variation CV2 (Ponce-Alvarez et al., 2010; Voges and Perrinet, 2010;  
817 Riehle et al., 2018), and per SU across slices the Fano factor FF (Nawrot et al., 2008; Nawrot, 2010;  
818 Riehle et al., 2018). For the REST recordings, we also calculated the commonly used coefficient of  
819 variation CV (Shinomoto et al., 2003; Ponce-Alvarez et al., 2010; Voges and Perrinet, 2010), shown  
820 in the additional Figure in Appendix 1 Sec. Transient activities.

821 CV and CV2 are based on the inter-spike-interval distribution of a SU (Shinomoto et al., 2003;  
822 Ponce-Alvarez et al., 2010; Voges and Perrinet, 2010; Riehle et al., 2018). They characterize the  
823 (ir-)regularity in neuronal firing. A value close to zero indicates regular spiking, a value of one  
824 indicates Poissonian spiking, and a value above one even more irregular firing. The CV2 corrects for  
825 transient firing rate changes which yield inappropriately high CV values (Ponce-Alvarez et al., 2010;  
826 Voges and Perrinet, 2010). The FF describes the variability in SU spike counts across trials (R2G) or  
827 time slices (REST) (Nawrot et al., 2008; Nawrot, 2010; Riehle et al., 2018).

828 We compared the FR and CV2 values obtained for each SU within each slice of RSS, RS, M, TM and  
829 PP states in two different ways, see Fig. 3. On the one hand, we averaged over time slices/trials to  
830 represent the variability with respect to SUs. On the other hand, we averaged the results obtained  
831 for each data slice/trial over SUs in order to analyse the variability of our measures in time. The  
832 significance of the differences between the behavioral states was assessed with a Kruskal-Wallis  
833 test including a Bonferroni-Holm correction, both when comparing all 5 states and in pairwise  
834 comparisons.

## 835 Covariances and dimensionality

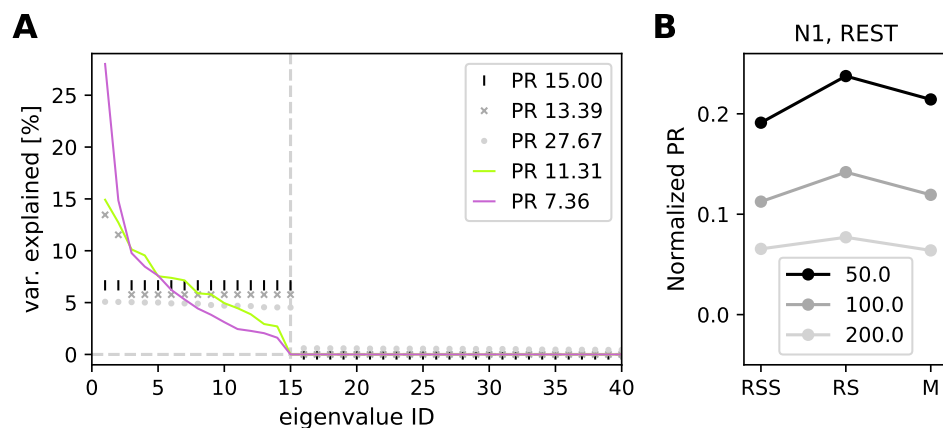
836 To measure the joint variability in rate modulation, we calculated the pairwise spike-count co-  
837 variances (COV, Cohen and Kohn (2011); Dahmen et al. (2019)). REST data were cut and R2G data  
838 concatenated into 3 s slices (state-resolved) and binned into 100 ms intervals. The bin size of 100 ms  
839 was a compromise between obtaining enough bins to calculate covariance values (given a slice  
840 length of 3 s), considering enough spikes for reliable estimation of covariance, and using a time  
841 scale appropriate for the examination of rate modulations. For R2G data this procedure implied  
842 that data from 6 consecutive trials contributed to a single COV value.

