

1 **Title (13 words; 50 words max)**

2 Frequency shifts and depth dependence of premotor beta
3 band activity during perceptual decision-making

4

5 **Abbreviated Title (50 char; 50 char max)**

6 Premotor beta band activity during decision-making

7

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17

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19

20 **AUTHOR CONTRIBUTIONS**

21 CC and KVS designed the experiments. CC performed the experiments, trained animals, and
22 performed neurophysiological recordings. IEB and CC performed analyses together. IEB, CC,
23 and KVS all wrote the paper. KVS was involved in all aspects of the manuscript.

24

25 **CONFLICT OF INTEREST**

26 KVS is a consultant for Neuralink Corp. and is on the scientific advisory board for CTRL-Labs
27 Inc., MIND-X Inc., Inscopix Inc. and Heal Inc.

28

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37

38 **WORD COUNTS**

39 Abstract - (243 words; 250 words max)

40 Significance Statement - (118 words; 120 words max)

41 Introduction - (647 words; 650 max)

42 Discussion - (1476 words; 1500 words max)

43 **ABSTRACT (243 words; 250 words max)**

44

45 Neural activity in the premotor and motor cortex shows prominent structure in the beta
46 frequency range (13-30 Hz). Currently, the behavioral relevance of beta band activity (BBA) in
47 premotor and motor regions is not well understood. The underlying source of motor BBA and
48 how it changes as a function of cortical depth is also unknown. Here, we addressed these
49 unresolved questions by investigating BBA recorded using laminar electrodes in the dorsal
50 premotor cortex (PMd) of two male rhesus macaques performing a visual reaction time (RT)
51 reach discrimination task. We observed robust BBA before and after the onset of the visual
52 stimulus but not during the arm movement. While post-stimulus BBA was positively correlated
53 with RT throughout the beta frequency range, pre-stimulus correlation varied by frequency. Low
54 beta frequencies (~15 to 20 Hz) were positively correlated with RT and high beta frequencies
55 (~25 to 30 Hz) were negatively correlated with RT. Simulations suggested that these frequency-
56 dependent correlations could be due to a shift in the component frequencies of the pre-stimulus
57 BBA as a function of RT, such that faster RTs are accompanied by greater power in high beta
58 frequencies. We also observed a laminar dependence of BBA, with deeper electrodes
59 demonstrating stronger power in low beta frequencies both pre- and post-stimulus. The
60 heterogeneous nature of BBA and the changing relationship between BBA and RT in different
61 task epochs may be a sign of the differential network dynamics involved in expectation,
62 decision-making, and motor preparation.

63

64 **SIGNIFICANCE STATEMENT (118 words; 120 words max)**

65

66 Beta band activity (BBA) has been implicated in motor tasks, in disease states, and as a signal
67 for brain-machine interfaces. However, the functional role of BBA and its laminar organization in
68 motor cortex are poorly understood. Here we addressed these unresolved issues using
69 simultaneous recordings from multiple cortical layers of the motor cortex of monkeys performing
70 a decision-making task. Our key finding is that BBA is not a monolithic signal. Instead, BBA
71 seems to be composed of at least two frequency bands. The relationship between BBA and
72 eventual behavior, such as reaction time, also dynamically changes depending on task epoch.
73 We also found that BBA is laminarly organized, with greater power in deeper electrodes for low
74 beta frequencies.

75

76 **INTRODUCTION (647 words; 650 max)**

77

78 Fluctuations in the beta (13-35 Hz) range of the local field potential (LFP) and spiking activity
79 are consistently observed in monkeys performing instructed delay (Sanes and Donoghue, 1993;
80 Zhang et al., 2008; Kilavik et al., 2012, 2013; Stetson and Andersen, 2014; Khanna and
81 Carmena, 2017) and cognitive tasks (Murthy and Fetz, 1992; Lee, 2003; Buschman and Miller,
82 2007; Pesaran et al., 2008; DePasquale and Graybiel, 2015; Sherman et al., 2016; Haegens et
83 al., 2017). Other studies demonstrated prominent BBA in humans performing motor and
84 cognitive tasks (Rubino et al., 2006; Tzagarakis et al., 2010; Zaepffel et al., 2013). Clinical
85 studies suggest that BBA changes with age (Rossiter et al., 2014b), is modulated in disease
86 states (Brown, 2006; Brittain et al., 2014; Rossiter et al., 2014a; Proudfoot et al., 2017), and

87 may be useful for brain machine interfaces (Bai et al., 2008; Flint et al., 2013; So et al., 2014;
88 Gilja et al., 2015; Stavisky et al., 2015; Pandarinath et al., 2017a). Despite insights gained about
89 BBA, questions about its role and origin still remain. Here, we focus on two unresolved
90 questions.

91
92 First, we wanted to understand the relevance of BBA in the motor system for decision-
93 making. Three hypotheses have been proposed for the role of BBA in the motor system –
94 postural holding, maintenance of the current state, and attention – each making specific
95 predictions relating BBA and RT (Figure 1, Khanna and Carmena, 2015). The postural holding
96 hypothesis posits that BBA is related to keeping the hand still during the hold period of
97 instructed delay tasks (Baker et al., 1999; Kristeva et al., 2007). A second hypothesis suggests
98 that BBA represents the desire to maintain the current state of being (e.g., resisting start of
99 movement) (Gilbertson et al., 2005; Pogosyan et al., 2009; Engel and Fries, 2010). The
100 attentional hypothesis emerged from the study of reach-target selection tasks and suggests that
101 BBA reflects attention (Bouyer et al., 1987; Murthy and Fetz, 1992; Zhang et al., 2008; Saleh et
102 al., 2010). Here, we addressed the behavioral relevance of BBA by examining the relationship
103 between RT and BBA recorded from PMd of two monkeys (Zhang et al., 2008; Saleh et al.,
104 2010; Tzagarakis et al., 2010; Kilavik et al., 2012; Khanna and Carmena, 2017). The monkeys
105 performed a visual reach decision-making task that engaged their attention, involved the
106 somatomotor system, and induced significant RT variability beyond the variability induced by the
107 different stimulus difficulties.

108
109 Second, we wanted to improve on the currently vague description of the laminar
110 organization of BBA in premotor and motor cortex. Some studies suggest that neurons in
111 deeper cortical layers of M1 (especially layer V) are involved in the generation of BBA (Wetmore
112 and Baker, 2004; Chen and Fetz, 2005; Roopun et al., 2006; Yamawaki et al., 2008). Others
113 suggest that all cortical layers in M1 are involved in BBA (Kondabolu et al., 2016; Sherman et
114 al., 2016). Identifying how BBA changes as a function of cortical depth is needed for developing
115 the next generation of computational models (Kopell et al., 2011; Lee et al., 2013; Bhatt et al.,
116 2016; Sherman et al., 2016). To study the laminar organization of BBA, we used multi-contact
117 electrodes that provided simultaneous recordings across different cortical depths.

118
119 We observed that both pre- and post-stimulus BBA was correlated to RT, thus ruling out
120 the postural holding hypothesis. Post-stimulus BBA was positively correlated with RT throughout
121 the 13-35 Hz range, while the correlation between RT and pre-stimulus BBA was positive in the
122 low beta frequencies (~15 to 20 Hz) and negative in the high beta frequencies (~25 to 35 Hz).
123 Through simulation, we identified that frequency-dependent correlations between RT and pre-
124 stimulus LFP power spectra could potentially emerge from a shift in pre-stimulus BBA to higher
125 frequencies for faster RTs. We also found that power spectra of LFPs recorded in deeper
126 electrodes demonstrated more power in low beta frequencies both pre- and post-stimulus.

127
128

129 **METHODS**

130

131 **EXPERIMENTAL DESIGN:**

132

133 Here we provide a brief description of the experimental design. Additional details about training
134 and surgery in addition to a description of single neuron responses during the various epochs
135 are found in a previous study (Chandrasekaran et al., 2017). This study focuses on analysis of
136 the pre-stimulus and post-stimulus LFP recorded during the same experiments.

137

138 **Subjects:** Our experiments were conducted using two adult male macaque monkeys (*Macaca*
139 *mulatta*; Monkey T, seven years, 14 kg; O, eleven years, 15.5 kg) trained to reach for visual
140 targets for a juice reward. Monkeys were housed in a social vivarium with a normal day/night
141 cycle. The protocols for our experiments were approved by the Stanford University Institutional
142 Animal Care and Use Committee. We initially trained monkeys to come out of the cage and sit
143 comfortably in a chair. After initial training, we performed sterile surgeries during which monkeys
144 were implanted with head restraint holders (Crist Instruments, cylindrical head holder) and
145 standard recording cylinders (Crist Instruments). Cylinders were centered over caudal PMd (+
146 16, 15 stereotaxic coordinates) and placed surface normal to the cortex. We covered the skull
147 within the cylinder with a thin layer of dental acrylic/palacos.

148

149 **Apparatus:** The general set-up for the experiments is shown in [Fig. 2a](#). Monkeys sat in a
150 customized chair (Crist Instruments, Snyder Chair) with the head restrained via the surgical
151 implant. The arm not used for reaching was gently restrained using a tube and a cloth sling.
152 Experiments were controlled and data collected under a custom computer control system (xPC
153 target and Psychophysics Toolbox). Stimuli were displayed on an Acer HN2741 computer
154 screen placed approximately 30 cm from the monkey. A photodetector (Thorlabs PD360A) was
155 used to record the onset of the visual stimulus at a 1 ms resolution. Each session we taped a
156 small reflective hemispherical bead (11.5 mm, NDI Digital passive spheres) to the middle digit of
157 the right hand (left hand for Monkey O). The bead was taped 1 cm from the tips of the fingers,
158 and the position of this bead was tracked optically in the infrared (60 Hz, 0.35 mm root mean
159 square accuracy; Polaris system; Northern Digital). Eye position was tracked with an overhead
160 infrared camera (estimated accuracy of 1°, Iscan, Burlington, MA). To get a stable eye image for
161 the overhead infrared camera which acquires the eye image, an infrared mirror transparent to
162 visible light was positioned at a 45° angle (facing upwards) immediately in front of the nose. This
163 mirror reflected the image of the eye in the infrared range while letting visible light pass through.
164 A visor placed around the chair prevented the monkey from bringing the bead to his mouth or
165 touching the infrared mirror or the juice tube.

