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Beyond the Status Quo: A Role for Beta Oscillations in Endogenous Content (Re-) Activation

Beta oscillations in endogenous content activation

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6

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39 **Abstract**

40 Among the rhythms of the brain, oscillations in the beta frequency range (approx. 13–30 Hz)
41 have been considered the most enigmatic. Traditionally associated with sensorimotor
42 functions, beta oscillations have recently become more broadly implicated in top-down
43 processing, long-range communication, and preservation of the current brain state. Here, we
44 extend and refine these views based on accumulating new findings of content-specific beta
45 synchronization during endogenous information processing in working memory and
46 decision-making. We characterize such content-specific beta activity as short-lived, flexible
47 network dynamics supporting the endogenous (re-)activation of cortical representations.
48 Specifically, we suggest that beta-mediated ensemble formation within and between cortical
49 areas may awake, rather than merely preserve, an endogenous cognitive set in the service of
50 current task demands. This proposal accommodates key aspects of content-specific beta
51 modulations in monkeys and humans, integrates with timely computational models, and
52 outlines a functional role for beta that fits its transient temporal characteristics.

53

54 **Significance statement**

55 Brain oscillations at frequencies of 13–30 Hz (the “beta” rhythm) are traditionally associated
56 with sensory and motor processing, but are increasingly implicated in various cognitive
57 functions, such as working memory and decision-making. Here, we review new evidence
58 that beta activity in these domains can be content-specific, that is, it can reflect the very
59 information that is currently being processed. Going beyond previous accounts that link beta
60 to maintenance of the current brain state, our review highlights the dynamic, often short-
61 lived nature of beta modulations during endogenous information processing. We integrate

62 these findings in a dynamic network view where beta synchronization supports the internally

63 driven (re-)activation of neuronal ensembles to represent currently task-relevant contents.

64

65 **Beta-band oscillations: beyond motor control**

66

67 Oscillations in the beta frequency range (approx. 13–30 Hz) have traditionally been
68 associated with sensorimotor processing (Hari and Salmelin, 1997; Pfurtscheller and Lopes
69 da Silva, 1999). During preparation and execution of movements, beta oscillations in
70 sensorimotor cortex show marked power decreases (assumed to reflect local
71 desynchronization), followed by a “rebound” of power (i.e., synchronization) after
72 movement (Kilavik et al., 2013). A similar sequence of beta power changes is observed in
73 somatosensation, with desynchronization in anticipation of and during stimulation, followed
74 by (re-)synchronization after stimulus offset (e.g., Bauer et al., 2006; Spitzer et al., 2010; Van
75 Ede et al., 2010). The dynamics of beta activity in sensorimotor cortex often resemble and/or
76 parallel modulations of alpha band activity (approx. 8–12 Hz), in that power decreases with
77 active engagement, for instance during spatial attention (Bauer et al., 2006; Schubert et al.,
78 2009; Jones et al., 2010; Van Ede et al., 2011; but see Haegens et al., 2012). However,
79 whereas alpha oscillations are widely linked to the inhibition of task-irrelevant areas
80 (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Haegens et al., 2011a), the precise
81 functional role of sensorimotor beta synchrony remains unclear. Initially believed to reflect
82 cortical idling (Pfurtscheller et al., 1996; Neuper and Pfurtscheller, 2001), more recent views
83 suggest a role in maintaining the current sensorimotor set, or “status quo” (Engel and Fries,
84 2010; cf. Jenkinson and Brown, 2011).

85

86 Beyond its established role as a sensorimotor rhythm, beta activity has been observed in
87 various different cortical areas and is increasingly implicated in a wider range of cognitive
88 functions (Engel and Fries, 2010). Modulations of beta oscillatory activity in non-

89 somatomotor areas (e.g., frontal, parietal, visual; Figure 1A) have been associated with visual
90 perception (Donner et al., 2007; Piantoni et al., 2010; Kloosterman et al., 2015), language
91 processing (for review, see Weiss and Mueller, 2012), working memory (Tallon-Baudry et al.,
92 1998; Deiber et al., 2007; Axmacher et al., 2008; Siegel et al., 2009), long-term memory
93 encoding and retrieval (Sederberg et al., 2006; Hanslmayr et al., 2009; Spitzer et al., 2009;
94 for review, see Hanslmayr et al., 2016), decision-making (Pesaran et al., 2008; Wimmer et al.,
95 2016; Wong et al., 2016), response inhibition (e.g., Jha et al., 2015), and reward processing
96 (for review, see Marco-Pallarés et al., 2015). In some of these contexts, beta-band
97 modulations occur in a relatively low frequency band (“lower” beta, approx. 13–20 Hz) and
98 in tandem with alpha (e.g., Hanslmayr et al., 2009). In other cases, beta-band rhythms of
99 varying frequencies (including “upper” beta, approx. 20–30 Hz) behave in ways more similar
100 to gamma activity (>30 Hz) and increase, rather than decrease, with task-related
101 engagement (e.g., Tallon-Baudry et al., 1998; Marco-Pallarés et al., 2015; Kornblith et al.,
102 2016).

