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1 ***Interneuronal correlations dynamically adjust to task demands***
2 ***at multiple time-scales***

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13
14 Key words: noise correlation, prefrontal cortex, macaque monkey, task difficulty, alpha
15 oscillations, beta oscillations, cognitive demand, cognitive flexibility, rhythmic cognition,

16 **Summary**

17 Functional neuronal correlations between pairs of neurons are thought to play an important
18 role in neuronal information processing and optimal neuronal computations during attention,
19 perception, decision-making and learning. Here, we report dynamic changes in prefrontal
20 neuronal noise correlations at multiple time-scales, as a function of task contingencies.
21 Specifically, we record neuronal activity from the macaque frontal eye fields, a cortical region
22 at the source of spatial attention top-down control, while the animals are engaged in tasks of
23 varying cognitive demands. First, we show that noise correlations decrease as cognitive
24 engagement and task demands increase, both across tasks and within-trials. Second, we
25 demonstrate, for the first time, rhythmic modulations of noise correlations in the alpha and
26 beta frequency ranges that account both for overt behavioral performance and for layer
27 specific modulations in spike-field coherence. All this taken together demonstrates a strong
28 functional role of noise correlations in cognitive flexibility.

29 **Introduction**

30 Optimal behavior is the result of interactions between neurons both within and across
31 brain areas. Identifying how these neuronal interactions flexibly adjust to the ongoing
32 behavioral demand is key to understand the neuronal processes and computations underlying
33 optimal behavior. Several studies have demonstrated that functional neuronal correlations
34 between pairs of neurons, otherwise known as noise correlations, play an important role in
35 perception and decision-making¹⁻⁹. Specifically, several experimental and theoretical studies
36 show that noise correlations have an impact on the amount of information that can be decoded
37 for neuronal populations^{4,10-12} as well as on overt behavioral performance^{4,10-15}. As a result,
38 understanding how noise correlations dynamically adjust to task demands is a key step toward
39 clarifying how neural circuits dynamically control information transfer, thereby optimizing
40 behavioral performance.

41 Several sources of noise correlations have been proposed, arising from shared
42 connectivity¹⁶, global fluctuations in the excitability of cortical circuits^{17,18}, feedback signals
43¹⁹ or internal areal dynamics²⁰⁻²², or bottom-up peripheral sensory processing²³. From a
44 cognitive point of view, noise correlations have been shown to change as a function of spatial
45 attention²⁴, spatial memory²⁵ and learning^{26,27}, suggesting that they are subject both to rapid
46 dynamic changes as well as to longer term changes, supporting optimal neuronal
47 computations²⁷.

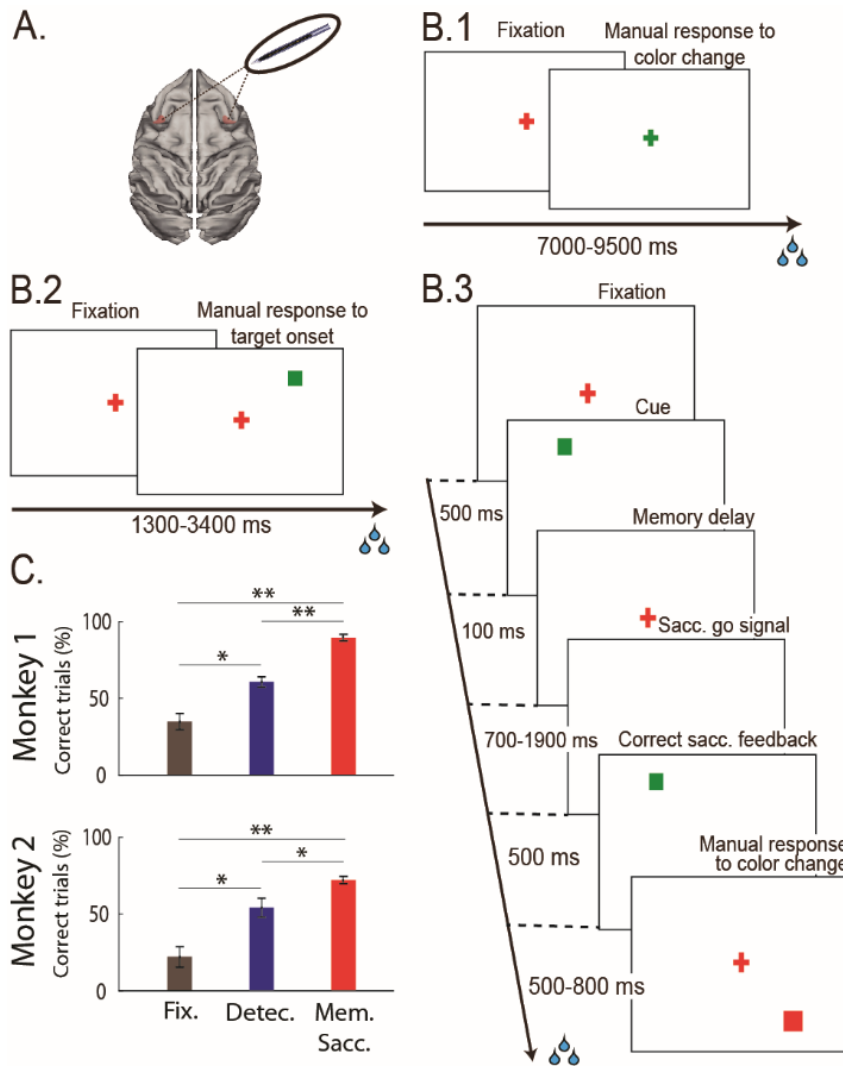
48 Here, we focus onto how multiple task contingencies induce dynamic changes in
49 prefrontal neuronal noise correlations at multiple time-scales. Specifically, we record
50 neuronal activity from the macaque frontal eye fields, a cortical region which has been shown
51 to be at the source of spatial attention top-down control^{15,28-30} while the animals are engaged
52 in tasks of varying cognitive demands, as assessed by their overt behavioral performance.
53 Overall, we demonstrate that noise correlations dynamically adjust to the cognitive demand,
54 decreasing as cognitive engagement and task demands increase. These dynamical changes
55 take place both across task, as a function of task demands, and within trials, as a function of
56 the probabilistic structure of the task, demonstrating a top-down control over this neuronal
57 process. We also demonstrate, for the first time, rhythmic modulations of noise correlation in
58 two specific functional frequency ranges: the alpha and beta frequency ranges. Crucially,
59 these rhythmic modulations in noise correlations account both for overt behavioral
60 performance and for layer specific modulations in spike-field coherence. All this taken
61 together demonstrates a strong functional role of noise correlations in cognitive flexibility.

62 These findings are discussed in relation with previously reported functional and structural
63 sources of variations in noise correlation and a comprehensive model of shared population
64 neuronal variability is proposed.

65

66 **Results**

67 Our main goal in this work is to examine how the degree of cognitive engagement and
68 task demands impact the neuronal population state as assessed from interneuronal noise
69 correlations. Cognitive engagement was operationalized through tasks of increasing
70 behavioral requirements. The easiest task (*Fixation task*, figure 1B.1) was a central fixation
71 task in which monkeys were required to detect an unpredictable change in color of the
72 fixation point, by producing a manual response within 150 to 800ms from color change. The
73 second task (*Target detection task*, figure 1B.2) added a spatial uncertainty on top of the
74 temporal uncertainty of the event associated with the monkeys' response. This was a target
75 detection task, in which the target could appear at one of four possible locations, at an
76 unpredictable time from fixation onset. The monkeys had to respond to this target
77 presentation by producing a manual response within 150 to 800ms from color change. In the
78 third task (*Memory guided saccade task*, figure 1B.3), monkeys were required to hold the
79 position of a spatial cue in memory for 700 to 1900ms and to perform a saccade towards that
80 memorized spatial location on the presentation of a go signal. This latter task thus involved a
81 temporal uncertainty but no spatial uncertainty. However, in contrast with the previous tasks,
82 it required the production of a spatially oriented oculomotor response rather than a simple
83 manual response. Accordingly, both monkeys had higher performances on the memory guided
84 saccade task than on the target detection task (Figure 1C, Wilcoxon rank sum test, Monkey 1,
85 $p < 0.01$, Monkey 2, $p < 0.05$), and higher performances on the target detection task than on the
86 fixation task (Wilcoxon rank sum test, $p < 0.05$).