166

167 **Task structure:** Experiments consisted of a sequence of trials, which each lasted a few
168 seconds; successful trials resulted in a juice reward, and unsuccessful trials resulted in a time-
169 out lasting 2-4 seconds. An example trial timeline is shown in [Fig. 2b](#). Monkeys used their
170 unrestrained arm (Monkey T used his right arm, Monkey O used his left arm) to reach to touch
171 either red or green targets based on the dominant color in a central, static checkerboard cue
172 composed of isoluminant red and green squares. For every trial, the monkey placed his

173 unrestrained arm on a central target (diameter = 24 mm) and fixated on a small white cross
174 (diameter = 6 mm). After ~350-400 ms had elapsed, two isoluminant colored targets appeared
175 100 mm to the right and left of the central target. The target configuration was randomized so
176 that colors were not always tied to reach directions: sometimes the red target was on the left
177 and green on the right, while other trials had the opposite configuration. After an additional hold
178 period (varying from 400 to 900 ms), a static checkerboard cue (15 x 15 grid of squares; each
179 square 2.5 mm x 2.5 mm) composed of isoluminant red and green squares appeared on the
180 screen around the fixation cross (example stimuli are shown in Fig. 2c). The monkeys reached
181 for the target whose color matched the dominant color in the central checkerboard cue. For
182 example, when there was more green than red in the central checkerboard cue, the monkey
183 had to choose the green target. To “choose” a target, the animals moved their hand from the
184 central hold point and stably held a target for a short duration (minimum of 200 ms). The task
185 was an RT paradigm, so the monkeys were free to initiate their reach whenever they felt there
186 was sufficient evidence for them to provide a response. We did not impose any delayed
187 feedback procedure in this task such as a delay between the time of reward and the completion
188 of a reach for a correct target. The juice reward was provided to the monkey immediately after
189 the monkey provided a correct response (Roitman and Shadlen, 2002).

190
191 We parameterized the checkerboard cue at several different levels from almost fully red
192 to almost fully green. We used 14 levels of red (ranging from 11 red squares to 214 red
193 squares) in the central checkerboard cue. Each level of red had a complementary green level
194 (e.g., 214 R, 11 G; and 214 G, 11 R-squares). This defined seven levels of color coherence
195 (defined as $C = \frac{100 \times |R-G|}{R+G}$), ranging from 4 – 90%. The corresponding signed color coherence
196 was estimated without taking the absolute value of the difference ($SC = \frac{100 \times (R-G)}{R+G}$). For Monkey
197 T, we used a uniform distribution of hold period durations between the onset of the targets and
198 the onset of the checkerboard cue. Monkey O attempted to anticipate the checkerboard cue
199 onset. To minimize this anticipation and reduce predictability we used an exponential hold
200 period duration (400 – 800 ms) between the onset of the targets and the onset of the
201 checkerboard cue.

202
203 **Electrophysiological Recordings:** Stereotactic coordinates, known response properties of
204 PMd and M1, and neural responses to muscle palpation served as our guides for
205 electrophysiological recordings. We placed the chambers surface normal to the cortex to align
206 with the skull of the monkey, and recordings were performed perpendicular to the surface of the
207 brain. Recordings were made anterior to the central sulcus, lateral to the spur of the arcuate
208 sulcus, and lateral to the precentral dimple. For both monkeys, we confirmed our estimate of the
209 upper and lower arm representation by repeated palpation at a large number of sites to identify
210 muscle groups associated with the sites. Monkey T used his right arm to perform tasks while O
211 used his left arm. Recordings were performed in PMd and M1 contralateral to the arm used by
212 the monkey.

213
214 We performed linear multi-contact electrode (U-probe) recordings in the same manner
215 as single electrode recordings with some minor modifications. We used a slightly sharpened

216 guide tube to allow the U-probe to penetrate the Dura more easily. We also periodically scraped
217 away any overlying tissue on the dura under anesthesia. Sharp guide tubes and scraping away
218 dura greatly facilitated penetration of the U-probe. We typically penetrated the brain at very slow
219 rates (~2 - 5 $\mu\text{m/s}$). Once we felt that we had a reasonable sample population of neurons
220 potentially spanning different cortical layers, we stopped and waited for 45-60 min for the
221 neuronal responses to stabilize. The experiments then progressed as usual. We used 180 μm
222 thick, 16-electrode U-probes with an inter-electrode spacing of 150 μm ; electrode contacts were
223 ~100 k Ω in impedance.

224
225 We attempted to minimize the variability in U-probe placement on a session-by-session
226 basis so that we could average across sessions. Our approach was to place the U-probe so that
227 the most superficial electrodes (electrodes 1, 2 on the 16 channel probe) were able to record
228 multi-unit spiking activity. Any further movement of the electrode upwards resulted in the spiking
229 activity for those electrodes disappearing and a change in the overall activity pattern of the
230 electrode (suppression of overall LFP amplitudes). Similarly, driving the electrodes deeper
231 resulted in multiphasic extracellular waveforms and also a change in auditory markers which
232 were characterized by decreases in overall signal intensity and frequency content; both markers
233 suggested that the electrode entered white matter (Cooper et al., 1969). We utilized these
234 physiological markers as a guide to place electrodes and thereby minimize variability in
235 electrode placement on a session-by-session basis. Recording yields and this careful electrode
236 placement were in general better in monkey T (average of ~16 units per session) than monkey
237 O (average of ~9 units per session). Random placement of U-probes on a day-to-day basis
238 would flatten out the average visuomotor index and dilute or entirely remove significant
239 differences in the discrimination time differences between superficial and deep electrodes.

240
241 The insertion technique necessitated a careful watch over the electrode while lowering to
242 ensure that it did not bend, break at the tip or excessively dimple the dura. We therefore were
243 unable to use a grid system to precisely localize the location of the U-probes on different days
244 and to provide a map of how laminar profiles change in the rostrocaudal direction.

245
246 **Local field potentials:** LFP recordings in T were performed using a 2 KHz sampled signal. We
247 then resampled this signal at 1 KHz and performed subsequent spectral analysis on appropriate
248 time epochs. For monkey O, two methods were used. For 17 of the sessions, we recorded LFP
249 at 2 KHz, as in T. For the remaining 27 sessions, we recorded broadband extracellular activity
250 at 30 KHz. We resampled this broadband extracellular signal at 1 KHz and then again used it for
251 subsequent spectral analysis. All resampling was performed using the MATLAB resample
252 command that first applies a delay compensating low pass filter and then subsequently
253 resamples the data avoiding antialiasing.

254
255 **Reaction Time:** Reaction time (RT) is defined as the time between stimulus onset and the
256 monkey's selection of a target. RT is described in units of milliseconds. A reaction time less than
257 or equal to 300 ms indicates that the monkey did not incorporate the presented stimulus into his
258 response. These trials are not representative of decision-making based on the provided
259 stimulus and were therefore removed from our analysis.

260

261 **STATISTICAL ANALYSIS:**

262

263 **Psychometric curves for accuracy:** For the analysis of the behavior, we used the same 24
264 sessions for monkey T (47,483 trials) and 44 sessions for monkey O (70,250 trials) from which
265 we examined electrophysiological data. Fits to psychometric curves and RT regressions were
266 performed on a per-session basis and then averaged over sessions. The behavior of an
267 average session was estimated from ~1500 trials. RT was estimated for each session by
268 including both correct and incorrect trials for each signed color coherence.

269

270 We fit psychometric curves that describe how discrimination accuracy changed as a
271 function of color coherence. For every experiment, we estimated the monkey's sensitivity to the
272 checkerboard cue by estimating the probability (p) of a correct choice as a function of the color
273 coherence of the checkerboard cue (C). We used the `psignifit` toolbox to fit this accuracy
274 function using a Weibull cumulative distribution function (Wichmann and Hill, 2001):

275

$$p(c) = 1 - 0.5e^{-(c/\alpha)^\gamma}$$

276

277 The discrimination threshold, α , is the color coherence level at which the monkey would make
278 81.6% correct choices. The second parameter, γ , describes the slope of the psychometric
279 function. The mean α parameter across sessions was used as the threshold. We fit threshold and
280 slope parameters on a session-by-session basis and averaged the estimates. The mean and
281 standard deviation of the threshold estimates are reported in [Fig. 2d](#).

282

283 **RT vs. coherence:** To examine if RT changed with color coherence, we adopted the procedure
284 from (Roitman and Shadlen, 2002) and used a linear regression between RT and log
285 coherence.

286

$$RT(c) = \text{intercept} + a_c \log_e(c)$$

287

288 We fit this regression model ([Fig. 2e](#)) with a_c as the slope of the regression.

289

290 **Power spectra:** To estimate the power spectra, we used the Chronux toolbox for MATLAB
291 (Mitra and Bokil, 2008; Mitra et al., 2016) which implements the multi-taper spectral estimation
292 method, with a time-bandwidth product of three and with five leading tapers. Choice of other
293 tapers did not result in any changes in our conclusions. We removed the DC offset from the LFP
294 time series and used a second-order IIR notch filter to remove line noise (Mitra and Bokil, 2008;
295 Mitra et al., 2016). Line noise, which is centered at 60 Hz, arises from radiative electrical pickup
296 from lights and power sockets, currents due to ground loops, and currents induced by magnets
297 in DC power supplies in the experimental setup (Mitra and Bokil, 2008). We centered the filter at
298 60 Hz and set the quality factor (related to the filter bandwidth) to 35. The power spectra have
299 arbitrary units (A.U.) before they are normalized.

300

301 We only plot the power spectra from 2 Hz to 50 Hz. We saw no significant activity in the

302 range of 50 Hz to 500 Hz. For the normalized power spectra from 2 to 90 Hz, the Z scores from
303 50 Hz through 90 Hz were below zero for all analyzed periods of the task (pre-stimulus, post-
304 stimulus, and post-movement).

305

306 **Normalization of power spectra:** For each trial, we normalized the power spectrum over all
307 power values (for each frequency for all electrodes) from all trials in that session. We calculated
308 the Z Score by subtracting the mean (of all power values from all trials in that session) from
309 each point and dividing by the standard deviation.

310

311 **Standard Error:** Standard error was defined as s/\sqrt{n} , where s is the standard deviation of the
312 power spectra for several sessions with respect to the sessions, and n is the number of
313 sessions. Standard error is shown in shading in plots of power spectra.