103

104 While a unifying theoretical account of cortical beta oscillations is currently lacking, some
105 mechanistic aspects have been tentatively identified. In particular, beta oscillations are
106 mostly associated with endogenous, top-down controlled processing (Buschman and Miller,
107 2007; for review, see Engel and Fries, 2010; Wang, 2010; Fries, 2015). Furthermore, in line
108 with a “communication through coherence” view (Fries, 2005, 2015), oscillations in the beta
109 frequency range are assumed to facilitate long-range interactions on a cortical network level
110 (Kopell et al., 2000; Varela et al., 2001; Benchenane et al., 2011; Kilavik et al., 2013). Both
111 these aspects have been integrated in a predictive coding framework, where gamma
112 synchronization serves feedforward (bottom-up) communication, whereas beta

113 synchronization affords feedback communication of top-down predictions (Arnal and Giraud,
114 2012; Bastos et al., 2012; Bastos et al., 2015; Michalareas et al., 2016). One of the many
115 persistent puzzles regarding beta, however, remains its unclear relation to neuronal activity
116 as measured in spike firing rates and/or blood-oxygen-level dependent (BOLD) signals.
117 Whereas oscillations in other frequency bands are known to correlate either positively (e.g.,
118 gamma) or negatively (e.g., alpha) with these activity measures, findings for beta have been
119 mixed (e.g., Michels et al., 2010; Hanslmayr et al., 2011), with some studies showing no
120 correlation at all (e.g., Whittingstall and Logothetis, 2009; Rule et al., 2017).

121

122 Perhaps surprisingly in light of the above, an increasing number of findings indicate that in
123 some task contexts, beta oscillatory activity can be content-specific, that is, it can reflect the
124 very information that is currently being processed (Figure 1B). Across human and monkey
125 species, content-specific beta activity was found to carry information about internalized task
126 rules (Buschman et al., 2012), stimulus categories (Antzoulatos and Miller, 2014, 2016;
127 Stanley et al., 2016), scalar magnitudes (Spitzer et al., 2010; Spitzer and Blankenburg, 2011;
128 Spitzer et al., 2014a) and other stimulus properties (Salazar et al., 2012; Mendoza-Halliday et
129 al., 2014; Lewis et al., 2016; Wimmer et al., 2016), as well as subjective comparison
130 outcomes (Haegens et al., 2011b; Herding et al., 2016). Such content-specific beta activity
131 has in particular been observed during endogenous information processing in working
132 memory and decision-making. Before considering these two domains in greater detail, we
133 briefly discuss by which neurophysiological mechanisms beta oscillations might be
134 generated.

135

136

137 *Generation of cortical beta oscillations*

138 Two main views exist in the literature, suggesting that (i) beta is generated in cortex (Jensen
139 et al., 2005; Roopun et al., 2006; Kramer et al., 2008; Kopell et al., 2011; Sherman et al.,
140 2016), or (ii) that beta is generated in the basal ganglia and propagated to cortex via the
141 thalamus (Holgado et al., 2010; McCarthy et al., 2011). Within the view of cortically
142 generated beta, one class of models suggests that beta is generated by local spiking
143 interactions among cells, either consisting of pyramidal cell-interneuron loops (Jensen et al.,
144 2005; Kramer et al., 2008; Kopell et al., 2011; Lee et al., 2013) or layer 5 pyramidal cells
145 coupled via gap junctions (Roopun et al., 2006). A more recent proposal (Sherman et al.,
146 2016) suggests an intermediate model, with beta being generated in cortex but depending
147 on a (laminae-specific) exogenous drive originating from subcortical and/or cortical
148 influences (see also Schmiedt et al., 2014, suggesting cortical beta generation driven by
149 thalamic and/or top-down cortical inputs).

150

151 Based on local generator models, it has been suggested that beta is ideally suited for flexibly
152 and dynamically forming cell assemblies (Roopun et al., 2008; Kopell et al., 2011), and for
153 long-distance inter-area communication (Kopell et al., 2000). These models rely on local
154 spiking interactions between excitatory and inhibitory neurons, and on intrinsic currents of
155 the underlying pyramidal cells (e.g., h-currents or m-currents, determining the cell's rebound
156 after hyperpolarization), defining the time constants for spike firing, thereby contributing to
157 beta rhythmogenesis (Roopun et al., 2008; Kopell et al., 2011). Kopell et al. (2011) suggest
158 that beta-synchronized cell assemblies are robust as they are self-sustaining after a long,
159 decaying excitatory input (contrary to PING based networks which need ongoing input;
160 PING: pyramidal-interneuron gamma, a model of local circuit gamma generation), and can

161 concurrently exist with other cell assemblies (again, contrary to PING assemblies which
162 compete with one another as they rely on the same inhibitory interneurons). The sustained
163 nature of these cell assemblies, spiking at a low beta rate (~ 15 Hz), would allow maintaining
164 of neuronal activity patterns, i.e., a mechanism for working memory, and the linking of past
165 and present inputs.