87

88 **Figure 1:** (A) **Recordings sites.** On each session, 24-contact recording probes were placed in
89 the left and right FEFs. (B.1) **Fixation task.** Monkeys had to fixate a red central cross and
90 were rewarded for producing a manual response 150ms to 800 ms following fixation cross
91 color change. (B.2) **Target detection task.** Monkeys had to fixate a red central cross and were
92 rewarded for producing a manual response 150ms to 800ms from the onset of a low
93 luminosity target at an unpredictable location out of four possible locations on the screen.
94 (B.3) **Memory-guided saccade task.** Monkeys had to fixate a red central cross. A visual cue
95 was briefly flashed in one of four possible locations on the screen. Monkeys were required to
96 hold fixation until the fixation cross disappeared and then produce a saccade to the spatial
97 location indicated by the cue within 300ms from fixation point offset. On success, the cue re-
98 appeared and the monkeys had to fixate it. They were then rewarded for producing a manual
99 response 150ms to 800ms following the color change of this new fixation stimulus. (C)
100 **Behavioral performance.** Average percentage of correct trials across sessions for each tasks
101 and each monkey with associated standard errors.

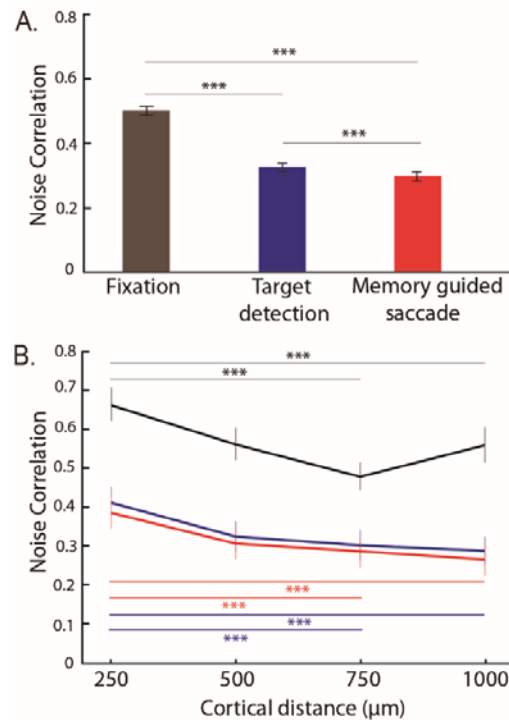
102

103 Neuronal recordings were performed in the prefrontal cortex, specifically in the frontal
104 eye field (FEF, figure 1A), a structure known to play a key role in covert spatial attention^{30–33}.
105 In each session, multi-unit activity (MUA) and local field potential (LFP) were recorded
106 bilaterally, while monkeys performed these three tasks. In the following, the noise
107 correlations between the different prefrontal signals of the same hemisphere were computed
108 on equivalent task fixation epochs, away from both sensory intervening events and motor
109 responses. In a first step, we analyzed how these noise correlations varied both across tasks,
110 as a function of cognitive engagement and within-tasks, as a function of the probabilistic
111 structure of the task. In a second step, we describe the temporal oscillatory structure of noise
112 correlations. We relate these rhythmic variations to cognitive engagement and we show that
113 they correlate with changes in the coupling between local field potentials and MUA spiking
114 activity, in specific functional frequency bands.

115 *Noise correlations decrease as cognitive engagement and task requirements*
116 *increase.*

117 In order to characterize how inter-neuronal noise correlations vary as a function of
118 cognitive engagement and task requirements, we proceeded as follows. In each session
119 (n=26), noise correlations were computed between each pair of task-responsive channels
120 (n=671, see Methods), over equivalent fixation task epochs, running from 300 to 500 ms after
121 eye fixation onset. This epoch was at a distance from a possible visual or saccadic foveation
122 response and in all three tasks, monkeys were requested to maintain fixation at this stage. It
123 was also still early on in the trial, such that no intervening sensory event was to be expected
124 by the monkey at this time. Importantly, fixation behavior, i.e. the distribution of eye position
125 in within the fixation window, did not vary between the different tasks (Friedman test,
126 $p < 0.001$). As a result, and because tasks were presented in blocks, any difference in noise
127 correlations across tasks during this “neutral” fixation epoch are to be attributed to general
128 non-specific task effects, i.e. differences in the degree of cognitive engagement and task
129 demands. Noise correlations were significantly different between tasks (Figure 2A, ANOVA,
130 $p < 0.001$). Specifically, they were higher in the fixation task than in the target detection task
131 (Figure 2A, Wilcoxon rank sum test, $p < 0.001$) and in the memory guided saccade task
132 (Wilcoxon rank sum test, $p < 0.001$). They were also significantly higher in the target detection
133 task than in the memory guided saccade task (Wilcoxon rank sum test, $p < 0.001$). Importantly,
134 these significant changes in noise correlations existed in the absence of significant differences
135 in mean firing rate (ANOVA, $p > 0.5$), standard error around this mean firing rate (ANOVA,

136 $p > 0.6$), and Fano factor (ANOVA, $p > 0.7$, data not shown). We thus describe that, in absence
137 of any sensory or cognitive processing, noise correlations are strongly modulated by cognitive
138 engagement and task demands.



139

140 **Figure 2:** (A) *Noise correlations as a function of task.* Average noise correlations across
141 sessions for each of the three tasks (mean \pm s.e., noise correlations calculated on the
142 neuronal activities from 300 to 500 after eye fixation onset. Black: fixation task; blue: target
143 detection task; red: memory guided saccade task. Stars indicate statistical significance
144 following a one-way ANOVA; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. (B) *Noise correlations as a*
145 *function of cortical distance.* Average noise correlations (mean \pm s.e.) across sessions,
146 for each task (conventions as in (A)), from 300 ms to 500ms after eye fixation onset, as a
147 function of distance between pairs of channels: 250 μ m; 500 μ m; 750 μ m; 1000 μ m. Stars indicate
148 statistical significance following a two-way ANOVA and ranksum post-hoc tests; * $p < 0.05$;
149 ** $p < 0.01$; *** $p < 0.001$.

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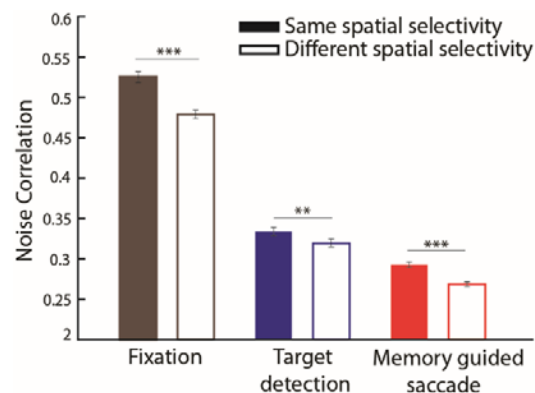
151 *Cortical distance, spatial selectivity and cortical layer effects on noise correlations*
152 *are task independent.*

153 The task differences in noise correlations described above could reflect changes in the
154 shared functional connectivity, within the large-scale parieto-frontal functional network the
155 cortical region of interest belongs to¹⁶ or to global fluctuations in the excitability of cortical
156 circuits^{34,35}. This large-scale hypothesis predicts that the observed changes in noise

157 correlations are independent from intrinsic connectivity as assessed by the distance, the spatial
158 selectivity or cortical layer between the pairs of signals across which noise correlations are
159 computed. Alternatively, these task differences in noise correlations could reflect a more
160 complex reweighing of functional connectivity and the excitatory/inhibitory balance in the
161 area of interest, due to local changes in the random shared fluctuations in the pre-synaptic
162 activity of cortical neurons^{4,16,36,37}. This local hypothesis predicts that the observed changes in
163 noise correlations depend onto intrinsic microscale connectivity. In the following, we
164 characterize task differences in noise correlations as a function of cortical distance, spatial
165 selectivity and cortical layer.

166 *Cortical distance effects.* Our recordings were performed as tangentially to FEF
167 cortical surface as possible. The distance between the different recording probe contacts is
168 thus a fair proxy to actual cortical tangential distance. Consistent with previous studies³⁸⁻⁴⁰,
169 noise correlations significantly decreased as the distance between the pair of signals across
170 which noise correlations were computed increased (Figure 2B). Importantly, this distance
171 effect was present for all tasks and expressed independently of the main task effect described
172 above (2-way ANOVA, Task x Distance, Task effect: $p < 0.001$; Distance effect: $p < 0.001$,
173 interaction: $p > 0.05$). Post-hoc analyses indicate that this distance effect is statistically
174 significant, for all tasks, beyond 500 μm (Wilcoxon rank sum test, Fixation task: $p < 0.001$ for
175 a cortical distance of 750 μm , $p < 0.005$ for 1000 μm ; Target detection task: $p < 0.001$ for 750
176 μm , $p < 0.001$ for 1000 μm ; Memory-guided saccade task: $p < 0.001$ for 750 μm , $p < 0.001$ for
177 1000 μm).