314

315 **Split into RT quantiles:** We first calculated the breaks for the RT percentiles for that monkey
316 on that session, separating the trials with RTs either greater than 85% of trials in that session
317 and the trials with RTs smaller than 15% of trials in that session. We then averaged the
318 normalized power spectra over trials within each RT quantile and finally averaged over all
319 electrodes within each quantile. Then within each quantile, we averaged over all sessions,
320 giving two normalized grand average power spectra each over all trials, channels, and sessions.

321

322 **Correlation between BBA and RT:** For each electrode, per session of data (several trials), we
323 computed the partial Spearman correlation between the normalized power at each frequency
324 with reaction time, controlling for the coherence of the checkerboard. We then averaged the
325 correlations over all electrodes and all sessions. Significance of the correlation values were
326 adjusted using the Benjamini & Hochberg (Benjamini and Hochberg, 1995) procedure for
327 controlling the false discovery rate (FDR) of a family of hypothesis tests (Groppe, 2016).

328

329 We decided to do a partial correlation in order to control for the confounding variable, the
330 coherence of the checkerboard, which we know affects the RT and also likely affects the LFP
331 power spectra and would therefore have otherwise given misleading correlation values.

332

333 **Simulating Relationships between BBA and RT:** In order to clarify the mathematical
334 relationship between BBA and RT, we ran a series of simulations (Fig. 6). We first randomly
335 generated an RT value within the range typically observed for our monkeys. Then, we created a
336 variety of LFP signals in which the frequency and amplitude were either constant or related in
337 some way to the RT that was generated. The relationship between frequency, amplitude, and
338 RT are specified in the equations below, where randn signifies a random number drawn from
339 the normal distribution. Within each frequency and amplitude relationship, we generated one
340 thousand RTs and corresponding LFP signals. We then calculated the power spectrum for each
341 simulated LFP signal before correlating the power spectra to the randomly generated RT. Each
342 frequency and amplitude relationship resulted in a different correlation with RT. The equations
343 below match the panels shown in Fig. 6.

344

345 i: Frequency = $28 + 1.2 \cdot \text{randn} + .003 \cdot \text{RT}$; Amplitude = 1;

346 **ii:** Frequency = $28 + 1.2 \cdot \text{randn} - .003 \cdot \text{RT}$; Amplitude = 1;
347 **iii:** Frequency = $28 + 1.2 \cdot \text{randn} - .003 \cdot \text{RT}$; Amplitude = $.3 + 5e-6 \cdot \text{RT}$;
348 **iv:** Frequency = $28 + 1.2 \cdot \text{randn} - .003 \cdot \text{RT}$; Amplitude = $.3 - 5e-6 \cdot \text{RT}$;
349 **v:** Frequency = $28 + 1.2 \cdot \text{randn}$; Amplitude = $.3 + 5e-6 \cdot \text{RT}$;
350 **vi:** Frequency = $28 + 1.2 \cdot \text{randn}$; Amplitude = $.3 - 5e-6 \cdot \text{RT}$;
351
352
353
354
355
356

357 RESULTS

358

359 Two trained monkeys (T and O) discriminated the dominant color of a central, static
360 checkerboard cue composed of mixtures of red and green squares and used an arm movement
361 to report the decision (Fig. 2a, Coallier et al., 2015). Fig. 2b depicts a trial timeline. The trial
362 began when the monkey touched the center target and fixated on the cross. After a variable
363 target viewing period, the red-green checkerboard cue appeared. The task of the monkey was
364 to make an arm movement toward the target (red vs. green) that matched the dominant color of
365 the checkerboard cue. We parameterized difficulty of the discrimination (example stimuli shown
366 in Fig. 2c) by a color coherence measure (C) defined as the absolute difference in the number
367 of red and green squares normalized by the total number of squares in the checkerboard ($C =$
368 $100 * |R - G| / (R + G)$). A corresponding signed color coherence measure (SC) is defined as $SC =$
369 $100 * (R - G) / (R + G)$. We previously reported the behavior of the monkeys while they performed
370 this task (Chandrasekaran et al., 2017). Here we present the psychometric and chronometric
371 curves for the sessions where we examined the LFP.

372

373 On average across sessions, decreases in color coherence resulted in more errors (Fig.
374 2d). We fit the proportion correct as a function of unsigned coherence (C) using a weibull
375 function to estimate slopes and thresholds (average R^2 , T: .99 (over 24 sessions, 47483 trials),
376 O: .99 (over 44 sessions, 70250 trials), slope (β), $M \pm SD$ over sessions, T: 1.30 ± 0.16 , O: $1.26 \pm$
377 0.15). Monkey T displayed more sensitivity than Monkey O (thresholds are computed on a per-
378 session basis and averaged over sessions at 81.6% correct, ($M \pm SD$): T, $9.87\% \pm 1.12\%$, O:
379 $15.05 \pm 1.79\%$, two-tailed test, Wilcoxon rank sum comparing median thresholds, $p = 1.292e-11$).

380

381 A decrease in color coherence also resulted in a slower mean RT (Fig. 2e, using a
382 regression to test if mean RT increases as \log_e coherence decreases (harder stimulus
383 difficulties as in (Roitman and Shadlen, 2002); average R^2 , T: 0.94, O: 0.59; slope of regression:
384 $M \pm SD$ over sessions, T: -41.1 ± 6.3 ms/ \log_e coherence (%), O: -8.6 ± 4.5 ms/ \log_e coherence (%)).
385 Monkey T had a larger range of RTs compared to Monkey O (Comparing the RT range between
386 easiest and hardest difficulties ($M \pm SD$) estimated over sessions; T: 115 ± 19 ms and O: 28 ± 11
387 ms, Wilcoxon ranksum comparing median ranges of RT, $p = 1.292e-11$).

388

389 Although color coherence explains considerable variation in RT, there is significant
390 variation that is not explained by the coherence. A linear regression between RT and stimulus
391 coherence only explained 10.8% of the variance in monkey T and only 1.3% in monkey O.
392 Variation in RT is readily apparent even within a given color coherence (Fig. 2f). Our hypothesis
393 is that this RT variability is at least in part related to fluctuations in BBA (See Figure 1,
394 Pogosyan et al., 2009; Kilavik et al., 2012; Khanna and Carmena, 2017).

395

396 LFP and neuronal responses during the pre-stimulus period show prominent beta band 397 activity

398

399 We first examined our LFPs recorded in PMd, specifically examining how the power across
400 different frequencies of the LFP changed throughout the reach decision task. BBA is apparent in

401 the pre-stimulus period (600 ms before the appearance of the checkerboard the stimulus),
402 decreases during the decision-formation period, and remains low during the movement epoch
403 (Fig. 3a, 3b). This pre-stimulus increase in power in the 15-35 Hz range is consistent with the
404 definition of BBA in both frequency (from 15 to 35 Hz) and timing within task behavior (Sanes
405 and Donoghue, 1993; Baker et al., 1997; Kilner et al., 1999; Riddle and Baker, 2006; Rubino et
406 al., 2006; Baker, 2007; Klostermann et al., 2007; Chakarov et al., 2009; Zaepffel et al., 2013).
407 Decreases in BBA after movement onset are also consistent with these and other prior reports
408 of beta event related desynchronization. Finally, activity in the delta band (0.5 to 4 Hz), theta
409 band (4 to 7 Hz), and alpha band (8 to 12 Hz) are present both before and after checkerboard
410 onset (Fig. 3a). We found that there was essentially no activity in the gamma band (40-100 Hz)
411 (Fig. 3a).

412
413 Several other analyses confirmed the existence of BBA during the pre-stimulus period.
414 Temporal fluctuations in the beta band were readily visible in individual trials of the LFP
415 suggesting that we are not artificially separating a broadband signal into signals of a specific
416 frequency (Fig. 3c). The power spectra for the trials shown in Fig. 3c corroborated this
417 observation of signals in the 15-35 Hz range (Fig. 3d). Finally, pre-stimulus BBA was
418 consistently observed in our population recordings (Fig. 3e & 3f). Figs. 3e & 3f plot the average
419 power spectrum over all trials, electrodes, and sessions for three different task periods: pre-
420 checkerboard cue, post-checkerboard cue, and post-movement. Both monkeys show significant
421 BBA during the pre-stimulus period, each with peak frequencies slightly below 30 Hz.

422
423 Across both monkeys, BBA observed after the checkerboard (during the post-
424 checkerboard period) differs from pre-stimulus BBA (Fig. 3e & 3f). After the checkerboard, BBA
425 has decreased peak power and a broader peak (covering more frequencies). The frequencies
426 present are still consistent with the frequency definition of BBA.

427 428 **RT covaries with BBA frequency and power**

429
430 Our first goal in this study was to better understand the relationship between BBA from the pre-
431 and post-stimulus periods and behavior. First, we examined if there were significant
432 relationships between pre-stimulus BBA and RT. As an initial, exploratory analysis, we
433 examined the extremes of the data by splitting the data into the (fastest) trials with the smallest
434 15% of RTs and the (slowest) trials with the largest 15% of RTs and compared the average
435 power spectra of the two groups for each monkey. Using the 5th and 95th percentiles suggested
436 similar patterns. Across both monkeys during the pre-stimulus period, we found that the faster
437 RTs have more power in the higher frequencies of BBA (approximately 25 to 30 Hz) (Fig. 4a &
438 4b). In Monkey T, in the lower frequencies of BBA (approximately 15 to 25 Hz), the slower RTs
439 have more power. Combined, this leads to a frequency shift between the RT quantiles, with the
440 power spectra for the slower RT trials slightly shifted towards the lower frequencies. In Monkey
441 O, however, the faster (smallest) RTs have more power for both the low and high frequencies of
442 BBA, so the perceived shift is not present.

443

444 To more rigorously quantify this relationship between RT and pre-stimulus BBA, we
445 examined the correlation between these two variables at each and every frequency. We
446 performed this analysis using partial correlations; i.e., we estimated the correlation between pre-
447 stimulus BBA and RT while using checkerboard coherence as a covariate. We then averaged
448 the partial correlations over the 16 electrodes. Correlation analyses exploiting the simultaneous
449 nature of our recordings were not notably different from the averaging analysis. So we only
450 report the results obtained from averaging partial correlations over electrodes.