166

167 More recently, Sherman et al. (2016) proposed a model building on prior work (Jones et al.,
168 2007; Jones et al., 2009; Sacchet et al., 2015), where cortical beta is generated in the apical
169 dendrites of large populations of spatially aligned pyramidal neurons, which span several
170 layers. Specifically, this model produces transient beta activity (<150 ms) by the integration
171 of simultaneous (subthreshold) excitatory drives to the proximal (closer to the soma) and
172 distal apical dendrites of pyramidal cells located in supragranular (layers 2/3) and
173 infragranular layers (layer 5). The weaker proximal drive (of approx. 100 ms duration) arrives
174 via granular (layer 4), the stronger distal drive (approx. 50 ms) via the supragranular layers,
175 with both extrinsic drives arising from thalamic or potentially higher-order cortical areas. The
176 model accurately generates beta “burst” events (<150 ms), with a nonsinusoidal waveform
177 as observed in spontaneous human, monkey and rodent recordings (Sherman et al., 2016).
178 Moreover, within this framework, when both drives arrive nearly synchronously at a 10-Hz
179 rate, a sustained beta rhythm can be produced. Note that a beta-rate input is neither
180 required nor sufficient for this model to produce realistic beta events (contrary to models
181 that assume generators in the basal ganglia), nor do individual cells fire at a beta rate (in
182 contrast with other local generator models). Rather, beta oscillatory activity arises from net
183 subthreshold dendritic fluctuations, relying on integration of feedforward (to granular layer)
184 and—critically—feedback inputs (to supragranular layers).

185 **Beta-band oscillations in working memory**

186

187 Numerous studies have reported beta power increases, concomitant with modulations in
188 other frequency bands, during working memory (WM) maintenance of visual (Tallon-Baudry
189 et al., 1998; Liebe et al., 2012; Lara and Wallis, 2014; Wimmer et al., 2016), verbal (Deiber et
190 al., 2007), or temporal information (Chen and Huang, 2016). Such effects occur in frontal,
191 parietal, and/or temporal areas, and can vary with WM load, i.e., the amount of to-be-
192 maintained information (Deiber et al., 2007; Honkanen et al., 2015; Chen and Huang, 2016;
193 see also Palva et al., 2011; Kornblith et al., 2016). In addition, several studies have shown
194 that WM demands can alter the degree to which beta oscillations are phase-synchronized,
195 both within and between cortical areas (Tallon-Baudry et al., 2001; Babiloni et al., 2004;
196 Tallon-Baudry et al., 2004; Axmacher et al., 2008; Salazar et al., 2012; Dotson et al., 2014).

197

198 Findings of enhanced beta activity in WM tasks appear consistent with a role in actively
199 maintaining the current cognitive set, i.e., the “status quo” (Engel and Fries, 2010). However,
200 overall changes of oscillatory activity during WM processing can depend on various task
201 factors and are also often found in frequency bands other than beta, especially theta (4–7
202 Hz), alpha, and gamma (for review, see Fell and Axmacher, 2011; Roux and Uhlhaas, 2014).
203 While overall activity changes may reflect involvement in WM, more direct insights into the
204 mechanisms of WM storage can be gained from delay activity that reflects the current
205 memory content, in terms of the task-relevant stimulus information that is to-be-maintained
206 on a given trial (Christophel et al., 2017). Such content-specific delay activity has traditionally
207 been observed in persistent neuronal spiking (e.g., Kubota et al., 1974; Miller et al., 1996),
208 local gamma band activity (Pesaran et al., 2002), as well as BOLD activity patterns (e.g.,

209 Harrison and Tong, 2009). However, a growing body of recent literature indicates that WM
210 contents can also be reflected in oscillatory brain signals, particularly in the beta frequency
211 range (e.g., Spitzer et al., 2010; Spitzer and Blankenburg, 2011; Salazar et al., 2012;
212 Mendoza-Halliday et al., 2014; Antzoulatos and Miller, 2016; Rose et al., 2016; Wimmer et
213 al., 2016).

214

215 *Content-specific modulations in scalar WM*

216 One line of evidence for content-specific delay activity in the beta band comes from studies
217 of WM for scalar magnitudes, such as the speed, intensity, or duration of a stimulus. The
218 neural basis of scalar information processing has been studied in great detail in a classic
219 somatosensory task (Mountcastle et al., 1967; Romo and de Lafuente, 2013), where
220 monkeys were trained to memorize the frequency of a brief tactile vibration (f_1) for delayed
221 comparison against a second vibration (f_2 ; see Figure 2A, top). As a seminal finding in this
222 task, the trial-specific f_1 frequency is encoded parametrically, i.e., in a monotonically graded
223 fashion, in neuronal firing rates throughout the cortical processing hierarchy (Romo and de
224 Lafuente, 2013). During the WM delay after f_1 , such parametric coding prevails in prefrontal
225 (PFC) and premotor cortex, with different cell populations either positively or negatively
226 tuned to the frequency of f_1 (Romo et al., 1999; Hernández et al., 2002; Barak et al., 2010).
227 In subsequent human EEG experiments, similar effects were observed in prefrontal beta
228 activity, with parametric modulations of oscillatory power as a function of f_1 frequency
229 (Spitzer et al., 2010; Spitzer and Blankenburg, 2011; Ludwig et al., 2016). Further studies
230 showed that such beta power modulations are not specific to vibrotactile frequency
231 information, but can also be observed for other analogue continua, like stimulus intensity,
232 motion speed, or approximate number (Spitzer et al., 2014a; Spitzer et al., 2014b; Wimmer

233 et al., 2016). A general picture emerging from this line of work is that at least some of the
234 computations underlying scalar WM are supramodal (Spitzer and Blankenburg, 2012;
235 Vergara et al., 2016; see also Nieder, 2012), potentially reflecting high-level abstractions of
236 the task-relevant magnitude, rather than concrete sensory information (Spitzer et al., 2014a;
237 Spitzer et al., 2014b; see also Christophel et al., 2017).