178



179

180 **Figure 3: Noise correlations as a function of spatial selectivity.** Average noise correlations
181 (mean +/- s.e.) across sessions, for each tasks (conventions as in figure 2), from 300ms to
182 500ms after eye fixation onset, as a function of whether noise correlations are calculated over

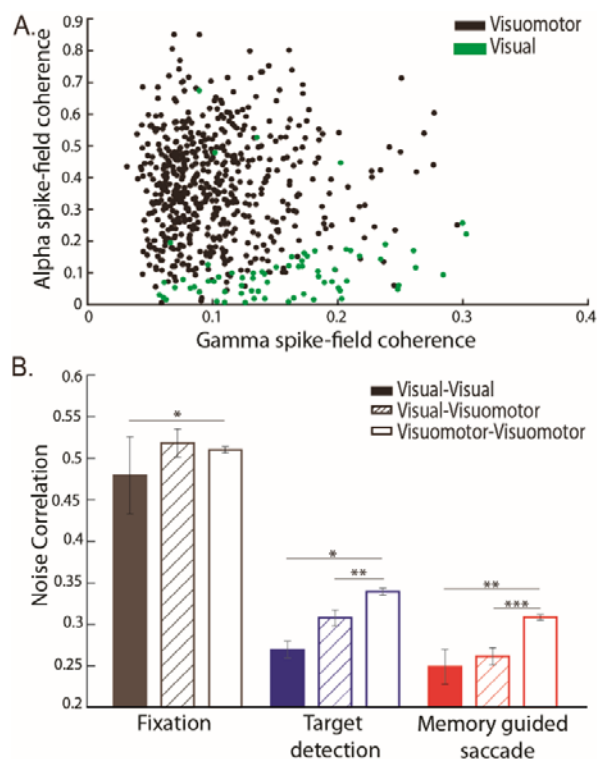
183 signals sharing the same spatial selectivity (full bars) or not (empty bars). Stars indicate
184 statistical significance following a two-way ANOVA and ranksum post-hoc tests; * $p < 0.05$;
185 ** $p < 0.01$; *** $p < 0.001$.

186

187 *Spatial selectivity effects.* The spatial selectivity of each task-related MUA in response
188 to cue presentation and saccade execution was assessed using an ANOVA (see methods). As
189 described previously^{41,42}, the receptive fields of FEF neurons are quite large and most MUA
190 responded to cue presentation or saccade execution in more than one quadrant (94% of
191 MUA). For each MUA, we further identified the visual quadrant that elicited maximal
192 neuronal response to cue or saccade execution, as well as, whenever possible the visual
193 quadrant that didn't elicit any response. In the following, and under the assumption of a
194 higher functional connectivity between pairs of MUA sharing the same spatial selectivity, we
195 compared noise correlations between pairs of neurons sharing the same preferred quadrant
196 and pairs for which the preferred quadrant of one MUA matched the unresponsive quadrant of
197 the other MUA. Consistent with previous studies³⁶, noise correlations were significantly lower
198 for different spatial selectivity pairs than for same spatial selectivity pairs (Figure 3). This
199 spatial selectivity effect was present for all tasks (2-way ANOVA, Task x Spatial selectivity,
200 Task effect: $p < 0.001$; Spatial selectivity effect: $p < 0.001$). Post-hoc analyses indicate that this
201 spatial selectivity effect is statistically significant for all tasks (Wilcoxon rank sum test,
202 Fixation task: $p < 0.001$; Target detection task: $p < 0.01$; Memory-guided saccade task:
203 $p < 0.001$). However, spatial selectivity effects were not constant across tasks, possibly
204 suggesting task-dependent functional changes in spatial selectivity based neuronal interactions
205 (Task x Spatial selectivity interaction: $p < 0.05$).

206 *Cortical layer effects.* FEF neurons are characterized by a strong visual, saccadic,
207 spatial memory and spatial attention selectivity^{30,42,43}. Previous studies have shown that pure
208 visual neurons are located in the input layers of the FEF while visuo-motor neurons are
209 located in its output layers^{42,44-48}. Independently, Buffalo et al. have shown that, in extrastriate
210 area V4, the ratio between the alpha and gamma spike field coherence discriminated between
211 LFP signals in deep (low alpha / gamma spike field coherence ratio) or superficial cortical
212 layers (high alpha / gamma spike field coherence ratio)⁴⁹. In our own data, because our
213 recordings were performed tangentially to FEF cortical surface, we have no direct way of
214 assigning the recorded MUAs to either superficial or deep cortical layers. However, the alpha
215 / gamma spike field coherence ratio provides a very reliable segregation of visual and visuo-

216 motor MUAs (figure 4A). We thus consider that, as has been described for area V4, this
217 measure allows for a robust delineation of superficial and deep layers in area FEF. In the
218 following, we computed inter-neuronal noise correlations between three different categories
219 of pairs based on their assigned cortical layer: superficial/superficial pairs, superficial/deep
220 pairs and deep/deep pairs, where superficial MUA correspond to predominantly visual, low
221 alpha/gamma spike field coherence ratio signals and deep MUA correspond to predominantly
222 visuo-motor, high alpha/gamma spike field coherence ratio signals. Noise correlations varied
223 as a function of cortical layer (Figure 4B). This cortical layer effect was present for all tasks
224 and expressed independently of the main task effect described above (2-way ANOVA, Task x
225 Cortical layer, Task effect: $p < 0.001$; Cortical layer effect: $p < 0.001$). As for spatial selectivity,
226 layer effects were not constant across tasks, possibly suggesting task-dependent functional
227 changes in within and across layer neuronal interactions (interaction: $p < 0.05$). Unexpectedly,
228 belonging to the same layer cortical layer didn't systematically maximize noise correlations.
229 Indeed, post-hoc analyses indicate significantly lower noise correlations between the
230 superficial/superficial pairs as compared to the deep/deep pairs (Wilcoxon rank sum test,
231 Fixation task: $p < 0.05$; Target detection task: $p < 0.05$; Memory-guided saccade task: $p < 0.01$).
232 Superficial/deep pairs sat in between these two categories and had significantly lower noise
233 correlations than the deep/deep pairs (Wilcoxon rank sum test, Fixation task: $p < 0.05$; Target
234 detection task: $p < 0.05$; Memory-guided saccade task: $p < 0.01$) and higher noise correlations
235 than the superficial/superficial pairs, though this difference was never significant.



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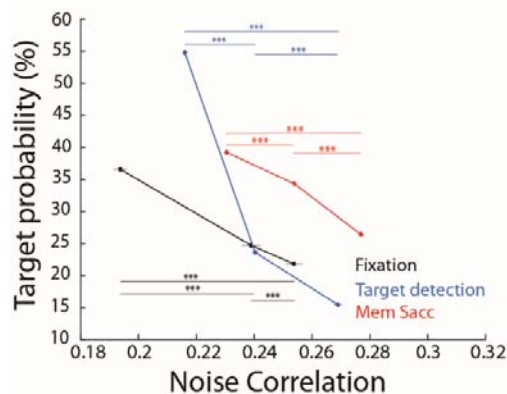
237 **Figure 4:** (A) *Distribution of alpha spike-field coherence (6-16Hz) as a function of gamma*
238 *(40-60Hz) spike-field coherence for visual and visuomotor frontal eye field sites.* Sites with
239 visual selectivity but no motor selectivity (green, putative superficial sites) demonstrated
240 stronger gamma-band spike-field coherence, whereas sites with visuomotor selectivity (black,
241 putative deep sites) demonstrated stronger alpha-band spike-field coherence. (B) *Noise*
242 *correlations as a function of pair functional selectivity.* Average of noise correlations (mean
243 +/- s.e.) across sessions, for each task (conventions as in figure 2), from 300ms to 500ms after
244 eye fixation onset, as a function of pair functional selectivity: visual-visual, visual-
245 visuomotor, visuomotor-visuomotor. Stars indicate statistical significance following a two-
246 way ANOVA and ranksum post-hoc tests; *p<0.05; **p<0.01; ***p<0.001.

247

248 Overall, these observations support the co-existence of both a global large-scale
249 change as well as a local change in functional connectivity. Indeed, task effects onto noise
250 correlations build up onto cortical distance, spatial selectivity and cortical layer effects,
251 indicating global fluctuations in the excitability of cortical circuits^{34,35}. On top of this global
252 effect, we also note more complex changes as reflected from statistical interactions between
253 Task and spatial selectivity or layer attribution effects. This points towards more local
254 changes in neuronal interactions, based on both 1) functional neuronal properties such as
255 spatial selectivity that may change across tasks⁵⁰⁻⁵³ and 2) the functional reweighing of top-
256 down and bottom-up processes^{28,30}.