451
452 Our analysis suggested a positive correlation between BBA and RT around 15 Hz (T:
453 peak at approx. 16 Hz, $r = 0.0785$, $p = 9.9341e^{-7}$; O: peak at approx. 12 Hz, $r = 0.0214$, $p =$
454 0.0056) and a negative correlation between BBA and RT around 35 Hz (T: minimum at approx.
455 31 Hz, $r = -0.1278$, $p = 9.9341e^{-7}$; O: not significant) (Fig. 4c & 4d). The presence of significant
456 correlations is inconsistent with the postural holding hypothesis. However, varying correlations
457 by frequency support both the maintenance hypothesis (purely positive correlations with BBA)
458 and the attentional hypothesis (purely negative correlations with BBA) within different sub-
459 regions of the beta band (maintenance for low BBA and attentional for high BBA).

460
461 We next performed the same analyses on the post stimulus (post-checkerboard) BBA to
462 better understand its relation to RT. Across both monkeys during the post-stimulus period, we
463 see that the slower (larger) RTs (85th percentile) have more power in the lower frequencies of
464 BBA (approximately 15 to 25 Hz) (Fig. 5a & 5b). In Monkey O, in the higher frequencies of BBA
465 (approximately 25-35 Hz), the faster (smaller) RTs have more power. Combined, this leads to a
466 frequency shift between the RT quantiles, with the power spectra for the slower RT trials slightly
467 shifted towards the lower frequencies. In Monkey T, however, the slower (larger) RTs have
468 more power for both the low and high frequencies of BBA, so the perceived shift is not present.
469 Across both monkeys, the correlation between post-stimulus activity and RT is positive for both
470 low and high beta (as well as some high alpha) (T: peak at approx. 21 Hz, $r = 0.13$, $p = 3.3114e^{-7}$;
471 O: peak at approx. 21 Hz, $r = 0.1167$, $p = 8.1205e^{-13}$) (Fig. 5c & 5d). The correlation is
472 negative for gamma activity in the low gamma band (T: minimum at approx. 37 Hz, $r = -0.06$, $p =$
473 $3.3114e^{-7}$; O: minimum at approx. 47 Hz, $r = -0.0708$, $p = 5.8103e^{-9}$).

474
475 These results for the post-stimulus period can also be more broadly viewed as a shift in
476 the component frequencies of the LFP, this time across multiple frequency bands. That is, on
477 faster RT trials, there is less overall beta band activity and slightly more gamma band activity.
478 The opposite is true for the slower RTs.

479
480 **Simulations suggest that a frequency shift in BBA is a plausible mechanism for the**
481 **observed pattern of correlation**

482
483 In order to better understand the mechanisms behind the frequency dependent correlation
484 between BBA and RT, we used a simulation analysis. The schematic for this analysis is shown
485 in Fig. 6a. First, we randomly generated RT values within the range of RTs typically observed
486 for our monkeys. Then, based on these values and a variety of governing equations for

487 frequency and amplitude, we simulated LFP signals for these hypothetical trials. The signal was
488 defined as

$$489 \quad \text{signal} = \text{Amplitude} * \sin(2\pi * \text{Frequency} * t),$$

491
492 where amplitude and frequency are either constants, linear increasing functions of RT, or linear
493 decreasing functions of RT. We then calculated the power spectra of these simulated signals
494 from these trials and correlated these power spectra to their corresponding RTs. For each group
495 of frequency and amplitude equations, we generated one thousand simulated trials with
496 corresponding RTs, simulated LFP signals, and power spectra. The correlation coefficient as a
497 function of frequency between the simulated power spectra and RTs is shown in Fig. 6b for the
498 six paradigms.

499
500 The correlations between pre-stimulus BBA and RT observed in the real data (shown in
501 Fig. 4c & 4d) most closely match the correlation when frequency is negatively related to RT.
502 This relationship is robust regardless of the relationship between amplitude and RT (shown in
503 Fig. 6b parts ii, iii, and iv). These findings indicate the presence of a relationship between pre-
504 stimulus BBA frequency composition and RT, suggesting that pre-stimulus BBA component
505 frequencies are negatively related with RT.

506
507 The correlations between post-stimulus BBA and RT observed in the real data (shown in
508 Fig. 5c & 5d) most closely match the correlation when frequency is not related to RT and
509 amplitude is positively related to RT (shown in Fig. 6b, part v). This indicates the presence of a
510 relationship between post-stimulus BBA amplitude and RT with no relationship between post-
511 stimulus BBA component frequencies and RT. We do recognize though that additional
512 processes that involve the dynamical balance between beta band activity and gamma band
513 activity can lead to shifts in the frequencies that, in turn, explain the negative correlations in the
514 gamma band but positive correlations in the beta band.

515
516 **Deeper cortical layers have stronger activity in the low beta range than the superficial**
517 **layers**

518
519 The next goal of our study was to understand how BBA changes as a function of cortical depth.
520 The use of linear multi-contact electrodes (Fig. 2g) provided us with simultaneous recordings
521 across several cortical depths and allowed us to examine whether there was a relationship
522 between cortical depth and BBA.

523
524 To examine the degree to which pre-stimulus power in the beta region varied with
525 electrode depth, we divided the electrodes into two groups: the superficial (electrodes 1:8) and
526 the deep (electrodes 9:16). In both monkeys, deeper electrodes (corresponding to deeper
527 cortical layers) have more power around the 10 to 20 Hz region (Fig. 7a & 7b). In one monkey
528 (Monkey O), this pattern of deeper electrodes having more power than surface electrodes
529 continues from approximately 10 Hz until 30 Hz, slightly past its peak frequency (Fig. 7b).

530

531 This pattern of deeper electrodes having more power than surface electrodes around the
532 10-20 Hz (low beta) region is also true of the post-stimulus period and is even more pronounced
533 (Fig. 8a & 8b). Again in Monkey O, the pattern of deeper electrodes having more power than
534 surface electrodes continues slightly past its peak frequency (Fig. 8b).

535

536 **Correlation between BBA and RT does not vary significantly by depth**

537

538 To examine whether BBA from certain cortical layers was more strongly tied with RTs, we
539 performed the correlation with RT over two depth groups: superficial (electrodes 1:8) and deep
540 (electrodes 9:16). For both pre-stimulus (Fig. 7c & 7d) and post-stimulus (Fig. 8c & 8d) BBA, the
541 correlations for each group of electrodes produced the same shape as the correlation over all
542 electrodes shown previously. The correlations for the superficial and deep electrodes are
543 essentially the same, i.e. the correlation for one depth group is not significantly greater in
544 magnitude than that of the other.

545

546

547 **DISCUSSION (1476 words; 1500 words max)**

548

549 The motivation for our study was to further understand the behavioral relevance of BBA and
550 how it is organized as a function of cortical depth. In a perceptual decision-making task, we
551 found that BBA was robustly present during the pre-stimulus and post-stimulus periods and was
552 related to the behavioral RT. During the pre-stimulus period, low beta frequencies (~15 to 20
553 Hz) were positively correlated with RT, while high beta frequencies (~25 to 30 Hz) were
554 negatively correlated. Through simulation, we found that the observed frequency-dependent
555 correlation corresponds to a negative relationship between RT and the component frequencies
556 of pre-stimulus BBA. During the post-stimulus period, all frequencies of BBA (~15-30 Hz) were
557 positively correlated to RT. We also found that deeper electrodes had higher power in the low
558 beta frequencies (~15 to 20 Hz) than superficial electrodes for both the pre- and post-stimulus
559 periods.

560

561 **“Maintenance of current state” and “attentional” hypotheses help explain BBA in PMd**

562

563 The nuanced relationship we discovered between BBA and RT is relevant for the ongoing
564 discussion regarding the role of BBA. Currently, three main hypotheses exist, and each
565 hypothesis has corresponding expected relationships between BBA and RT.

566

567 The postural hypothesis posits that BBA is a result of the maintained holding of a hand
568 position and has no relationship to eventual behavior. For our experiment, one would predict no
569 relationship between BBA and RT (Baker et al., 1999; Kristeva et al., 2007) – a hypothesis
570 inconsistent with our findings that both pre-stimulus and post-stimulus BBA were related to RT.

571

572 Correlations between BBA and RT during the pre-stimulus period support both of the two
573 remaining hypotheses. The maintenance hypothesis asserts that BBA represents a willingness
574 to maintain the current state of either rest or movement. In this hypothesis, greater levels of
575 BBA reflect the “desire” to maintain the hold position, which would result in slower movement
576 and an increase in RT (Gilbertson et al., 2005; Pogosyan et al., 2009; Engel and Fries, 2010).
577 Our finding of a positive correlation between BBA and RT for low beta frequencies is consistent
578 with the maintenance hypothesis. The attentional hypothesis, which suggests that greater BBA
579 reflects more attentional engagement with the task, would suggest a negative correlation
580 between BBA and RT (Bouyer et al., 1987; Murthy and Fetz, 1992; Zhang et al., 2008; Saleh et
581 al., 2010). The negative correlation between BBA and RT for high beta frequencies supports the
582 attentional hypothesis.

583

584 During the post-stimulus period, we found that BBA was positively correlated with RT for
585 both low and high frequencies, which supports the maintenance hypothesis. During this period,
586 it appears that BBA of any frequency (low or high) reflects more willingness to maintain the
587 current state of being.

588

589 This constellation of results suggest that the beta band is not a monolithic signal and
590 consists of activity in at least two frequency sub-bands that dynamically emerge in different task

591 epochs, perhaps reflecting distinct behavioral demands placed on the animal (Buschman et al.,
592 2012; Spitzer and Haegens, 2017). We expand on this theme in the next section.

593

594 **BBA is better understood when split into two frequency bands**

595

596 By examining the correlation at each frequency, rather than averaging over the whole beta
597 frequency band, we found that BBA is better understood as being composed of at least two
598 frequency sub-bands: low beta (~13 to 20 Hz) and high beta (~25 to 30 Hz).