238

239 *Content-specific (de-)synchronization within and across areas*

240 The modulations of beta activity in scalar WM tasks were observed in power measures,
241 which are thought to reflect the local (de-)synchronization of neuronal ensembles within a
242 brain area (Pfurtscheller and Lopes da Silva, 1999). However, using more complex stimuli,
243 content-specific WM activity in the beta band has also been observed on a larger-scale
244 cortical network level. For instance, in simultaneous recordings from prefrontal and parietal
245 cortex in behaving monkeys, information about memorized visual objects could be decoded
246 not only from sustained spiking in either region, but also from the level of beta-band
247 synchronization between regions (Salazar et al., 2012). Similarly, beta synchronization of
248 prefrontal networks was found to reflect currently relevant task-rules (Buschman et al.,
249 2012) and stimulus categories (Antzoulatos and Miller, 2014, 2016; Stanley et al., 2016). In
250 another recent study, memory-coding neurons in monkey lateral PFC were found to be
251 synchronized via beta oscillations to motion-sensitive area MT, in which the memorized
252 motion information was also reflected in local field potential (LFP) power but not in spiking
253 activity (Mendoza-Halliday et al., 2014). The latter findings were interpreted as evidence for
254 top-down signaling from PFC to lower-level visual areas, in line with the emerging notion of
255 beta oscillations as a communication channel for top-down and feedback information across
256 cortex (Buschman and Miller, 2007; Bastos et al., 2015).

257 *A role in (re-)activating WM content*

258 Several lines of evidence suggest that content-specific beta oscillations do not reflect a
259 persistent memory trace *per se*, but rather, a class of endogenous processes that are
260 auxiliary to WM processing. For instance, content-dependent beta activity is typically not
261 sustained throughout entire memory delays (of several seconds), but relatively short-lived,
262 often lasting only several hundreds of milliseconds (e.g., Spitzer and Blankenburg, 2011;
263 Salazar et al., 2012). Furthermore, unlike WM codes in neuronal spiking (e.g., Romo et al.,
264 1999; Barak et al., 2010), prefrontal beta modulations are usually absent during stimulation,
265 and seem to emerge only at particular times during WM retention (Figure 2A-D). More
266 specifically, in standard delay tasks, beta modulations are mostly found late in the delay
267 (e.g., Spitzer et al., 2010; Salazar et al., 2012; Spitzer and Blankenburg, 2012; Wimmer et al.,
268 2016), when WM information might be endogenously (re-)activated or “refreshed”
269 (Johnson, 1992) in preparation for the imminent comparison task (Spitzer et al., 2010; Myers
270 et al., 2015; Wimmer et al., 2016). In contrast, when participants were explicitly (retro)-cued
271 to update WM with one of two previously presented stimuli for further maintenance,
272 prefrontal beta was modulated early after the cue, and therein selectively reflected the cued
273 stimulus information (Spitzer and Blankenburg, 2011; Spitzer et al., 2014b). Similarly, in tasks
274 where the scalar magnitude of a stimulus could only be assessed after integration over time
275 (e.g., the number of pulses in a sequence), beta modulations occurred promptly after the
276 accumulation period, as if the task-relevant scalar was “activated” in WM as soon as it was
277 internally computed (Spitzer et al., 2014a; Spitzer et al., 2014b). Taken together, rather than
278 a substrate of persistent memory storage *per se*, prefrontal beta modulations seem to
279 reflect the momentary updating, or (re-)activation, of WM content in the service of the task
280 at hand.

281 To our knowledge, content-specific beta activity in WM has thus far only been observed
282 during single-item maintenance (e.g., Salazar et al., 2012; Dotson et al., 2014; Mendoza-
283 Halliday et al., 2014), and several findings suggest that the capacity of beta-associated WM
284 updating might be limited to a single piece of information in the current focus of attention
285 (Spitzer and Blankenburg, 2011; Spitzer et al., 2014b; Antzoulatos and Miller, 2016; Wimmer
286 et al., 2016; cf. Oberauer, 2002). However, one recent study showed that an additional,
287 currently unattended memory item can be pushed into an active WM state by transcranial
288 magnetic stimulation (TMS) of WM-coding areas (Rose et al., 2016). Interestingly, whereas
289 the currently attended memory information could be decoded from various EEG frequency
290 bands, the TMS-induced reactivation of the unattended memory item was exclusively
291 evident in content-specific beta activity. In other words, beta activity specifically marked the
292 transition of “latent” WM contents (see below; Mongillo et al., 2008; Stokes, 2015) into an
293 active memory, consistent with a role of beta in updating, or reactivating, information in the
294 current focus of WM.