257 ***Impact of the probabilistic structure of the task onto noise correlations.***

258 Up to now, we have shown that noise correlations vary as a function of cognitive
259 engagement and task demands. This suggests an adaptive mechanism that adjusts noise
260 correlations to the ongoing behavior. On task shifts, this mechanism probably builds up
261 during the early trials of the new task, past trial history affecting noise correlations in the
262 current trials. In⁵⁴ we show that, in a cued target detection task, while noise correlations are
263 higher on miss trials than on hit trials, noise correlations are also higher on both hit and miss
264 trials, when the previous trial was a miss as compared to when it was a hit. Here, one would
265 expect that on the first trials of task shifts, noise correlations would be at an intermediate level
266 between the previous and the ongoing task. Task shifts being extremely rare events in our
267 experimental protocol, this cannot be confirmed. On top of this slow dynamics carry on effect,
268 one can also expect faster dynamic adjustments to the probabilistic structure of the task. This
269 is what we demonstrate below.



270

271 **Figure 5: Noise correlations decrease as function of expected response probability.**

272 Average noise correlations (mean +/- s.e.) across sessions, for each task (conventions as in
273 figure 2), calculated on 200 ms before the target (Fixation and Target detection tasks) onset or
274 saccade execution signal onset (memory guided saccade task), as a function of expected target
275 probability. Each data point corresponds to noise correlations computed over trials of different
276 fixation onset to event response intervals, i.e. over trials of different expected response
277 probability. Stars indicate statistical significance following a two-way ANOVA and ranksum
278 post-hoc tests; *p<0.05; **p<0.01; ***p<0.001.

279

280 In each of the three tasks, target probability (saccade go signal probability in the case of
281 the memory guided saccade task) varied as a function of time. As a result, early target onset
282 trials had a different target probability than intermediate target onset trials than late target

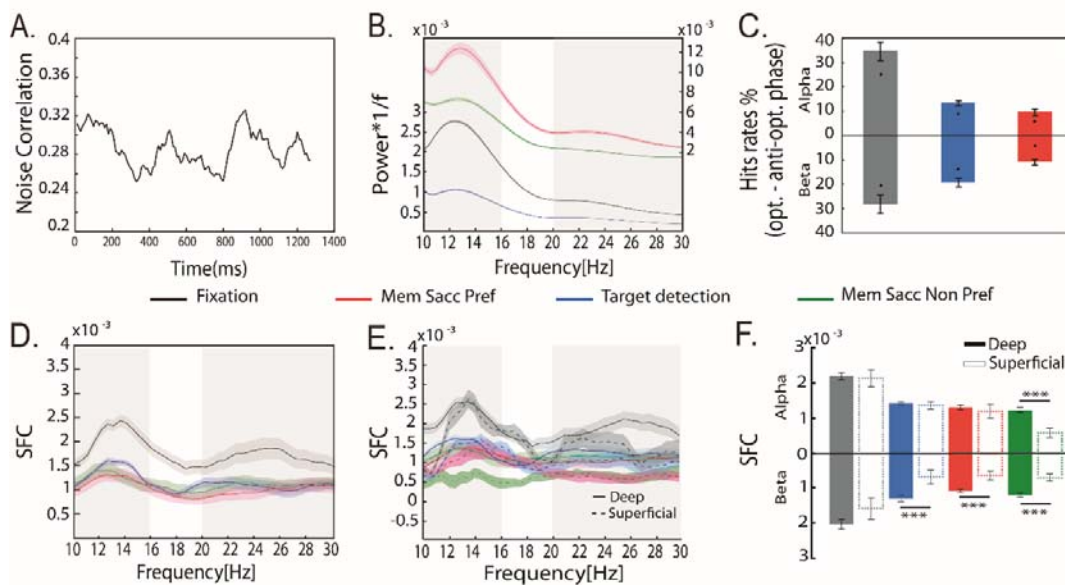
283 onset trials. Our prediction was that if monkeys had integrated the probabilistic structure of
284 the task, this should reflect onto a dynamic adjustment of noise correlations as a function of
285 target probability. Figure 5 confirms this prediction. Specifically, for all tasks, noise
286 correlations were lowest in task epochs with highest target probability (Wilcoxon non-
287 parametric test, $p < 0.001$ for all pair-wise comparisons). These variations between the highest
288 and lowest target probability epochs were highly significant and in the order of the 15% or
289 more (Fixation task: 15%, Target detection task: 40%, Memory-guided saccade task: 14%).
290 This variation range was lower than the general task effect we describe above but yet quite
291 similar across tasks. Overall, this indicates that noise correlations are dynamically adjusted to
292 the task structure, and are lowest at the time of highest behavioral demand in the trial.

293 *Rhythmic fluctuations in noise correlations.*

294 Up to now, we have described within and across task-related variations in noise
295 correlations, building up onto intrinsic connectivity influences as reflected by cortical
296 distance, spatial selectivity and layer attribution effects. Looking at noise correlations in time
297 (figure 6A) reveals an additional source of variation, namely rhythmic changes in noise
298 correlation levels, phase locked to fixation onset (Fixation and target detection task) or cue
299 presentation (Memory guided saccade task). These rhythmic fluctuations take place in two
300 distinct frequency ranges: a high alpha frequency range (10-16 Hz) and a beta frequency
301 range (20-30Hz), as quantified by a wavelet analysis (figure 6B). These oscillations can be
302 described in all of the three tasks, this in spite of an overall higher background spectral power
303 during the memory guided saccade task, both when noise correlations are calculated on trials
304 in which spatial memory was instructed towards the preferred or the non-preferred location of
305 the MUA signals (figure 6B, red and green curves respectively). Because spatial selective
306 processes are at play in the memory guided saccade task, both for trials in which spatial
307 memory is oriented towards the preferred MUA location (excitatory processes) or towards the
308 non-preferred location (inhibitory processes), we will mostly focus on the fixation and the
309 target detection tasks. When compensating the rhythmic modulations of noise correlations for
310 background power levels (assuming an equal frequency power between all conditions beyond
311 30Hz), frequency power in the two ranges of interest are higher in the fixation task than in the
312 target detection task (Friedman non-parametric test, all pairwise comparisons, $p < 0.001$), in
313 agreement with the proposal that cognitive flexibility coincides with lower amplitude beta
314 oscillations⁵⁵ and that attentional engagement coincides with lower amplitude alpha
315 oscillations^{56,57}. Importantly, these oscillations are absent from the raw MUA signals

316 (Friedman non-parametric test, all pairwise comparisons, $p > 0.2$), as well as when noise
 317 correlations are computed during the same task epochs but from neuronal activities aligned
 318 onto target presentation (or saccade go signal in the memory guided saccade task, Friedman
 319 non-parametric test, all pairwise comparisons, $p > 0.2$).

320 Importantly, in all of the three tasks, behavioral performance, defined as the proportion
 321 of correct trials as compared to error trials, varied as a function of alpha and beta noise
 322 correlation oscillations. Indeed, on a session by session basis, we could identify an optimal
 323 alpha (10-16Hz) phase for which the behavioral performance was maximized, in antiphase
 324 with a bad alpha phase, for which the behavioral performance was lowest (figure 6C). These
 325 effects were highest in the fixation task (34.6% variation in behavioral performance) and
 326 lowest though significant in the memory-guided saccade task (13.3% in the target detection
 327 task and 9.5% in the memory guided saccade task). Similarly, an optimal beta (20-30Hz)
 328 phase was also found to modulate behavioral performance in the same range as the observed
 329 alpha behavioral modulations (28.3% variation in behavioral performance in the fixation task,
 330 19.2% in the target detection task and 11% in the memory guided saccade task). As a result,
 331 Alpha and beta oscillation phase in noise correlations were predictive of behavioral
 332 performance, and the strength of these effects co-varied with alpha and beta oscillation
 333 amplitude in noise correlations, being higher in the fixation task, than in the target detection
 334 task than in the memory guided saccade task.



335

336 **Figure 6: Rhythmic fluctuations in noise correlations modulate behavioral response**
 337 **and spike-field coherence in upper input cortical layers.** (A) Single memory guided saccade

338 session example of noise correlation variations as a function of trial time. (B) 1/f weighted
339 power frequency spectra of noise correlation in time (average +/- s.e.m), for each task,
340 calculated from 300ms to 1500ms from fixation onset (Fixation and Target detection tasks) or
341 following cue offset (Memory guided saccade task). (C) Hit rate modulation by alpha (top
342 histogram) and beta (bottom histogram) noise correlation at optimal phase as compared to
343 anti-optimal phase for all three tasks (color as in (B), average +/- s.e., dots represent the 95%
344 confidence interval under the assumption of absence of behavioral performance phase
345 dependence). (D) Spike field coherence between LFP and spike data as a function of
346 frequency, time intervals as in (B). (E) Spike field coherence calculated as in (C) but as a
347 function of the layer attribution of each signal, time intervals as in (B). (F) Average SFC (+/-
348 s.e.) in alpha (10-16Hz, top histogram) and beta (20-30Hz, bottom histogram) for each task
349 and both of superficial and deep cortical layer signals (t-test, ***: $p < 0.001$).