599

600 Our nuanced view of BBA has some precedent in literature, with human EEG and rat
601 studies referring to a beta1 band (~ 15 Hz) and a beta2 band (~ 25 Hz) (Haenschel et al., 2000;
602 Kramer et al., 2008; Kopell et al., 2011; Cannon et al., 2014). In monkeys, Kilavik and
603 collaborators examined motor cortical BBA during a visual multiple delay reaching task and
604 suggested a similar separation (Kilavik et al., 2012). They posited that low beta frequencies
605 were the result of widespread networks involved in top-down (conscious) processing and
606 expectation of movement-related visual information, while higher beta frequencies emerged
607 from bottom-up visual information processing and movement preparation (Kilavik et al., 2012).

608

609 The pre-stimulus period of our task incorporates the behavioral components identified by
610 Kilavik and collaborators for both types of BBA – the monkey is expecting the visual
611 checkerboard stimulus, is viewing relevant reach targets, and is preparing for one of two arm
612 movements. We take the stance that the frequency composition of the pre-stimulus period
613 reflects these different processes in the decision-making task. Therefore, it is not unreasonable
614 that we see both low and high beta frequencies and positive and negative correlations between
615 BBA and RT.

616

617 As the task progresses, the visual checkerboard (a bottom-up visual stimulus) appears.
618 We speculate that the appearance of the checkerboard triggers a cognitive process that
619 involves deliberation on the visual stimulus and likely movement preparation for the arm
620 movement to report the decision. In the framework proposed by Kilavik and collaborators, such
621 processes should induce activity in multiple beta frequencies, which is consistent with the
622 broader frequency range of BBA we see in the post stimulus period. It remains to be understood
623 why increased beta of any frequency during this period is associated with slower RTs.

624

625 **Beyond the LFP**

626

627 Our study has focused on BBA in the LFP and behavior. We chose to analyze the LFP because
628 it provides a population level, spatially averaged description of neural activity. We anticipate
629 similar effects in spiking neurons, and preliminary analysis of our spike trains suggested BBA in
630 many neurons and multi-units. However, analysis of single-neuron spike trains is often difficult
631 because of the mixture of both poisson and non-poisson variability in these spike trains. Typical
632 noise-reduction steps, such as convolution of spike trains with various filters, end up low pass
633 filtering spike trains, which would lead to severe attenuation of signals at beta frequencies and
634 the overemphasis of slower dynamics. We take the view these spikes are emerging from a

635 dynamical system with activity at multiple time scales and that there is a need for collectively
636 understanding both slow and fast dynamics in spiking activity. Single-trial analysis methods that
637 use recurrent neural networks would facilitate such analyses (Pandarinath et al., 2017b).

638

639 **Greater low frequency beta in deeper electrodes is consistent with hypotheses about the** 640 **generation of BBA**

641

642 We found that electrodes placed deeper in the cortex, whose position approximately
643 corresponds to layer V, have higher power in the low beta range (~15 to 20 Hz) than
644 superficially placed electrodes during both the pre- and post-stimulus periods. The power and
645 depth relation differed across our two monkeys for high beta frequencies (~25 to 30 Hz). The
646 difference between monkeys for the power and depth relation in higher frequencies could arise
647 due to variations in recording locations across animals or could be endogenous to the individual.
648 This possibility would need to be studied with a variety of experiments and a larger test
649 population.

650

651 Two main hypotheses exist regarding the generation of BBA: it is either generated
652 locally, perhaps in layer V of motor cortex, or it is generated distally and transmitted from
653 elsewhere (Khanna and Carmena, 2015; Spitzer and Haegens, 2017). Our finding of greater
654 power in low beta frequencies for deeper electrodes is consistent with both predominant
655 hypotheses; greater power could either indicate the BBA being generated in that layer (local
656 hypothesis), or it could indicate that the distally generated BBA is projected into that layer (distal
657 hypothesis).

658

659 Few studies have examined relationships between BBA and cortical depth. One study
660 examined synchronization of BBA at various depths in the inferior temporal cortex during the
661 passive repetition of visual stimuli (Kaliukhovich and Vogels, 2012). However, the passive
662 nature of the task meant that they could not relate BBA to behavior. A recent laminar study of
663 LFPs power in frontal cortex, including PMd, found greater power for low frequencies of BBA in
664 deeper cortical layers (Bastos et al., 2018) – a result consistent with our observations here.

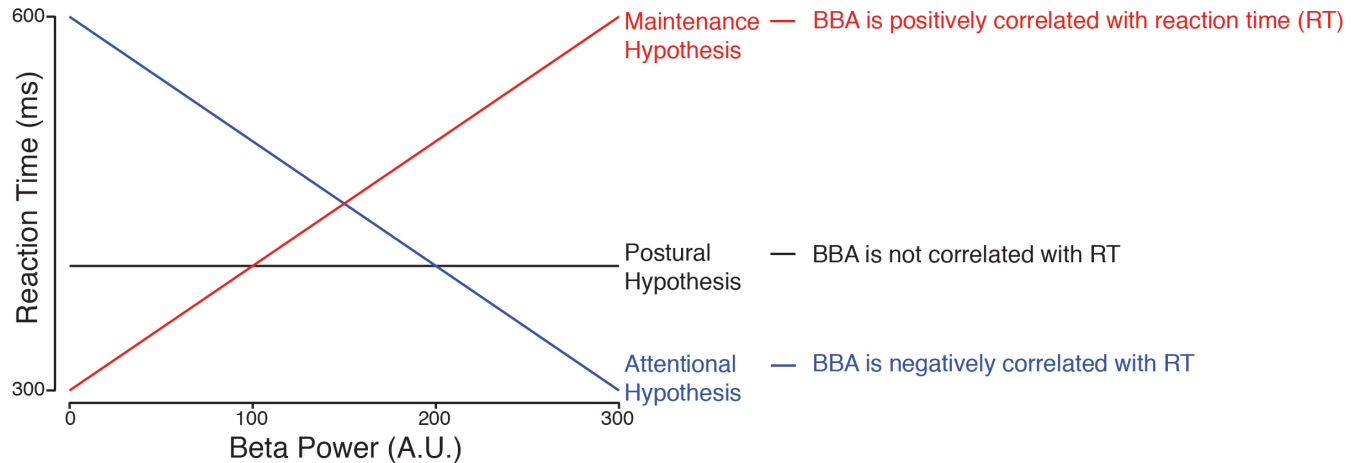
665

666 Even though few studies focus on how BBA changes as a function of cortical depth,
667 many have hypothesized about its origin and built computational models (Lee et al., 2013;
668 Cannon et al., 2014). Despite these studies advancing our understanding of the biophysical
669 basis of BBA, we still lack clarity about its underlying generators, because these modeling
670 studies focus on results from in-vitro experiments in sensory cortices, with only one study
671 focusing on the motor areas. Our study provides some of the first descriptions of BBA in
672 premotor cortical areas in monkeys performing demanding cognitive tasks that also involve the
673 somatomotor system. We anticipate that our data showing greater power in the lower
674 frequencies of BBA will help constrain computational models of BBA. Studies involving laminar
675 recordings in other BBA associated structures are needed to build the next generation of
676 computational models of BBA. Ideally, these future studies would include decision-making,
677 instructed delay, and somatosensory perturbation tasks that engage the different processes that
678 are postulated to be associated with beta band activity.

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FIGURES

Figure 1

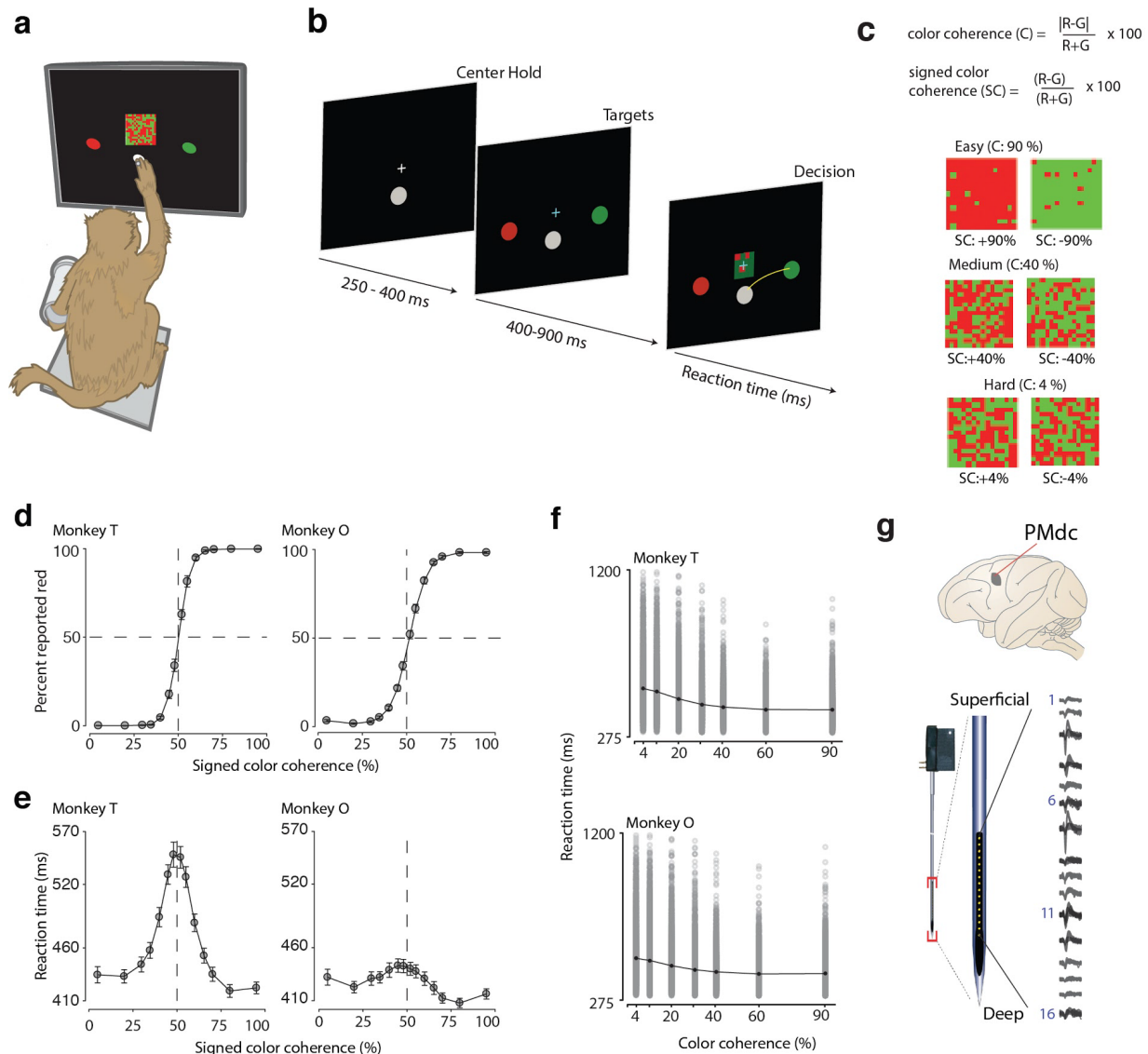


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Figure 1 – Existing hypotheses about the role of BBA

Three existing hypotheses about the relation between pre-stimulus BBA and RT. The black, horizontal line corresponds to the postural hypothesis of BBA, where there is no relationship between BBA and RT. The red, positively sloped line corresponds to the maintenance hypothesis of BBA, because increased BBA would be tied with longer RTs. The blue, negatively sloped line corresponds to the attentional hypothesis of BBA, because more BBA would be tied to greater attention on the task and therefore shorter RTs. Each dot in the figure is a random, hypothetical RT and beta power used to illustrate the relationship between the two.