295

296 *Neurocomputational perspectives on beta oscillations in WM*

297 A role of beta oscillations in WM has also been put forward in computational modeling work
298 (e.g., Kopell et al., 2011; Lundqvist et al., 2011; Dipoppa and Gutkin, 2013). Simulations by
299 Kopell et al. (2011), for instance, showed beta oscillations to be uniquely suited to form and
300 coordinate cell assemblies for sustained stimulus processing in the absence of further input,
301 eventually permitting the co-existence of past and present stimulus information in the same
302 network. In this view, beta rhythms may scaffold functional assemblies for active WM
303 processing. Another line of modeling studies, with a focus on multi-item WM, suggests a
304 sequential replay of individual WM items (see also Lisman and Jensen, 2013), in terms of

305 alternations between “ground” and “active” states (see below), where the former is
306 dominated by alpha/beta and the latter by gamma (Lundqvist et al., 2010; Lundqvist et al.,
307 2011). Corroborating this idea, Lundqvist et al. (2016) reported a dissociation between beta
308 and gamma during multi-item WM in monkey PFC, where gamma bursts were associated
309 with stimulus encoding and decoding in spikes, whereas beta bursts prevailed during
310 memory maintenance. However, it was not analyzed whether beta and/or gamma bursts
311 themselves carried information about the WM contents, leaving the question of content-
312 specific beta activity in multi-item WM to future research (but see Siegel et al., 2009, for a
313 potential role of beta phase in multi-item WM).

314

315 **Beta-band oscillations in decision-making**

316

317 Given the well-documented involvement of beta-band oscillations in movement preparation
318 (Murthy and Fetz, 1992; Sanes and Donoghue, 1993; Crone et al., 1998; Pfurtscheller and
319 Lopes da Silva, 1999), it seems not surprising that sensorimotor beta effects are routinely
320 observed in decision-making tasks where choices are to be communicated via a motor
321 response (e.g., Kaiser et al., 2007; Zhang et al., 2008; Bidet-Caulet et al., 2012). During
322 perceptual discrimination of auditory stimuli, for instance, the latency of preparatory beta
323 power modulation was found to mimic response time differences across varying levels of
324 task difficulty (Kaiser et al., 2007). Such effects typically manifest as sensorimotor power
325 decreases contralateral to the to-be-moved limb, and are commonly assessed using
326 lateralization indices (e.g., contrasting left- vs. right-hemispheric activity associated with
327 right/left hand choices; Donner et al., 2009; Gould et al., 2012; Wyart et al., 2012). A
328 traditional view is that beta oscillations in decision-making reflect motor preparation only,

329 i.e., a serial processing view where the effector-specific motor plan is the final step, after
330 higher-order areas have reached a decision based on sensory input. However, as will be
331 outlined below, accruing evidence points to a more direct involvement of beta oscillations in
332 decision formation, which may or may not be linked to a specific motor plan.

333

334 *Dynamic accumulative updating*

335 Several recent studies suggest that lateralized beta activity during decision-making tasks may
336 not only reflect terminal movement preparation, but a dynamic process of accumulatively
337 updating a motor plan as a decision evolves (Donner et al., 2009; Gould et al., 2012;
338 O'Connell et al., 2012; Wyart et al., 2012; Kubanek et al., 2013; Wyart et al., 2015). For
339 instance, analyzing human MEG activity in a visual motion-detection task, Donner et al.
340 (2009) reported a slowly evolving, gradual beta power lateralization in (pre-)motor cortex
341 that tracked the current state of evidence accumulation, as inferred from the temporal
342 integral of gamma activity in motion-sensitive area MT (Figure 3A). Similar observations
343 were made in human EEG studies where participants integrated sequential samples of
344 decision information over extended periods of time (Gould et al., 2012; Wyart et al., 2012;
345 Kubanek et al., 2013; Wyart et al., 2015). In these studies, sensorimotor beta was found to
346 reflect the integral of accumulated decision information in the form of a gradual response
347 preparation signal, downstream to the encoding of sample-level decision information in
348 parietal EEG signals (Gould et al., 2012; Wyart et al., 2012; Kubanek et al., 2013).

349

350 Together, these studies support a role for beta in dynamic updating of the decision outcome
351 as mapped onto a motor response. However, a key point in the above studies is that they *a*
352 *priori* operationalized beta activity as a response-related signal. More specifically, they used

353 a fixed mapping between decision outcomes and motor responses (usually left/right hand
354 action), and assessed sensorimotor beta activity in terms of lateralization indices, relying on
355 the contra-lateralized nature of sensorimotor activity. Critically, this approach disregards
356 choice-related activity that might occur independent of the associated left/right response
357 mapping. In fact, when the fixed link between decision outcomes and left/right effectors is
358 removed, the effects in sensorimotor beta lateralization typically disappear (O'Connell et al.,
359 2012; Twomey et al., 2016).