350

351 High alpha and beta oscillations in the local field potentials (LFP) are ubiquitous and
352 are considered to reflect long-range processes. Beta oscillations have been associated with
353 cognitive control and cognitive flexibility. On the other hand, alpha oscillations are associated
354 with attention, anticipation^{56,57}, perception⁵⁸⁻⁶⁰, and working memory⁶¹. We hypothesized a
355 functional link between these LFP oscillations and the rhythmic oscillatory pattern of noise
356 correlations. Figure 6D represents spike field coherence (SFC) between spiking activity and
357 LFP signals (see Materials and Methods) computed during a 1200ms time interval starting
358 300ms after either fixation onset (Fixation and Target detection task) or cue offset (Memory
359 guided saccade task). SFC peaks at both the frequency ranges identified in the noise
360 correlation spectra, namely the high alpha range (10-16Hz) and the beta range (20-30Hz).
361 Importantly, this SFC modulation is highest for the fixation task as compared to the target
362 detection task, thus matching the oscillatory power differences observed in the noise
363 correlations. SFC are lowest in the memory guided saccade task whether considering
364 preferred or non-preferred spatial processing. This is probably due to the fact that the cue to
365 go signal interval of the memory guided saccade task involves memory processes that are
366 expected to desynchronize spiking activity with respect to the LFP frequencies of interest⁴⁹.
367 This will need to be further explored.

368 In figure 4, we show layer specific effects onto noise correlations that build up onto
369 the global task effects. An important question is whether these layer effects result from layer
370 specific changes in SFC. Figure 6E represents the SFC data of figure 6D, segregated on the
371 bases of the attribution of the MUA to either superficial or deep cortical FEF layers. While
372 SFC modulations are observed in the same frequencies of interest as in figure 6D, clear layer

373 specific differences can be observed (figure 6F). Specifically, beta range SFC are markedly
374 significantly lower in the superficial layers than in the deep layers, for both the detection task
375 and the memory guided saccade task. This points towards a selective control of correlated
376 noise in input, superficial FEF layers. In contrast, alpha range SFC are significantly lower in
377 the superficial layers than in the deep layers only in the memory guided saccade, and
378 specifically when spatial memory is oriented towards a non-preferred location. This points
379 towards overall weaker layer differences for alpha SFC. Alternatively, alpha SFC could result
380 from a different mechanism than beta SFC. This will need to be further explored. Thus in
381 spite of the fact that a comprehensive layer effect of alpha SFC is still lacking at this stage,
382 both alpha and beta noise correlation rhythmicity co-vary with 1) selective SFC modulations
383 in the alpha and beta frequency ranges (these latter being more pronounced in the superficial
384 input cortical layers than in the deeper cortical layers) as well as with 2) pronounced
385 variations in overt behavioral performance.

386

387 Overall, we thus identify a last functional oscillatory source of variations in noise
388 correlations in the alpha and beta ranges that both have an important functional relevance, as
389 they coincide with systematic variations in behavioral performance. These oscillations reflect
390 selective changes in SFC, more pronounced in the superficial than in the deep cortical layers.
391 This oscillatory source of variation in noise correlations adds up on top of the previously
392 identified sources of variation, namely global task demands and the probabilistic structure of
393 the task.

394

395 **Discussion**

396 In this work, our main goal was to examine the impact of cognitive engagement and
397 task demands onto the neuronal population shared variability as assessed from interneuronal
398 noise correlations at multiple time scales. Recordings were performed in the macaque frontal
399 eye fields, a cortical region in which neuronal noise correlations have been shown to vary as a
400 function of spatial attention²⁴ and spatial memory^{25,62}. Noise correlations were computed over
401 equivalent behavioral task epochs, prior to response production, during a delay in which eyes
402 were fixed and in the absence of any intervening sensory event or motor response. As a result,
403 any observed differences in noise correlations are to be assigned to an endogenous source of
404 shared neuronal variability.

405 Overall, we demonstrate, for the first time, that noise correlations dynamically adjust
406 to task demands at different time scales. Specifically, we show that noise correlations
407 decrease as cognitive engagement and task demands increase. These task-related variations in
408 noise correlations co-exist with within-trial dynamic changes related to the probabilistic
409 structure of the tasks as well as with long- and short-range oscillatory brain mechanisms.
410 These findings are discussed below in relation with previously reported functional and
411 structural sources of variations in noise correlation and a comprehensive model of shared
412 population neuronal variability is proposed.

413 ***Shared neuronal population response variability dynamically adjusts to the***
414 ***behavioral demands.***

415 Noise correlations have been shown to vary with learning or changes in behavioral
416 state (V1^{40,63-65}, V4^{24,66-68} and MT^{4,69,70}). For example, shared neuronal population response
417 variability was lower in V1 in trained than in naïve monkeys²⁶. More recently, Ni et al.
418 describe, within visual areas, a robust relationship between correlated variability and
419 perceptual performance, whether changes in performance happened rapidly (attention
420 instructed by a spatial cue) or slowly (learning). This relationship was robust even when the
421 main effects of attention and learning were accounted for²⁷. Here, we question whether
422 changes in noise correlations can be observed simultaneously at multiple time scales. We
423 describe two different times scales at which noise correlations dynamically adjust to the task
424 demands.

425 The first adjustment in noise correlations we describe is between tasks, that is between
426 blocked contexts of varying cognitive demand, the monkeys knowing that general task
427 requirements will be constant over a hundred of trials or more. Task performance is taken as a
428 proxy to cognitive adjustment to the task demands and negatively correlates with noise
429 correlations in the recorded population. Shared neuronal population variability measure is
430 largest in the fixation task as compared to the two other tasks, by almost 30%. The difference
431 between noise correlations in the target detection task as compared to the guided memory
432 saccade task is in the range of 2%, closer to what has been previously reported in the context
433 of noise correlation changes under spatial attention²⁴ or spatial memory manipulations.
434 Importantly, these changes in noise correlations are observed in the absence of significant
435 variations in individual neuronal spiking statistics (average spiking rates, spiking variability
436 or associated Fano factor). To our knowledge, this is the first time that such task effects are
437 described onto noise correlations. This variation in noise correlations as a function of
438 cognitive engagement and task requirements suggests an adaptive mechanism that adjusts

439 noise correlations to the ongoing behavior. Such a mechanism is expected to express itself at
440 different timescales, ranging from the task level, to the across trial level to the within trial
441 level. This is explored next.

442 It is unclear whether the transitions between high and low noise correlation states
443 when changing from one task to another are fast (over one or two trials) or slow (over tens of
444 trials). In⁵⁴, we show that noise correlations vary as a function of immediate trial past history.
445 Specifically, noise correlations are significantly higher on error trials than on correct trials,
446 both measures being higher if the previous trial is an error trial than if the previous trial is a
447 correct trial. We thus predict a similar past history effect to be observed on noise correlations
448 at transitions between tasks, and we expect for example, noise correlations to be lower in
449 fixation trials that are preceded by a target detection trial, than in trials preceded by fixation
450 trials. In our experimental design, task transitions are unfortunately rare events, precluding the
451 computation of noise correlations on these transitions.

452 However, our experimental design affords an analysis at a much finer timescale, i.e.
453 the description of a dynamical adjustment in noise correlations within trials. Specifically, we
454 show that noise correlations dynamically adjust to the probability of occurrence of a
455 behaviorally key task event associated with the reward response production (target
456 presentation on the fixation and target detection tasks or saccade go signal on the memory
457 guided saccade task). In other words, shared neuronal population response variability
458 dynamically adjusts to higher demand task epochs. As expected from the general idea that low
459 noise correlations allow for optimal signal processing^{12,71,72}, we show that, on each of the
460 three tasks, at any given time in the fixation epoch prior to response production, the higher the
461 probability of having to initiate a response, the lower the noise correlations.

462 Overall, this supports the idea that noise correlations is a flexible physiological
463 parameter that dynamically adjusts at multiple timescales to optimally meet ongoing
464 behavioral demands, as has been demonstrated in multisensory integration⁷³ and through
465 learning and attention²⁷. The mechanisms through which this possibly takes place are
466 discussed below.

467 ***Long-range and short-range mechanisms for noise correlation dynamics.***

468 As described by previous studies, in all the three tasks, interneuronal noise correlations
469 significantly decay as a function of cortical distance^{40,74,75}. Likewise, in all the three tasks,
470 noise correlations are significantly higher among neurons sharing the same spatial selectivity
471 as compared to between neurons with different spatial selectivity^{4,13,36,40,69,71,76}, supporting a

472 functional role for noise correlations⁷ in the framework of biased competition models of
473 perception⁷⁷. Last, in all three tasks, noise correlations depend on the functional selectivity of
474 the neurons. Indeed, noise correlations were lowest for visual MUA pairs, highest for
475 visuomotor MUA pairs and intermediate for visuo-visuomotor MUA pairs layers^{42,44-48}. This
476 thus points towards local layer specific noise correlation mechanisms.