843 The COV between spike trains  $i$  and  $j$  was defined as:

$$844 \text{COV}(i, j) = \frac{\langle b_i - m_i, b_j - m_j \rangle}{l - 1}, \quad (1)$$

845 with  $b_i$  and  $b_j$ —binned spike trains,  $m_i$  and  $m_j$  being their mean values,  $l$  the number of bins, and  
846  $\langle x, y \rangle$  the scalar product of vectors  $x$  and  $y$ . Thus, for each 3 s slice of a particular state we obtained  
847 a COV matrix  $\mathbf{M} \in \mathbb{R}^{N_{SU} \times N_{SU}}$  with  $N_{SU}$ —number of SUs.

848 Based on the COV matrices, we calculated the participation ratio PR to characterize the dimen-  
849 sionality of activity in different behavioral states, see Mazzucato and La Camera (2016); Gao et al.  
850 (2017). Eigenvalue decomposition of COV matrix  $\mathbf{M}$  yields  $N_{SU}$  eigenvalues  $\lambda$  with corresponding  
851 eigenvectors  $v$ , such that  $\mathbf{M}v_i = \lambda_i v_i$ . The eigenvalues were used to calculate the participation ratio



**Figure 8.** Participation ratio to characterize the dimensionality. **(A)** Sketch showing relation between the eigenvalue spectrum and PR. In case of first  $N$  eigenvalues explaining equal amounts of variance and the rest vanishing, the PR equals  $N$  (black vertical lines). If a few eigenvalues are much higher than the others, the resulting PR decreases (dark grey crosses). If, on the contrary, a uniformly distributed random value is added to each eigenvalue from the first case, the calculated PR becomes higher (light grey circles). Experimental data is typically a mixture of the second and the third case. Continuous traces show exemplary results for a single 3 s data slice of RS (green) and M (pink) in session N1. **(B)** Participation ratio, calculated with different bin sizes (50, 100, 200 ms) in exemplary session N1.

851 of the neuronal dynamics:

$$PR = \frac{(\sum \lambda_i)^2}{\sum \lambda_i^2}. \quad (2)$$

852 The PR thus quantifies how many eigenvectors are necessary to explain a significant part of variance  
853 in dynamics described by **M**, see Fig. 8A.

854 The PR is low if most of the variability is captured by the first few eigenvectors. A large PR  
855 indicates that many eigenvectors are necessary to capture the dynamics—a sign of high complexity.  
856 In order to test the robustness of our results, we performed our analysis with different bin sizes.  
857 The result is shown in (Fig. 8B). Here, all bin sizes revealed the same PR-dependent ordering of  
858 behaviors. This suggests that our results are robust to the choice of bin size.

859 The value of the PR depends on the number of SUs present in the analysis: It can take values  
860  $1 \leq PR \leq N_{SU}$ . In order to make the PRs comparable across recording sessions, we normalize with  
861 the number of SUs measured in the respective experiment,  $PR' = PR / N_{SU}$ , thus giving rise to values  
862 in a range [0, 1]. The box plots in Fig. 4 visualize the distributions of normalized PRs obtained in  
863 all non-overlapping 3 s time slices from all recording sessions of a given type (REST or R2G) per  
864 monkey. The time-resolved visualization of  $PR'$  in panel B of the same Figure was calculated in a  
865 sliding-window fashion with 3 s slices and 2 s overlap. Each data point in this plot is located at the  
866 center of the respective window.

## 867 Balance

868 The multiscale balance between putative excitatory (bs SUs) and inhibitory (ns SUs) population  
869 firing was examined similarly to the procedure proposed in *Dehghani et al. (2016)*. We considered  
870 timescales from 1 ms to 10 s. For a given timescale, pooled spikes from bs and ns units were binned  
871 and z-scored separately, resulting in bs and ns population activities (whole recording, no separation  
872 into behavioral states). Then, the putative inhibitory population activity was subtracted from the  
873 putative excitatory activity (see Fig. 5A). If this difference was close to zero, i.e., if pooled ns and bs  
874 spike counts were nearly identical, the network activity was called balanced. If this was the case for  
875 multiple time scales (i.e., bin sizes), it was called multiscale balance.

876 Since we observed some deviations from balance for bin sizes larger than 30 ms, we quantified  
877 these deviations in a state-resolved manner. For each REST and R2G session of a given monkey,

878 we binned the 3 s time slices (concatenated from six consecutive trials of 0.5 s for R2G data) into  
879 100 ms bins. Next, we applied two methods to quantify the balance between population activities.