360

361 *A content-specific decision signal?*

362 Several recent studies go beyond this approach, and demonstrate a role for beta oscillations
363 in perceptual decision tasks that appears independent of motor-response mapping (Haegens
364 et al., 2011b; Herding et al., 2016; Stanley et al., 2016; Wimmer et al., 2016). Haegens et al.
365 (2011b) used a variant of the somatosensory frequency discrimination task described earlier
366 (Mountcastle et al., 1967; Romo and de Lafuente, 2013). As outlined above, during the
367 retention period of such tasks, the first stimulus frequency (f_1) is reflected parametrically in
368 (pre-)frontal areas, both in terms of single-cell firing rates (e.g., Romo et al., 1999; Barak et
369 al., 2010; Vergara et al., 2016) and in upper beta activity (Spitzer et al., 2010). Notably,
370 during the ensuing decision period (i.e., after f_2 is presented), Haegens et al. (2011b) found
371 that the level of beta power in monkey sensorimotor cortex (including somatosensory,
372 premotor and motor areas) signaled the categorical outcome of the f_1 - f_2 comparison (i.e.,
373 " $f_2 > f_1$ " or " $f_1 < f_2$ "). This effect proved independent of the absolute frequencies of f_1 and f_2
374 (or their exact numerical difference) and reflected the monkey's categorical choices even on
375 error trials (Figure 3B). Importantly, this choice-related beta activity was not merely related
376 to motor planning, as all choices were reported with the left hand, and the effect

377 disappeared in a control condition in which the same motor response but no f1-f2
378 comparison was required. These findings complement previous reports on spike firing rate
379 modulation in the same paradigm: during the comparison period, firing rates of
380 sensorimotor and prefrontal cells gradually reflected a categorical response, corresponding
381 to the decision outcome (Hernández et al., 2002; Romo et al., 2002; Hernández et al., 2010).
382 Therein, similar to the “parametric” WM ensembles described earlier (Romo et al., 1999),
383 decision-coding cells fall into two complementary classes, with one group of cells positively
384 tuned (i.e., increasing its firing) to the “f2>f1” choice and another negatively tuned
385 (Hernández et al., 2002).

386

387 A beta-band effect replicating and extending the monkey findings by Haegens et al. (2011b)
388 was recently observed in human EEG recordings (Herding et al., 2016). Here too, during
389 vibrotactile frequency discrimination, the level of non-lateralized beta power in premotor
390 areas was modulated according to participants’ decision outcomes (f2>f1 or f2<f1) in a
391 categorical fashion (Figure 3C). Again, this effect reflected subjective choices, including
392 errors, as inferred from Bayesian modeling of f1-f2 choice behavior. Furthermore,
393 capitalizing on a larger subject sample, this effect was found to be invariant across motor
394 response mappings: even when the response scheme (index or middle finger of the right
395 hand) was flipped (across participants), the beta modulations remained unchanged (Herding
396 et al., 2016). In a follow-up study, virtually identical beta patterns were observed when
397 saccades rather than button-presses were used to communicate the decision. Now decision-
398 selective beta activity was localized to more lateral premotor areas (including the frontal eye
399 fields), suggesting a degree of effector-specificity in terms of areas involved, but with a
400 consistent role for beta (Herding et al., 2017).

401 Combined, these studies suggest that in scalar comparison tasks, sensorimotor beta
402 oscillations can reflect the categorical, potentially abstract content of a decision, even
403 independent of a concrete motor plan. One possibility is that such non-lateralized, content-
404 dependent beta activity relates to the endogenous activation of categorical, conceptual
405 information prior to local translation into an effector-specific response. This interpretation is
406 in line with a recent study recording LFPs in lateral PFC of macaques performing a visual
407 categorization task, which reported different patterns of beta coherence for different
408 categories of morphed stimuli (ranging for instance from cat to dog), “as if low-beta
409 coherence was helping to form the neural ensembles that represented the categories”
410 (Stanley et al., 2016). In further support of this view, when macaques had to judge random-
411 dot motion stimuli, beta activity in lateral PFC signaled the categorical decision outcome
412 (here, “same” or “different”), with beta modulation in different recording sites
413 corresponding to the different outcomes (Wimmer et al., 2016). As for the somatosensory
414 studies discussed above, this observation complemented findings from single unit spike
415 recordings in the same paradigm (Hussar and Pasternak, 2012): different cells increased their
416 firing rate either for “same” or for “different” choices. Thus, there appear to be parallels
417 between modulations of local beta activity and single unit firing rates, in that both signal the
418 emergence of a categorical decision outcome.