477 Noise correlations are thought to vary due to global fluctuations in the excitability of
478 cortical circuits at large^{34,35} as well as to fluctuations specific to a given functional network¹⁶.
479 Alternatively, variations in shared neuronal population response variability are also proposed
480 to result from changes in local processes, due to a reweighing of local functional connectivity,
481 local excitatory/inhibitory balance and/or a change in the random shared fluctuations in the
482 pre-synaptic activity of cortical neurons^{4,16,36,37}. These two hypotheses are not mutually
483 exclusive. The question is whether the task demand effects we describe here affect noise
484 correlations irrespective of cortical distance, neuronal spatial selectivity and functional/layer
485 specificity, or whether an interaction can be identified between task demand effects and
486 cortical distance, neuronal spatial selectivity and functional/layer specificity. An absence of
487 interactions would point towards a global noise correlation modulatory mechanism while an
488 interaction would point towards more local noise correlation modulatory mechanism.

489 Our observations support the co-existence of both long-range global mechanisms and
490 short-range local mechanisms. Indeed, we identify a very clear scaling of cortical distance,
491 neuronal spatial selectivity and functional/layer specificity effects by general task demand,
492 reflecting global influences onto noise correlations. On top of these global effects, we also
493 note more complex changes in noise correlations that point towards local changes in neuronal
494 interactions. Indeed, while task demand modulates noise correlations independently of
495 cortical distance effects, we describe statistical interactions between task demand effects and
496 neuronal spatial selectivity and functional/layer specificity effects. Specifically, neuronal
497 spatial selectivity effects are more pronounced in the less demanding fixation task, than in the
498 more demanding target detection and memory-guided saccade tasks. This suggests an active
499 mechanism whereby noise correlations across neurons sharing the same spatial selectivity are
500 selectively decreased under task demand, irrespectively of changes in noise correlations in the
501 neurons of different spatial selectivity. Alternatively these selective changes in noise
502 correlation can result from task-related dynamic changes in the neuronal spatial selectivity⁵⁰⁻
503 ⁵³. On the other hand, layer specificity effects are less pronounced in the less demanding
504 fixation task, than in the more demanding target detection and memory-guided saccade tasks.

505 This suggests an active mechanism whereby noise correlations across visual neuronal pairs
506 (and to a lesser degree visuo-visuomotor neuronal pairs) are selectively decreased under task
507 demand, irrespectively of changes in noise correlations in the visuomotor neuronal pairs,
508 possibly relying on a dynamic functional reweighing of top-down and bottom-up processes
509 ^{28,30}.

510 All this taken together indicates that changes in noise correlations in the FEF as a
511 function of task demand both depend onto long-range global mechanisms and short-range
512 functional and layer specific mechanisms.

513 *Rhythmic fluctuations in noise correlations.*

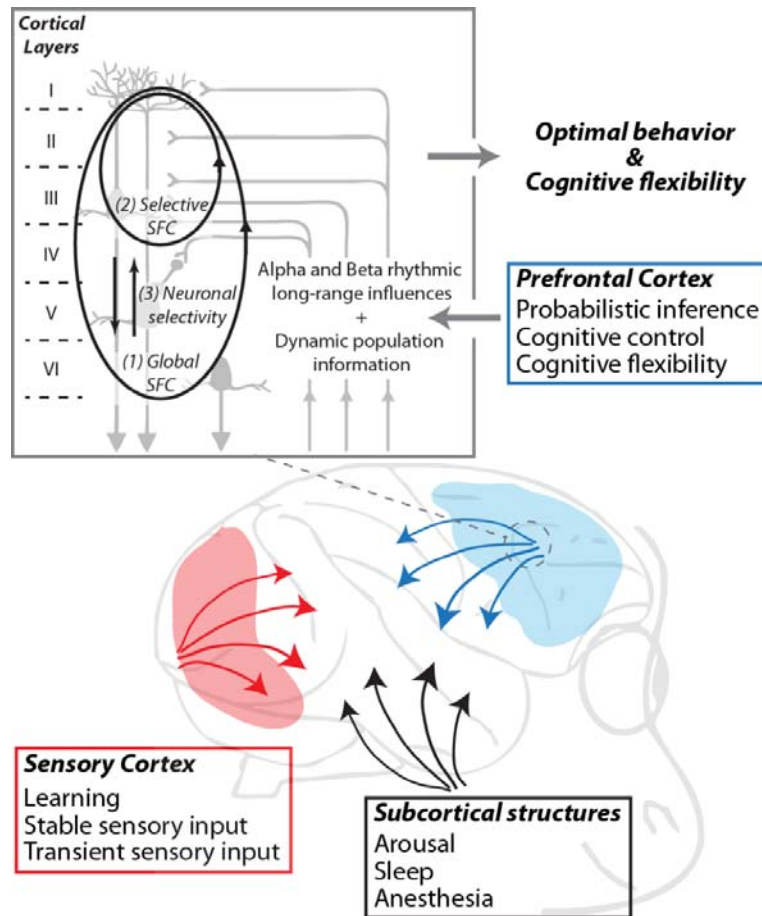
514 In the above, we describe changes in noise correlations between tasks as a function of
515 the cognitive demand, as well as within trials, as a function of the probabilistic structure of
516 each task. In addition to these task-related dynamics, we also observe rhythmic fluctuations in
517 noise correlations. These fluctuations are clearly identified in the high alpha frequency range
518 (10-16 Hz) and to a lesser extent in the low gamma frequency range (20-30Hz). To our
519 knowledge, this is the first time that such rhythmic variations in noise correlations are
520 reported. The question is whether these oscillations have a functional relevance or not.

521 From a behavioral point of view, we show that overt behavioral performance in the
522 three tasks co-vary with both the 10-16Hz and 20-30Hz noise correlation oscillations. In other
523 words, these oscillations account for more than 10% of the behavioral response variability,
524 strongly supporting a functional role for these alpha and beta oscillations.

525 From a functional point of view, attention directed to the receptive field of neurons has
526 been shown to both reduce noise correlations²⁴ and spike-field coherence in the gamma range
527 (V4⁷⁸, it is however to be noted that Engel et al. describe increased spike-field coherence in
528 V1, the gamma range under the same conditions, hinting towards areal specific differences⁷⁹).
529 In our hands, the rhythmic fluctuations in noise correlations co-exist with increased spike-
530 field coherence in the very same 10-16Hz and 20-30Hz frequency ranges we identify in the
531 noise correlations. This suggests that changes in shared neuronal variability possibly arise
532 from changes in the local coupling between neuronal spiking activity and local field
533 potentials. Supporting such a functional coupling, both the rhythmic fluctuations in noise
534 correlations and spike-field coherence in the frequencies of interest are highest in the fixation
535 task as compared to the other two tasks.

536 Beta oscillations in the local field potentials (LFP) are considered to reflect long-range
537 processes and have been associated with cognitive control and flexibility^{28,55,79–82} as well as
538 with motor control^{83–85}(for review see⁵⁵). Specifically, lower beta power LFPs has been
539 associated with states of higher cognitive flexibility. In our hands, lower beta in noise
540 correlations correspond to higher cognitive demands. We thus hypothesize a functional link
541 between these two measures, LFP oscillations locally changing spiking statistics, i.e. noise
542 correlations, by a specific spike-field coupling in this frequency range. Supporting a long-
543 range origin of these local processes (figure 7, inset), we show that spike-field coherence in
544 this beta range strongly decreases in the more superficial cortical layers as compared to the
545 deeper layers, as task cognitive demand increases. On the other hand, alpha oscillations are
546 associated with attention, anticipation^{56,57}, perception^{58–60}, and working memory⁶¹. As for beta
547 oscillations, lower alpha in noise correlations, and accordingly in spike-field coherence,
548 correspond to higher cognitive demands. In contrast with what is observed for beta spike-field
549 coherence, alpha spike-field coherence does not exhibit any layer specificity across task
550 demands. Thus overall, alpha and beta rhythmicity account for strong fluctuations in
551 behavioral performance, as well as for changes in spike-field coherence. However, beta
552 processes seem to play a distinct functional role as compared to the alpha processes, as their
553 effect is more marked in the superficial than in the deeper cortical layers. These observations
554 coincide with recent evidence that cognition is rhythmic^{86,87} and that noise correlations play a
555 key role in optimizing behavior to the ongoing time-varying cognitive demands²⁷.

556



557

558 **Figure 7:** Schematic representation of local and long-range mechanisms for the dynamic and
559 flexible adjustment of noise correlations to ongoing task demands.

560

561 **Conclusion.**

562 We thus demonstrate that noise correlations are highly dynamic, adjusting to the
563 ongoing behavioral demands, both across tasks and within trials. They are also rhythmic, time
564 varying in the alpha and beta frequency ranges. These rhythmic changes account both for
565 overt behavioral performance as well as for selective changes in spike-field coupling in
566 prefrontal superficial input cortical layers.