697 **Figure 2**



698

699 **Figure 2 – Recording locations, techniques, task, and discrimination behavior**

700

701 **a:** An illustration of the experimental setup for data gathering in the discrimination task. We
 702 gently restrained the resting arm with a plastic tube and cloth sling. We tracked a reflective IR
 703 bead taped on the middle digit of the unrestrained hand to mimic a touch screen and to provide
 704 an estimate of instantaneous arm position. We tracked eye position using an infrared reflective
 705 mirror placed in front of the monkey's nose.

706

707 **b:** Example timeline of the discrimination task.

708

709 **c:** Examples of different stimulus ambiguities used in the experiment parameterized by the color

710 coherence of the checkerboard defined as $C = \frac{100 \times |R-G|}{R+G}$. The corresponding signed color

711 coherence is defined as $SC = \frac{100 \times (R-G)}{R+G}$. Positive values of signed color coherence denote

712 more red than green squares and vice-versa.

713

714 **d-e:** Average discrimination performance (d) and reaction time (RT) (e) over sessions of the two
715 monkeys as a function of the signed color coherence of the checkerboard. RT plotted here
716 includes both correct and incorrect trials for each session and then averaged across sessions.
717 Gray markers show measured data points along with 2x(standard error) estimated over
718 sessions, though variation is so small that they are difficult to see in (d). The black line
719 segments are drawn in between these measured data points to guide the eye. For most data
720 points in (d), the error bars lie within the markers. X-axes in both (d) and (e) depict the signed
721 color coherence in %. Y-axes depict the percent responded red in (d) and RT in (e). Also shown
722 in (d) are discrimination thresholds ($M \pm SD$ over sessions) estimated from a Weibull fit to the
723 overall percent correct as a function of coherence. The discrimination threshold is the color
724 coherence level at which the monkey made 81.6% correct choices. 24 sessions for monkey T
725 (47483 trials) and 44 sessions for monkey O (70,250 trials) went into these averages.

726

727 **f:** RT as a function of checkerboard coherence. For each coherence, the mean RT is shown in
728 black and connected linearly, with gray markers showing individual RTs. There is large variation
729 of RTs both across and within coherences.

730

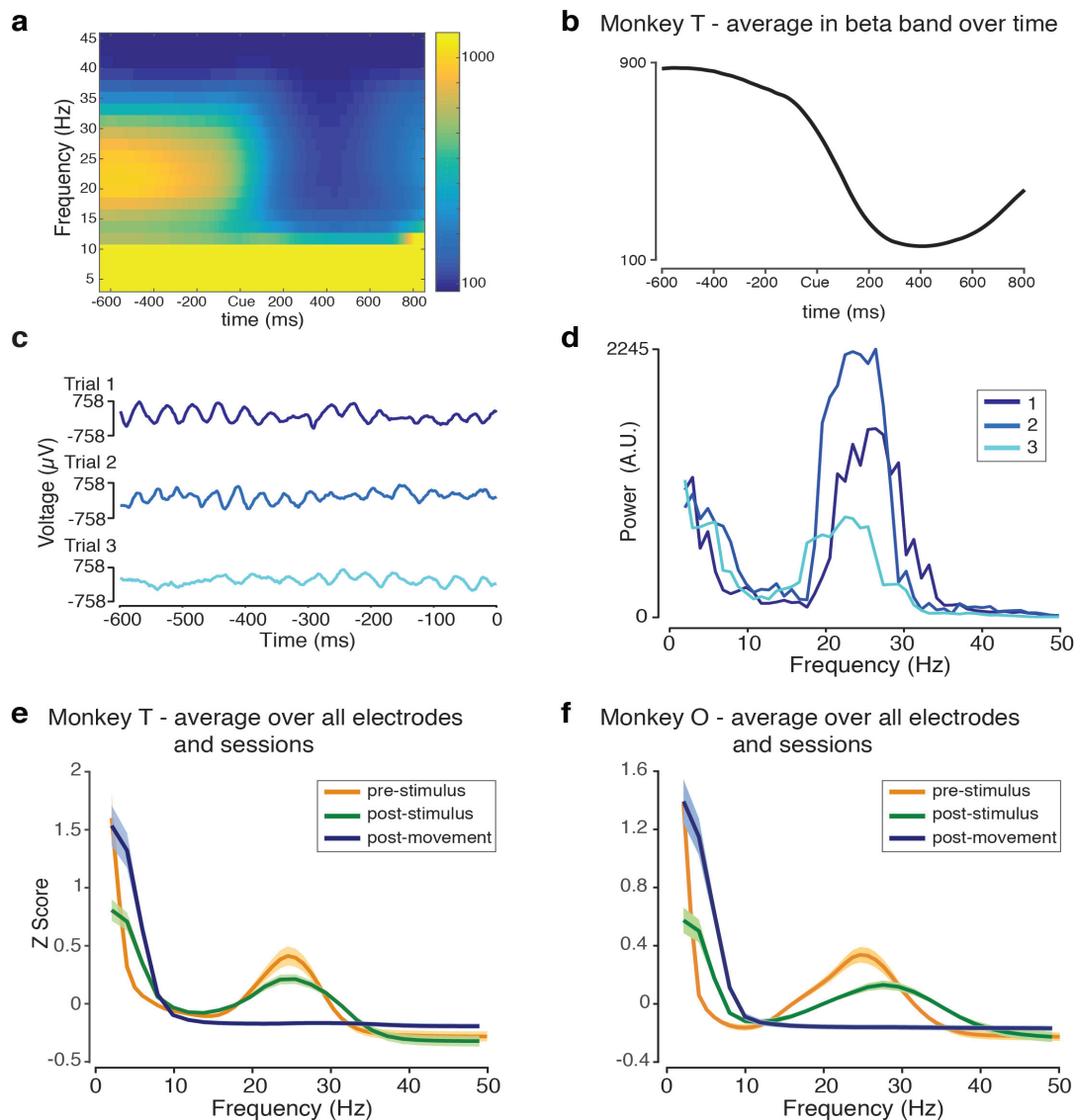
731 **g:** Location of PMd along with an example recording from a 16 electrode, 150 μm spacing U-
732 probe.

733

734

735

736 **Figure 3**



737

738 **Figure 3 – Existence of BBA during hold period before the visual stimulus**

739

740 **a:** Spectrogram aligned to checkerboard onset (indicated with Cue), averaged over all
741 electrodes, trials, and sessions for Monkey T. The Y-Axis represents frequency and is shown in
742 Hertz. The X-axis represents time in milliseconds. Color represents power in arbitrary units
743 (A.U.). Clear presence of pre-stimulus BBA is seen, with lower-power post-stimulus BBA.
744

745 **b:** Activity in the beta band (13-30 Hz) over time, averaged over all electrodes, trials, and
746 sessions for Monkey T. The Y-Axis is power in (A.U.) and the X-axis represents time in
747 milliseconds.
748

749 **c:** The LFP time series of three trials of Electrode 2 during a single session. The colors are
750 unique to each trial and consistent with subplot (d). The time series are shown as microvolts per

751 millisecond.

752

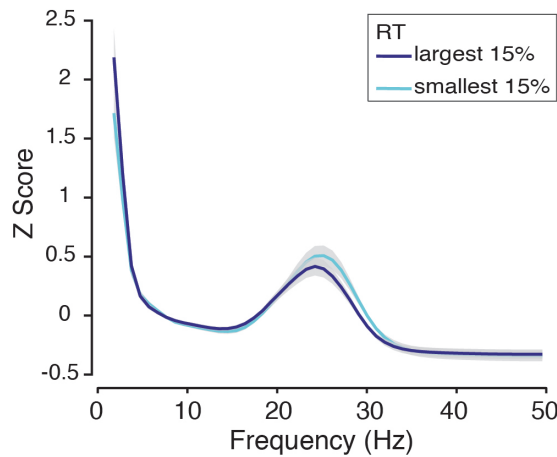
753 **d:** Power spectra of three example trials during the epoch before the checkerboard. Power in
754 (A.U.) is plotted against frequency (Hertz).

755

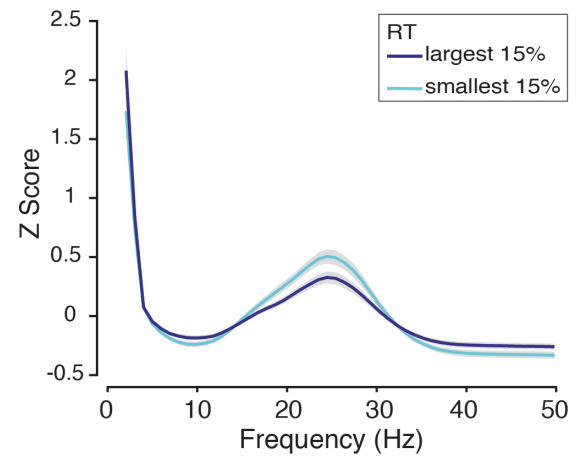
756 **e-f:** Normalized power spectra of the LFP during the epoch before the checkerboard (orange),
757 after the checkerboard (green), and after movement (blue). (e) Monkey T grand average over all
758 electrodes, trials and sessions. (f) Monkey O grand average over all electrodes, trials, and
759 sessions. The power spectra have been normalized, and their Z Scores are plotted against
760 frequency (Hertz). Standard error over sessions is shaded.