419

420 *Decision circuits*

421 The role of beta oscillations in decision-making might be extended to include long-range
422 interactions, again in line with WM findings discussed earlier. The decision effects observed
423 by Haegens et al. (2011b), for instance, included a distributed network of somatosensory
424 and (pre)motor areas. More direct support for a role in network-level processing comes from

425 a reach-planning study, demonstrating higher beta-band spike-field coherence (SFC; the
426 synchronization of spikes to oscillatory phase) between premotor cortex and the parietal
427 reach region when monkeys were freely making choices as compared to instructed choices
428 (Pesaran et al., 2008). The authors proposed that here, beta coherence reflected a decision
429 circuit between frontal and parietal cortex, which was more activated under free choice
430 conditions. Similarly, beta-band SFC in posterior parietal cortex reflected decisions in a
431 reward-guided choice task (Hawellek et al., 2016). In this study, information about
432 movement choice in firing rates was quantified and related to the phase of beta and gamma
433 oscillations. While for gamma, peak firing rate and maximum information content coincided,
434 for beta the highest spike count preceded maximum information. These differences in
435 temporal alignment were linked to the idea that gamma reflects local, bottom-up
436 processing, while beta links distributed ensembles for computations on a larger scale.
437 Further evidence for beta facilitating long-range communication was obtained in a recent
438 auditory perceptual decision-making study, in which large-scale network dynamics in the
439 beta band predicted decision speed (Alavash et al., 2017).

440

441 To summarize, a growing body of evidence suggests that content-specific beta oscillations
442 can signal the endogenous activation of a categorical decision outcome prior to translation
443 into a concrete motor response. Several studies show that such content-specific decision
444 activity in the beta band can be observed beyond sensorimotor regions, both within and
445 between distributed cortical areas.

446

447

448

449 **A role for beta oscillations in endogenous content (re-)activation**

450

451 In the previous sections, we have discussed research in the domains of working memory and
452 decision-making, showing that beta activity can be modulated in a content-specific manner.
453 Here, we outline a framework for beta oscillations in endogenous (re-)activation of cortical
454 content representations (illustrated in Figure 4A). We presume that active cortical
455 representations of task-relevant information are reflected in the (spiking) activity of content-
456 specific neuronal ensembles (Figure 4A, first panel). We further assume that in the absence
457 of stimulation or endogenous prioritization, representations of task-related information can
458 persist without sustained ensemble spiking, for instance, in patterns of synaptic weights
459 (e.g., Jonides et al., 2008). Such dormant, or “latent” memory representations (Figure 4A,
460 second panel) may for instance be characterized by short-term synaptic facilitation (Mongillo
461 et al., 2008; Stokes, 2015) for just presented stimuli, and/or by long-term synaptic
462 potentiation (Hebb, 1949) for overlearned (e.g., abstract/categorical) contents. A general
463 assumption in this framework is that latent memory information can be endogenously
464 restored into an “active” (i.e., spiking) cortical representation (Figure 4A, last panel), for
465 instance by top-down attentional prioritization (e.g., Warden and Miller, 2007; Jonides et al.,
466 2008; Jacob and Nieder, 2014; Watanabe and Funahashi, 2014; Sprague et al., 2016). The
467 mechanisms by which such endogenous (re-)activation might occur, however, have thus far
468 remained unclear. Here, based on the accumulating evidence reviewed above, we propose
469 that this role is filled by content-specific beta band activity. More specifically, we suggest
470 that episodes of content-specific beta synchronization support the endogenous transition
471 from latent to active cortical representations (Figure 4A, third panel), in the service of
472 current task demands.

473 Oscillatory synchronization is associated with fluctuations in local network excitability
474 (Bishop, 1932), and faster rhythms (>15 Hz) in particular are proposed to support flexible
475 information routing by providing windows of efficient inter-areal communication (Fries,
476 2015; Palmigiano et al., 2017). Oscillations in the beta band seem particularly well suited to
477 fill these roles during endogenously driven information processing, given (i) their association
478 with top-down processing (Engel and Fries, 2010; Wang, 2010) and (ii) long-range
479 communication (Kopell et al., 2000; Varela et al., 2001; Sherman et al., 2016), (iii) their burst-
480 like temporal dynamics (Jones, 2016), (iv) their presumed role in the flexible formation and
481 manipulation of functional cell assemblies (Roopun et al., 2008; Kopell et al., 2011), and (v)
482 their capacity to modulate impact of neuronal firing (Buzsáki and Draguhn, 2004; Wang,
483 2010). While several of these characteristics may also apply to other rhythms, the
484 combination of all these aspects appears unique to beta.

485

486 Mechanistically, the association of endogenously driven ensemble activation with beta
487 oscillations is in line with models of beta generation that rely on integration of concurrent
488 inputs along the proximal and distal locations of the apical dendrites of pyramidal cells
489 (Sherman et al., 2016; Jones et al., 2009). This integration includes both feedforward
490 (lemniscal thalamic) input via the granular layer, and, critically, feedback (higher-order
491 cortical and/or nonlemniscal thalamic) drives to the supragranular layers (essential for beta
492 emergence in the model), permitting top-down driven synchronization of a cell assembly,
493 mitigated via cortico-(thalamo)cortical drives. Furthermore, based on models that rely on
494 beta-rate spiking-interactions within local cortical circuits (Kopell et al., 2011), it has been
495 argued that beta-synchronized ensembles are less susceptible to competition (unlike
496 PING/gamma networks). In the present context, this property of beta might permit

497 endogenous content activation to operate in a “protected” oscillatory regime that is
498 relatively robust to distractor interference, e.g., from concurrent sensory inputs.