567 These dynamic adjustments in noise correlations correspond to a top-down control
568 (Figure 7, blue) over local neuronal processes, mediated through long-range inter-areal
569 influences. Alpha and beta rhythmicity appear to play a major role in this process, beta
570 rhythmicity being involved in a selective superficial SFC modulation (Figure 7, inset, (2)),
571 and alpha rhythmicity being involved in a more global SFC modulation (Figure 7, inset, (1)).
572 These rhythmic processes co-exist with selective changes in noise correlations as a function of

573 neuronal selectivity (Figure 7, inset, (3)). These top-down dynamic adjustments in noise
574 correlations are expected to add up onto state-related changes in noise correlations (Figure 7,
575 black), possibly mediated through neuromodulatory mechanisms, and sensory bottom-up
576 induced changes in noise correlations (Figure 7, red).

577 Overall, neuronal correlations are to be considered as a key neuronal mechanism
578 through which top-down and bottom-up neuronal influences are integrated to optimize
579 behavioral performance, along the same integrative rules as described for other neuronal
580 activity statistics.

581

582 ***Material and methods***

583 **Ethical statement**

584 All procedures were in compliance with the guidelines of European Community on
585 animal care (Directive 2010/63/UE of the European Parliament and the Council of 22
586 September 2010 on the protection of animals used for scientific purposes) and authorized by
587 the French Committee on the Ethics of Experiments in Animals (C2EA) CELYNE registered
588 at the national level as C2EA number 42 (protocole C2EA42-13-02-0401-01).

589 **Surgical procedure:**

590 As in⁵⁴, two male rhesus monkeys (*Macaca mulatta*) weighing between 6-8 kg
591 underwent a unique surgery during which they were implanted with two MRI compatible
592 PEEK recording chambers placed over the left and the right FEF hemispheres respectively
593 (figure 1a), as well as a head fixation post. Gas anesthesia was carried out using Vet-Flurane,
594 0.5 – 2% (Isoflurane 100%) following an induction with Zolétil 100 (Tiletamine at
595 50mg/ml, 15mg/kg and Zolazepam, at 50mg/ml, 15mg/kg). Post-surgery pain was controlled
596 with a morphine pain-killer (Buprecare, buprenorphine at 0.3mg/ml, 0.01mg/kg), 3 injections
597 at 6 hours interval (first injection at the beginning of the surgery) and a full antibiotic
598 coverage was provided with Baytril 5% (a long action large spectrum antibiotic, Enrofloxacin
599 0.5mg/ml) at 2.5mg/kg, one injection during the surgery and thereafter one each day during
600 10 days. A 0.6mm isomorphic anatomical MRI scan was acquired post surgically on a 1.5T
601 Siemens Sonata MRI scanner, while a high-contrast oil filled grid (mesh of holes at a
602 resolution of 1mmx1mm) was placed in each recording chamber, in the same orientation as
603 the final recording grid. This allowed a precise localization of the arcuate sulcus and
604 surrounding gray matter underneath each of the recording chambers. The FEF was defined as
605 the anterior bank of the arcuate sulcus and we specifically targeted those sites in which a
606 significant visual and/or oculomotor activity was observed during a memory guided saccade
607 task at 10 to 15° of eccentricity from the fixation point (figure 1A). In order to maximize task-
608 related neuronal information at each of the 24-contacts of the recording probes, we only
609 recorded from sites with task-related activity observed continuously over at least 3 mm of
610 depth.

611 **Behavioral task:**

612 During a given experimental session, the monkeys were placed in front of a computer
613 screen (1920x1200 pixels and a refresh rate of 60 Hz) with their head fixed. Their water
614 intake was controlled so that their initial daily intake was covered by their performance in the
615 task, on a trial by trial basis. This quantity was complemented as follows. On good
616 performance sessions, monkeys received fruit and water complements. On bad performance
617 sessions, water complements were provided at a distance from the end of the session. Each
618 recording session consisted of random alternations of three different tasks (see below and
619 figure 1b), so as to control for possible time in the session or task order effects. For all tasks,
620 to initiate a trial, the monkeys had to hold a bar in front of the animal chair, thus interrupting
621 an infrared beam. (1) **Fixation Task** (figure 1B.1): A red fixation cross ($0.7 \times 0.7^\circ$), appeared
622 in the center of the screen and the monkeys were required to hold fixation during a variable
623 interval randomly ranging between 7000 and 9500ms, within a fixation window of $1.5 \times 1.5^\circ$,
624 until the color change of the central cross. At this time, the monkeys had to release the bar
625 within 150-800 ms after color change. Success conditioned reward delivery. (2) **Target**
626 **detection Task** (figure 1B.2): A red fixation cross ($0.7 \times 0.7^\circ$), appeared in the center of the
627 screen and the monkeys were required to hold fixation during a variable interval ranging
628 between 1300 and 3400 ms, within a fixation window of $1.5 \times 1.5^\circ$, until a green squared target
629 ($0.28 \times 0.28^\circ$) was presented for 100 ms in one of four possible positions ($(10^\circ, 10^\circ)$, $(-10^\circ, 10^\circ)$,
630 $(-10^\circ, -10^\circ)$ and $(10^\circ, -10^\circ)$) in a randomly interleaved order. At this time, the monkeys had to
631 release the bar within 150-800 ms after target onset. Success conditioned reward delivery. (3)
632 **Memory-guided saccade Task** (figure 1B.3): A red fixation cross ($0.7 \times 0.7^\circ$) appeared in the
633 center of the screen and the monkeys were required to hold fixation for 500 msec, within a
634 fixation window of $1.5 \times 1.5^\circ$. A squared green cue ($0.28 \times 0.28^\circ$) was then flashed for 100ms at
635 one of four possible locations ($(10^\circ, 10^\circ)$, $(-10^\circ, 10^\circ)$, $(-10^\circ, -10^\circ)$ and $(10^\circ, -10^\circ)$). The
636 monkeys had to continue maintain fixation on the central fixation point for another 700–1900
637 ms until the fixation point disappeared. The monkeys were then required to make a saccade
638 towards the memorized location of the cue within 500-800ms from fixation point
639 disappearance, and a spatial tolerance of $4^\circ \times 4^\circ$. On success, a target, identical to the cue was
640 presented at the cued location and the monkeys were required to fixate it and detect a change
641 in its color by a bar release within 150-800 ms from color change. Success in all of these
642 successive requirements conditioned reward delivery.

643 **Neural recordings:**

644 On each session, bilateral simultaneous recordings in the two FEFs were carried out
645 using two 24- contact Plexon U-probes. The contacts had an interspacing distance of 250 μm .
646 Neural data was acquired with the Plexon Omniplex® neuronal data acquisition system. The
647 data was amplified 400 times and digitized at 40,000 Hz. The MUA neuronal data was high-
648 pass filtered at 300 Hz. The LFP neuronal data was filtered between 0.5 and 300 Hz. In the
649 present paper, all analyses are performed on the multi-unit activity recorded on each of the 48
650 recording contacts. A threshold defining the multi-unit activity was applied independently for
651 each recording contact and before the actual task-related recordings started. All further
652 analyses of the data were performed in Matlab™ and using FieldTrip⁸⁸ and the Wavelet
653 Coherence Matlab Toolbox⁸⁹, both open source Matlab™ toolboxes.

654 **Data Analysis**

655 **Data preprocessing.** Overall, MUA recordings were collected from 48 recording
656 channels on 26 independent recording sessions (13 for M1 and 13 for M2). We excluded from
657 subsequent analyses all channels with less than 5 spikes per seconds. For each session, we
658 identified the task-related channels based on a statistical change (one-way ANOVA, $p < 0.05$)
659 in the MUA neuronal activity in the memory-guided saccade task, in response to either cue
660 presentation ([0 400] ms after cue onset) against a pre-cue baseline ([-100 0] ms relative to
661 cue onset), or to saccade execution go signal and to saccade execution (i.e. fixation point off,
662 [0 400] ms after go signal) against a pre-go signal baseline ([-100 0] ms relative to go signal),
663 irrespective of the spatial configuration of the trial. In total, 671 channels were retained for
664 further analyses out of 1248 channels.

665 **Distance between recording sites.** For each electrode, pairs of MUA recordings were
666 classified along four possible distance categories: D1, spacing of 250 μm ; D2, spacing of 500
667 μm ; D3, spacing of 750 μm and D4, spacing of 1mm. These distances are an indirect proxy to
668 actual cortical distance, as the recordings were performed tangentially to cortical surface, i.e.
669 more or less parallel to sulcal surface.

670 **MUA spatial selectivity.** FEF neurons are characterized by a strong visual, saccadic,
671 spatial memory and spatial attention selectivity^{30,42,43}. We used a one-way ANOVA ($p < 0.05$)
672 to identify the spatially selective channels in response to cue presentation ([0 400] ms
673 following cue onset) and to the saccade execution go signal ([0 400] ms following go signal).