761 **Figure 4**

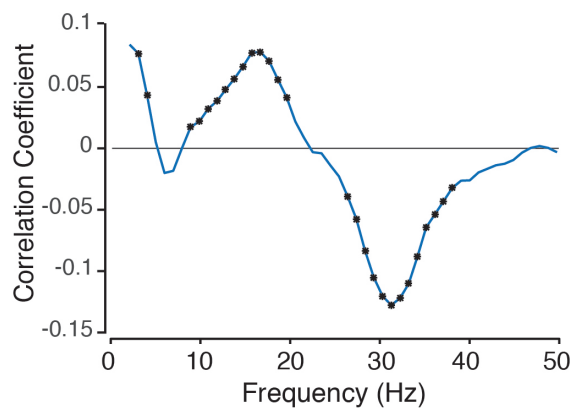
a Monkey T



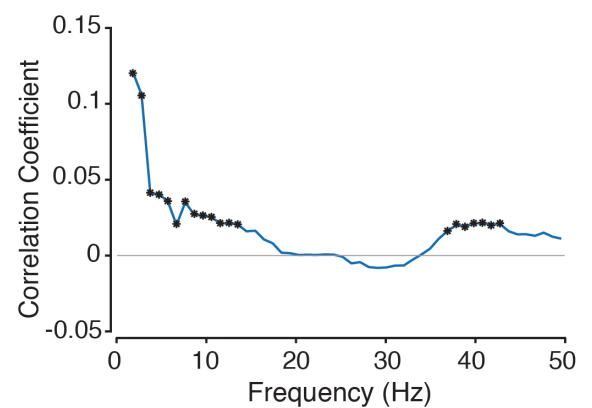
b Monkey O



c Monkey T



d Monkey O



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Figure 4 – Relation between pre-stimulus BBA and Reaction Time

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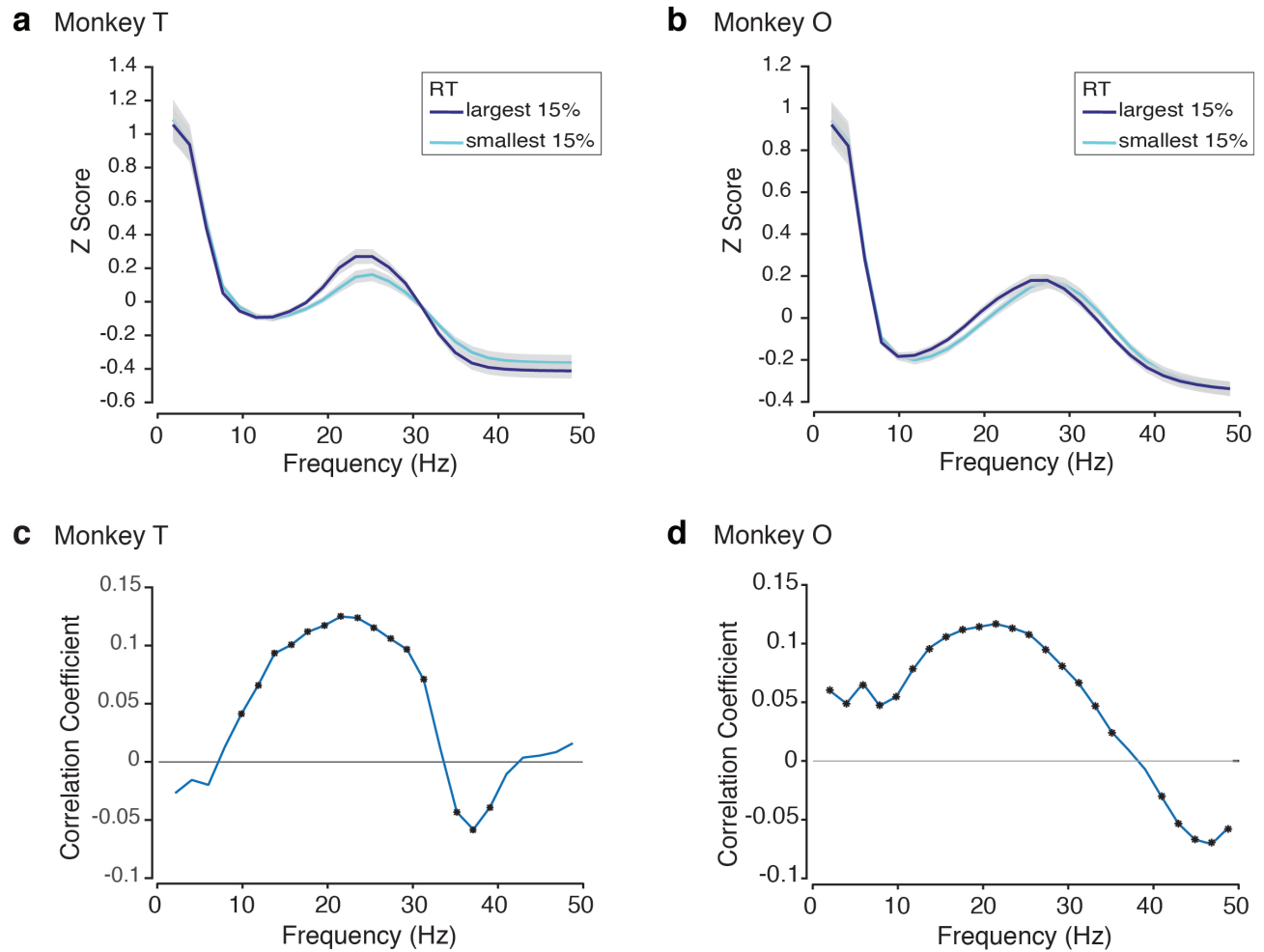
775

776

a,b: Normalized pre-stimulus power spectra grouped into two reaction time quantiles and averaged over all trials within that group, all electrodes, and all sessions for Monkey T (a) and Monkey O (b). The two quantiles are the 15% largest (slowest) reaction times and the 15% smallest (fastest) reaction times. The power spectra have been normalized and their Z Scores are plotted against frequency (Hertz). Standard error over sessions is shown in gray.

c,d: Correlation between normalized pre-stimulus power spectra with RT as a function of frequency for Monkey T (c) and Monkey O (d). Asterisks indicate points along the curve where the correlation is significant (adjusted p-value less than 0.05).

777 **Figure 5**



778

779 **Figure 5 – Relation between post-stimulus BBA and Reaction Time**

780

781 **a,b:** Normalized post-stimulus power spectra grouped into two reaction time quantiles and
782 averaged over all trials within that group, all electrodes, and all sessions for Monkey T (a) and
783 Monkey O (b). The two quantiles are the 15% largest (slowest) reaction times and the 15%
784 smallest (fastest) reaction times. The power spectra have been normalized and their Z Scores
785 are plotted against frequency (Hertz). Standard error over sessions is shown in gray.
786

787

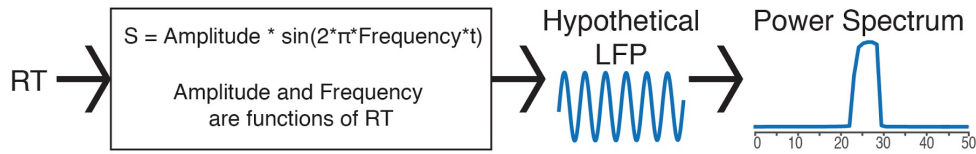
788 **c-e:** Correlation between normalized post-stimulus power spectra with RT as a function of
789 frequency for Monkey T (c) and Monkey O (d). Asterisks indicate points along the curve where
790 the correlation is significant (adjusted p-value less than 0.05).
791

790

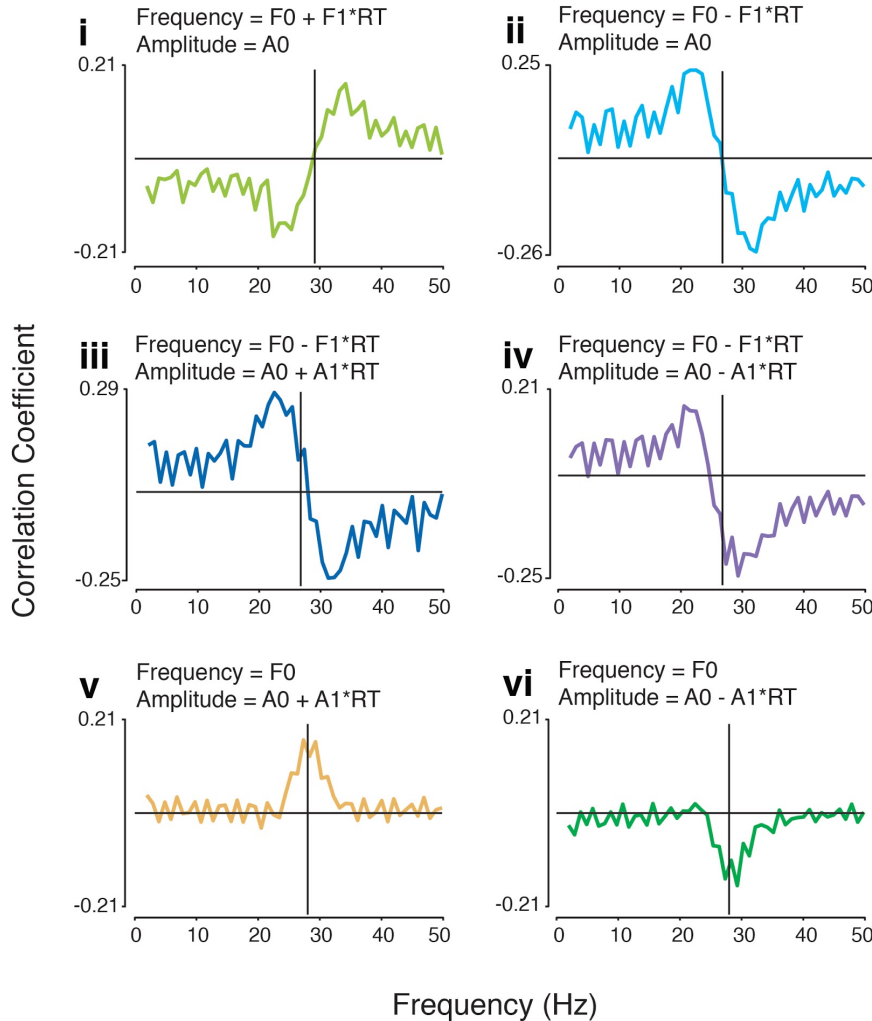
791

792 **Figure 6**

a



b Correlation (RT, Power Spectrum)