880 Firstly, the same as for the multiscale balance, we z-scored the population activities, using  
881 the respective mean and standard deviation of the whole recording (not state-specific). Then, we  
882 calculated, separately for each state, the difference between the z-scored bs and ns population  
883 activity of each 100 ms bin in each time slice: A negative value indicated a domination of ns activity  
884 while a positive value meant that the bs activity was higher. Fig. 5C shows the corresponding  
885 state-resolved histograms.

886 Secondly, we calculated the Spearman rank correlation between raw bs and ns population  
887 activities for each time slice: The higher the correlation  $\rho(\text{bs}, \text{ns})$ , the more strict the instantaneous  
888 balancing between the ns and bs populations (cf. (*Renart et al., 2010; Tetzlaff et al., 2012*)). The  
889 state-resolved results are presented in box plots (Fig. 6A).

890 To investigate the relationship between balance and dimensionality, we calculated the Spearman  
891 rank correlation between  $\rho(\text{bs}, \text{ns})$  and PR' for each monkey, pooled over all REST and R2G sessions,  
892 respectively (Fig. 6C, D and Tab. 6).

### 893 Acknowledgments

894 This project has received funding from the Deutsche Forschungsgemeinschaft Grant GR 1753/4-2 &  
895 DE 2175/2-1 Priority Program (SPP 1665), the Helmholtz Association through the Helmholtz Portfolio  
896 Theme Supercomputing and Modeling for the Human Brain (SMHB), and from the European Union's  
897 Horizon 2020 Framework Programme for Research and Innovation under Specific Grant Agreement  
898 No. 720270 & 785907 (Human Brain Project SGA1 & SGA2). We thank Tom Tetzlaff and Alper  
899 Yegenoglu for fruitful discussions.

### 900 Competing interests

901 No competing interests declared.

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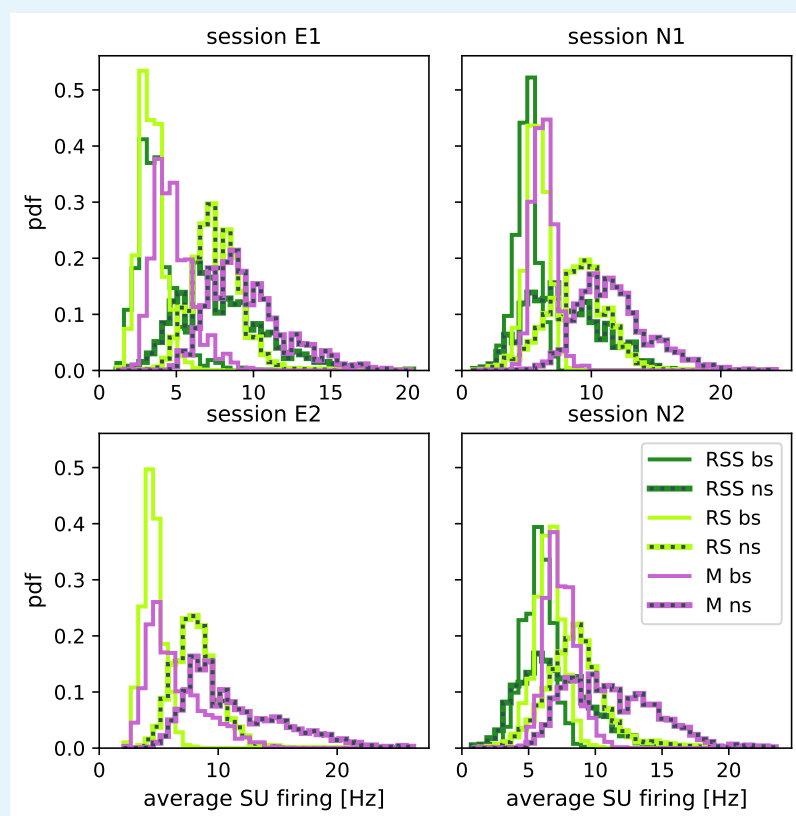
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## 1099 Appendix 1