674 Post-hoc t-tests served to further order, for each channels, the neuron's response in
675 each visual quadrant from preferred (p1), to least preferred (p4). By convention, positive

676 modulations were considered as preferred and negative modulations as least preferred. For
677 example, in a given session, the MUA signal recorded on channel 1 of a probe placed in the
678 left FEF, could have as best preferred position p1 the upper right quadrant, the next best
679 preferred position p2 the lower right quadrant, the next preferred position p3 the upper left
680 quadrant and the least preferred position p4 the lower left quadrant. The MUA signal recorded
681 on channel 14 of this same probe, could have as best preferred position p1 the lower right
682 quadrant, the next best preferred position p2 the upper right quadrant, the next preferred
683 position p3 the lower left quadrant and the least preferred position p4 the upper left quadrant.
684 Positions with no significant modulation in any task epoch were labeled as p0 (no selectivity
685 for this position). Once this was done, for each electrode, pairs of MUA recordings were
686 classified along two possible functional categories: pairs with the same spatial selectivity
687 (SSS pairs, sharing the same p1) and pairs with different spatial selectivities (DSS pairs, such
688 that the p1 of one MUA is a p0 for the other MUA). For the sake of clarity, we do not
689 consider partial spatial selectivity pairs (such that the p1 of one MUA is a non-preferred, p2,
690 p3 or p4 for the other MUA).

691 ***MUA layer attribution.*** As stated above, our recordings are not tangential to cortical
692 surface. As a proxy to attribute a given recording channel to upper or lower cortical layers we
693 proceeded as follows. For each electrode and each channel, we estimated, at the time of cue
694 onset in the memory-guided saccade task (100ms-500ms from cue onset), the spike-field
695 coherence in the alpha range (6 to 16 Hz) and the gamma range (40 to 60 Hz). Based on
696 previous literature⁹⁰, we used the ratio between the alpha and gamma spike field-coherence as
697 a proxy to assign the considered LFP signals to a deep cortical layer site (high alpha / gamma
698 spike-field coherence ratio) or to a superficial cortical layer site (low alpha / gamma spike-
699 field coherence ratio). We also categorized MUA signals into visual, visuo-motor and motor
700 categories, as in Cohen et al. (2009). Briefly, average firing rates were computed in 3 epochs:
701 [-100 0] ms before cue onset (baseline), [0 200] ms after cue onset (visual), and [0 200] ms
702 before saccade onset (movement). Neurons with activity statistically significantly different
703 from the baseline (Wilcoxon rank-sum test, $P < 0.05$) after cue onset were categorized as
704 visual. Neurons with activity statistically significantly different from the baseline (Wilcoxon
705 rank-sum test, $P < 0.05$) before saccade onset were categorized as oculomotor. Neurons that
706 were active in both epochs were categorized as visuo-movement neurons. The LFP
707 categorization along the alpha to gamma spike-field coherence ratio strongly coincided with
708 the classification of the MUA signals into purely visual sites (low alpha and gamma spike-

709 field coherence ratio, input FEF layers) and visuo-motor sites (high alpha and gamma spike-
710 field coherence ratio, output FEF layers, figure 4).

711 **Noise Correlations.** The aim of the present work is to quantify task effects onto the
712 spiking statistics of the FEF spiking activity during equivalent task-fixation epochs. The
713 statistics that we discuss is that of noise correlations between the MUA activities on the
714 different simultaneously recorded signals. For each channel, and each task, intervals of
715 interest of 200ms were defined during the fixation epoch from 300 ms to 500 ms from eye
716 fixation onset. Specifically, for each channel i , and each trial k , the average neuronal response
717 $r_i(k)$ for this time interval was calculated and z-score normalized into $z_i(k)$, where $z_i(k)=r_i(k)-$
718 μ_i/std_i and μ_i and std_i respectively correspond to the mean firing rate and standard deviation
719 around this mean during the interval of interest of the channel of interest i . This z-score
720 normalization allows to capture the changes in neuronal response variability independently of
721 changes in mean firing rates. Noise correlations between pairs of MUA signals during the
722 interval of interest were then defined as the Pearson correlation coefficient between the z-
723 scored individual trial neuronal responses of each MUA signal over all trials. Only positive
724 significant noise correlations are considered, unless stated otherwise. In any given recording
725 session, noise correlations were calculated between MUA signals recorded from the same
726 electrode, thus specifically targeting intra-cortical correlations. This procedure was applied
727 independently for each task. Depending on the question being asked, noise correlations were
728 either computed on activities aligned on fixation onset, or on activities aligned on target
729 (Fixation and Target detection task) or saccade execution (memory guided saccade task)
730 signals.

731 In order to control for the fact that the observed changes in noise correlations cannot
732 be attributed to changes in other firing rate metrics, several statistics were also extracted, from
733 comparable task epochs, from 300 to 500ms following trial initiation and fixation onset. None
734 of these metrics were significantly affected by the task. Specifically, we analyzed (a) mean
735 firing rate (ANOVA, $p>0.5$), (b) the standard error around this mean firing rate (ANOVA,
736 $p>0.6$), and (c) the corresponding Fano factor (ANOVA, $p>0.7$). These data, reproducing
737 previous reports^{54,91} are not shown.

738 **Oscillations in noise correlations.** To measure oscillatory patterns in the noise
739 correlation time-series data, we computed, for each task, and each session ($N=12$), noise
740 correlations over time (over successive 200ms intervals, sliding by 10ms, running from
741 300ms to 1500ms following eye fixation onset for Fixation and Target detection tasks and

742 from 300ms to 1500ms following cue offset form Memory-guided saccade task). A wavelet
743 transform⁸⁸ was then applied on each session's noise correlation time series. Statistical
744 differences in the noise correlation power frequency spectra were assessed using a non-
745 parametric Friedman test. When computing the noise correlations in time, we equalized the
746 number of trials for all tasks and all conditions so as to prevent any bias that could be
747 introduced by unequal numbers of trials. To control that oscillations in noise correlations in
748 time cannot be attributed to changes in spiking activity, a wavelet analysis was also run onto
749 MUA time series data (data not shown).

750 ***Spike field Coherence (SFC)***. In our study monkeys performed three tasks with
751 different task engagement levels. For each selected channel, SFC spectra were calculated
752 between the spiking activity obtained in one channel and the LFP activity from the next
753 adjacent channel in the time interval running from 300ms to 1500ms following eye fixation
754 onset (Fixation and Target detection task) or cue offset (Memory guided saccade task). We
755 used a single Hanning taper and applied convolution transform to the Hanning-tapered trials.
756 We equalized the number of trials for all tasks so as to prevent any bias that could be
757 introduced by unequal numbers of trials. We used a 4 cycles length per frequency. The
758 memory guided saccade task is known to involve spatial processes during the cue to target
759 interval that bias spike field coherence. In this task, SFC was thus measured separately for
760 trials in which the cued location matched the preferred spatial location of the channel and
761 trials in which the cued location did not match the preferred spatial location of the channel.
762 Statistics were computed across channels x sessions, using a non-parametric Friedman test.

763

764 ***Modulation of behavioral performance by phase of noise correlation alpha and beta***
765 ***rhythmicity***. To quantify the effect of noise correlation oscillations onto behavioral
766 performance, we used a complex wavelet transform analysis (Fieldtrip, Oostenveld et al.
767 2011) to compute, for each session and each task, in the noise correlations, the phase of the
768 frequencies of interest (alpha / beta) following eye fixation onset (for the Fixation and Target
769 detection tasks) or cue offset (for the Memory guided saccade task). For each session, we
770 identified hit and miss trials falling at zero phase of the frequency of interest ($\pm \pi / 140$) with
771 respect to target presentation or fixation point offset time. In the fixation task, premature
772 fixation aborts by anticipatory manual response or eye fixation failure were considered as
773 misses. Hit rates (HR) were computed for this zero phase bin. We then shifted this phase
774 window by $\pi / 70$ steps and recalculated the HR, repeating this procedure to generate phase-
775 detection HR functions, across all phases, for each frequency of interest⁹². For each session,

776 the phase bin for which hit rate was maximal was considered as the optimal phase. The effect
777 of a given frequency (alpha or beta) onto behavior corresponds to the difference between HR
778 at this optimal phase and HR at the anti-optimal phase (optimal phase + π). To test for
779 statistical significance, observed hit/miss phases were randomized across trials so as to shuffle
780 the temporal relationship between phases and behavioral performance. This procedure was
781 repeated 1000 times. 95% CI was then computed and compared to the observed behavioral
782 data.
783
784

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796

797 ***Authors contributions***

798 Conceptualization, S.B.H. S.B.H.H. and C.G.; Methodology, S.B.H., S.B.H.H., C.G., E.A.,
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