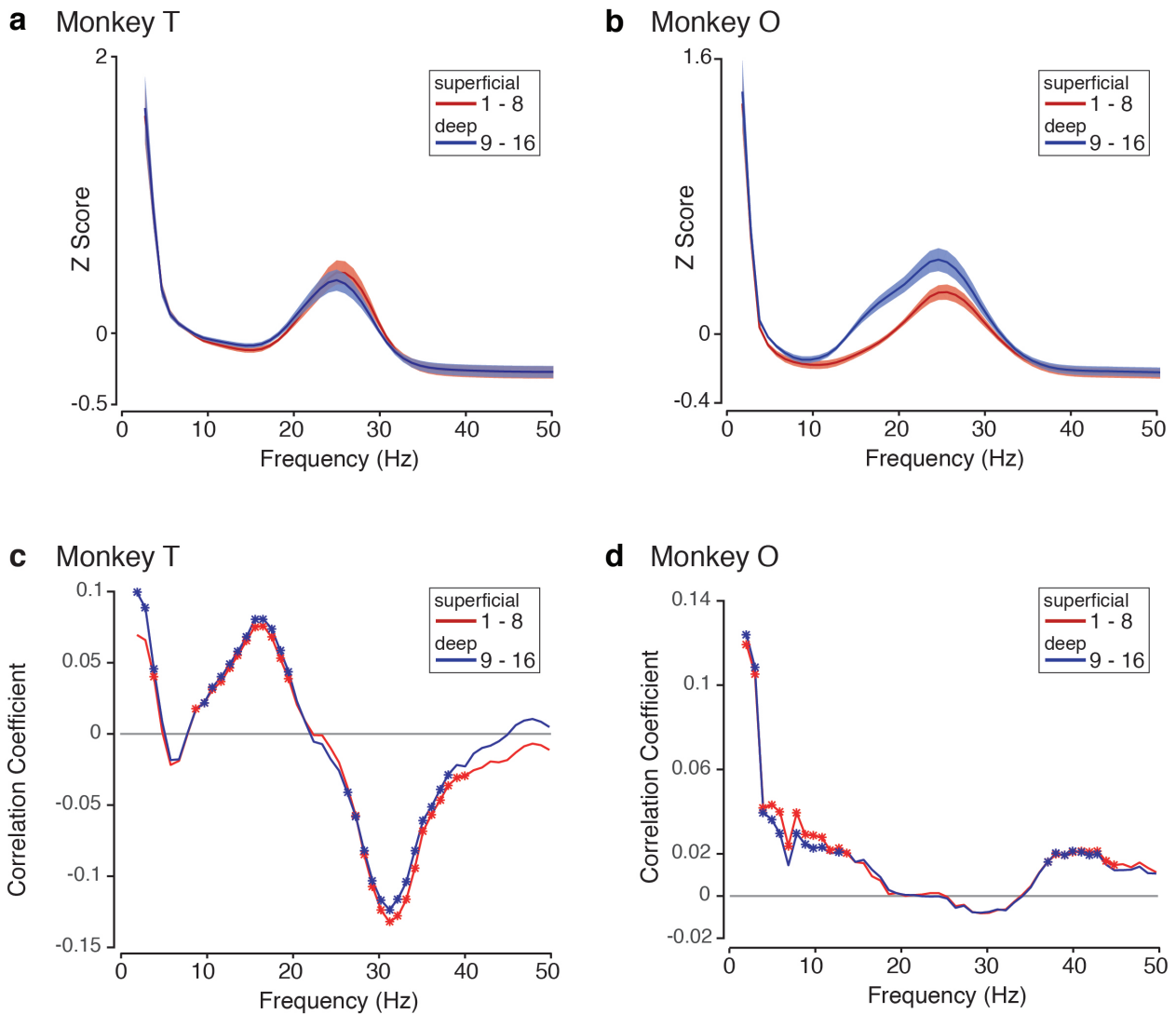


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794
795

Figure 6 - Simulations of Relation between BBA and Reaction Time

796 Process (a) and results (b) of a simulation that generated synthetic LFP signals as
797 $Amplitude * \sin(2 * \pi * Frequency * t)$. The Amplitude and Frequency of the LFP were defined
798 differently for each case, either as a constant or a function of reaction time. Power spectra were
799 made from these LFP signals, and they were then correlated with RT to create the shown plots
800 of correlation coefficients as a function of frequency for each of the six cases. The amplitude
801 and frequency relationships with RT for each case are shown with the correlations.

802 **Figure 7**



803

804 **Figure 7 – Pre-stimulus BBA by depth**

805

806 **a,b:** Normalized pre-stimulus power spectra grouped into two electrode groupings and averaged
807 over all trials, all electrodes within that group, and all sessions for Monkey T (a) and Monkey O
808 (b). The power spectra have been normalized, and their Z Scores are plotted against frequency
809 (Hertz). The average over the superficial electrodes is plotted in red, and the average over the
810 deep electrodes is plotted in blue. Standard error over sessions is shaded.

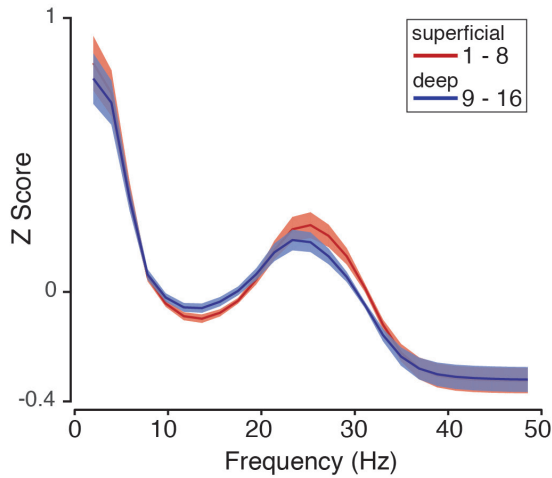
811

812 **c,d:** Depth dependent correlation between normalized pre-stimulus power spectra with RT as a
813 function of frequency for Monkey T (c) and Monkey O (d). The correlation over the superficial
814 electrodes is plotted in red, and the correlation over the deep electrodes is plotted in blue.

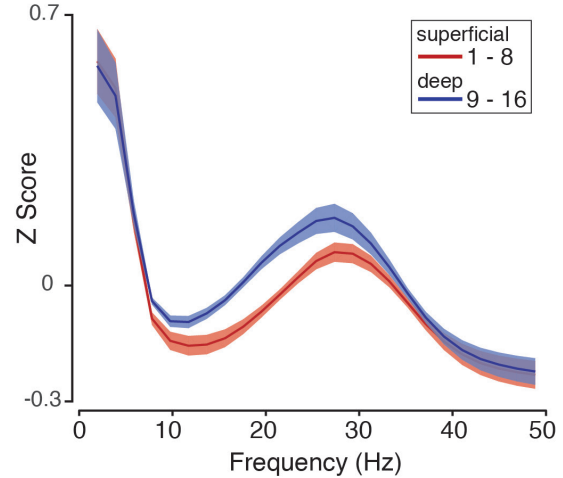
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816 **Figure 8**

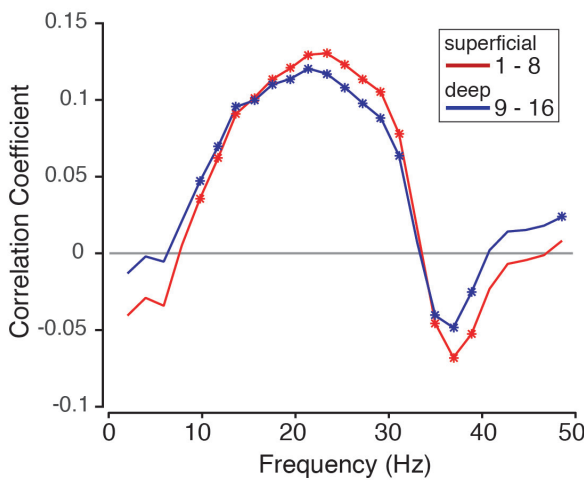
a Monkey T



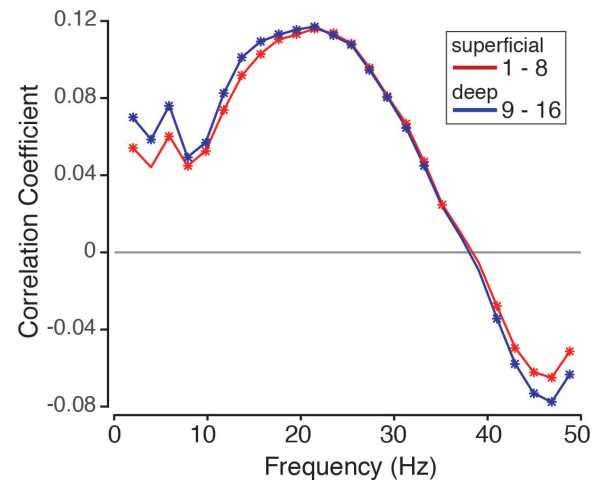
b Monkey O



c Monkey T



d Monkey O



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818 **Figure 8 – Post-stimulus BBA by depth**

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820 **a,b:** Normalized post-stimulus power spectra grouped into two electrode groupings and
821 averaged over all trials, all electrodes within that group, and all sessions for Monkey T (a) and
822 Monkey O (b). The power spectra have been normalized, and their Z Scores are plotted against
823 frequency (Hertz). The average over the superficial electrodes is plotted in red, and the average
824 over the deep electrodes is plotted in blue. Standard error over sessions is shaded.

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826 **c,d:** Depth dependent correlation between normalized post-stimulus power spectra with RT as a
827 function of frequency for Monkey T (c) and Monkey O (d). The correlation over the superficial
828 electrodes is plotted in red, and the correlation over the deep electrodes is plotted in blue.

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