### 1100 Transient activities

1101 To analyze the instantaneous balance, we correlate putative excitatory and inhibitory popula-  
1102 tion activities in different behavioral states (sleepy rest RSS, rest RS, and movements M). We  
1103 find a significantly reduced correlation (i.e., balance) during RS compared to M for monkey E,  
1104 and during RS and M compared to RSS in monkey N, significantly only between M and RSS  
1105 (cf. 6A and B). We also observe numerous transient increases in the population spike counts  
1106 (Fig. 5B). Such simultaneous peaks contribute to higher correlation values between the two  
1107 neuronal populations. The prevalence of this deviations differs between behavioral states.  
1108 Fig. 1 and Tab. 1 below show that the distributions of population activities during M (monkey  
1109 N, ns population) or both RSS and M (monkey E, both populations) are characterized by  
1110 higher standard deviations than expected from higher mean values. RSS of monkey N shows  
1111 lower means and slightly higher standard deviations than RS in ns population, pointing to  
1112 the same conclusion. Both relations serve as footprints of an increased number of narrow  
1113 peaks in population spiking during non-resting states.

1114 Given the transient peaks in the population spike counts during M and RSS, we suspect the  
1115 following relationship between balance and transients in the population activity: Whenever  
1116 one of the population activities transiently increases, the other one is forced to do the same  
1117 due to the recurrent coupling between putative excitatory and inhibitory neurons, yielding  
1118 higher correlation value and thus more balance.



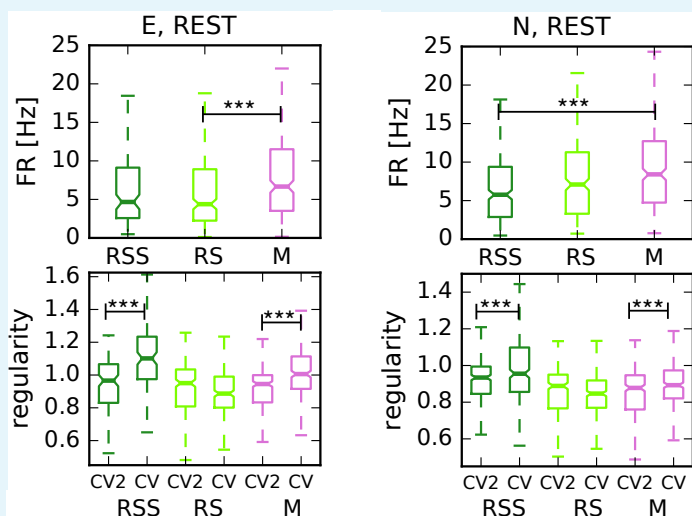
1119 **Appendix 1 Figure 1.** Population spiking in REST recordings. Distributions of the population spiking  
1120 activities calculated in 100 ms bins, separately for each REST session (left column—monkey E,  
1121 right—monkey N, colors indicate behavioral states, solid lines—bs, dashed lines—ns). Notice different  
1122 ranges of the x axes.  
1123



Session	RSS	RS	M
E1	$3.67 \pm 1.23$	$3.36 \pm 0.77$	$4.76 \pm 1.28$
	$7.81 \pm 2.75$	$7.56 \pm 1.54$	$9.56 \pm 2.49$
E2		$4.50 \pm 0.88$	$6.37 \pm 2.38$
		$8.10 \pm 1.84$	$11.31 \pm 4.06$
N1	$4.96 \pm 0.86$	$5.79 \pm 0.86$	$6.30 \pm 0.85$
	$7.88 \pm 2.91$	$8.85 \pm 2.29$	$11.68 \pm 2.74$
N2	$5.71 \pm 1.10$	$6.52 \pm 1.07$	$7.43 \pm 1.14$
	$6.92 \pm 2.53$	$8.52 \pm 2.37$	$11.18 \pm 3.34$

**Appendix 1 Table 1.** Mean values and standard deviations of distributions of population spiking activities visualized in Fig. 1 above. First line per session: bs, second line: ns population.

Complementary to the above discussed population activity, we now look at the firing on the level of SUs (considering 3 s time slices), shown in the top row of Fig. 2. We expect higher firing rates (mean and standard deviation) for states with more transient activities (M&RSS) which show an increased balance in the population activities. For monkey E, the reduced balance in RS compared to M (cf. Fig. 6A) coincides with a significant average firing rate reduction in RS compared to M. However, for monkey N, the reduced balance in M compared to RSS (cf. Fig. 6B) coincides with a significant firing rate increase in M compared to RSS. Since SU firing rate cannot be directly related to instantaneous balance, we examine another feature of firing, namely its regularity. The bottom row of Fig. 2 compares the results obtained for two different regularity measures, CV and CV2: only CV2 accounts for transient firing rate changes which typically yield erroneously high CV values (Ponce-Alvarez et al., 2010; Voges and Perrinet, 2010). Thus, a significant difference between CV and CV2 suggests the presence of such transient firing rate changes. Indeed, we observe significantly higher CV during RSS and M. Obviously, this is no proof but only an indication for transient changes in the firing rates on the level of SU firing during movements and sleep rest.



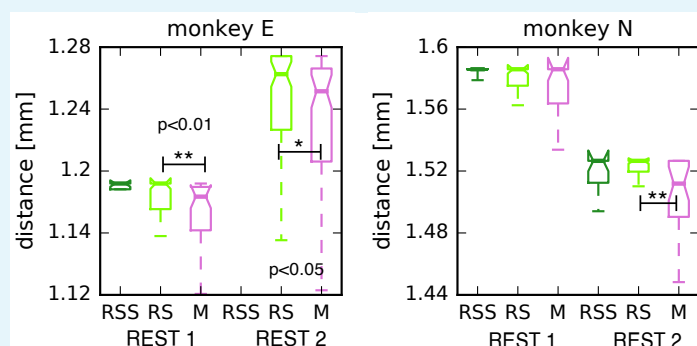
**Appendix 1 Figure 2.** Transient activities in REST recordings. Box plots of average firing rates (top row) and two different regularity measures (bottom row) of the three states defined for REST recordings (RSS in dark green, RS in light green, and M in magenta) of monkey E (left) and monkey N (right). CV2 and CV characterize the (ir-)regularity in spiking, but only CV2 accounts for transient changes in the firing rates which typically yield misleadingly high CV values. In both monkeys, CV yields significantly higher values than CV2 during M and RSS states but not during RS.

## 1152 Appendix 2

### 1153 Spatial activity distribution

1154 The participation ratio quantifies the dimensionality in the network activity space. One could  
1155 ask how this relates to the distribution of neuronal activity in physical space. In analogy  
1156 to large-scale resting state studies which find widely distributed networks of brain areas  
1157 that are particularly active during rest (Biswal *et al.*, 1995; Raichle, 2009; Deco *et al.*, 2011),  
1158 we estimated the spatial spread of active SUs in the different behavioral states of the REST  
1159 recordings. To this end, we calculated the average spatial distance from each active SU to  
1160 the center of mass of the spiking activity during sleepy rest (RSS), rest (RS), and movements  
1161 (M). An *active* SU emitted at least one spike during the respective 3 s slice; the center of mass  
1162 is given by the average coordinates of all active SUs. We thus characterized the mean spatial  
1163 spread of the activity around the center of mass in each behavioral state.

1164 Figure 1 (below) shows the results obtained for our four REST sessions. The distinct  
1165 scales on the y-axis are a result of the different implantations of the Utah arrays in the  
1166 two monkeys (number and placement of active versus inactive electrodes), see Riehle *et al.*  
1167 (2018). The differences in the spatial confinement of active SUs were small but consistent  
1168 across sessions and monkeys. For monkey E, we find that the activity during RS exhibits a  
1169 higher spatial spread than during M, even if the difference is only weakly significant ( $p < 0.01$   
1170 in session E1 and  $p < 0.05$  in session E2). In monkey N, only the second session shows a  
1171 significant difference, namely a larger spatial spread in RS compared to M ( $p < 0.01$ ). In  
1172 summary, we show a tendency of the SU activity during rest to be distributed over a larger  
1173 spatial region than during movement, which may relate to higher dimensionality quantified  
1174 by PR.



1175 **Appendix 2 Figure 1.** Spatial arrangement of active SUs on the Utah array. Box plots of the radial  
1176 spatial distance to the center of mass for the two REST recording sessions of monkey E (left panel) and  
1177 N (right panel).  
1178