499

500 We may further speculate that beta is an ideal “transit” band for endogenously driven (re-
501)activation, bridging the frequency space between alpha, which is commonly associated with
502 top-down inhibition (Klimesch et al., 2007; Haegens et al., 2011a), and gamma, which is
503 positively linked to population spiking (e.g., Whittingstall and Logothetis, 2009). Relatedly,
504 previous modeling work (Lundqvist et al., 2010; Lundqvist et al., 2011) has characterized
505 (WM-)reactivation as a transition from a low-frequency (alpha/beta) oscillatory regime
506 (associated with a non-coding “ground”- or “default” state) to a higher frequency/gamma
507 regime (associated with “active” stimulus coding), similar to our conceptualization of latent
508 and (re-)activated representations (cf. Figure 4A, second and fourth panels). Superficially,
509 the association of beta with a “default” state (Lundqvist et al., 2016; see also Engel and Fries,
510 2010) appears inconsistent with a role in content (re-)activation. However, the two
511 perspectives can be reconciled when considering that content-specificity (in terms of
512 experiment-related information; which might be dissociable from less specific, ongoing beta
513 rhythmicity, see *Future Perspectives* below) emerges only during the critical transition
514 between representational states (Figure 4A, third panel).

515

516 Our proposal captures various hallmarks of content-specific beta activity in the domains of
517 WM and decision-making. First, under this framework, content-specific beta episodes are
518 expected to be relatively short-lived (see also Jones, 2016; Sherman et al., 2016), since they
519 would reflect neither latent nor active representations per se, but only a—presumably
520 brief—transition period between the two (Figure 4A). Consistently, content-specific beta

521 modulations in WM tasks are typically observed in circumscribed time windows, in which
522 participants should bring back past information into the focus of attention (e.g., Spitzer and
523 Blankenburg, 2011; Spitzer et al., 2014b; Wimmer et al., 2016). Similarly, beta-oscillatory
524 representations of task rules in monkey prefrontal cortex were short-lived (see Figure 2F)
525 and appeared only while a stimulus was to be evaluated according to the current rule
526 (Buschman et al., 2012). Notably, in the Buschman et al. study, rules were only switched
527 between blocks of trials, likely leading to a (latent) memory of the current rule that persisted
528 across trials. A representation of such memory in beta synchrony was indeed absent
529 throughout large portions of the trial, and emerged only shortly before the to-be-evaluated
530 stimulus, as if the current rule was endogenously (re-)activated for task-oriented processing.
531 Before and after this brief episode, prefrontal firing rates—but not beta synchrony—
532 encoded just-presented cues, consistent with our differentiation of purely endogenous (re-
533)activation processes in the beta band from “active” neuronal representations per se (Figure
534 4A).

535

536 In a similar vein, the proposed framework can explain findings of content-specific beta
537 activity during categorization and decision-making, in dissociation from traditional indices of
538 motor preparation. In categorization tasks, subjects are asked to select one of two (or more)
539 internalized prototype concepts, which in our framework entails the endogenous activation
540 of a stored content representation. Indeed, category-selective beta synchronization during
541 stimulus categorization was found only after extensive category learning (Antzoulatos and
542 Miller, 2014, 2016), corroborating the idea that beta is especially involved in *re-activating*
543 cortical representations. Likewise, modulations of beta activity according to categorical
544 decision outcomes, such as in the vibrotactile frequency comparison tasks described earlier,

545 can be understood in terms of endogenously activating an abstract concept representation,
546 e.g., “higher” (“ $f_2 > f_1$ ”) or “lower” (“ $f_2 < f_1$ ”). Indeed, on any given trial in the above tasks, the
547 concepts or categories in question may co-exist in form of latent representations, one of
548 which will be activated at the time of choice, as reflected in content-specific beta activity.

549

550 Our framework is further consistent with a non-trivial relationship between beta oscillations
551 and spiking activity (e.g., Whittingstall and Logothetis, 2009; Rule et al., 2017). Conceiving of
552 content-specific beta activity as a transition period (Figure 4A), temporal correlations with
553 spike firing can be weakly negative or positive, depending on how strongly beta episodes
554 overlap in time with (still) dormant or (already) activated representations. Furthermore,
555 rather than in- or decreases of net firing rates in a given area, we assume a (content-specific)
556 distribution of neuronal firing within and/or between functional ensembles. This idea is in
557 line with the spatio-temporal coincidence of local beta modulations with a shifting of firing
558 rates between oppositely tuned cell populations (Romo et al., 1999; Hernández et al., 2002;
559 Barak et al., 2010; Spitzer et al., 2010; Haegens et al., 2011b; Hussar and Pasternak, 2012;
560 Wimmer et al., 2016). In these contexts, beta activity may appear content-specific to the
561 extent that population-level recordings (such as M/EEG or LFP) register the oscillatory
562 signatures of individual subpopulations with different sensitivity (Figure 4B). As a corollary of
563 this view, the sign of content-dependent beta modulations (e.g., whether local beta activity
564 in- or decreases for a given content) might be non-informative and dependent on the
565 particular recording setting. However, the precise relation between beta oscillations and
566 spiking ensemble activity remains speculative and awaits further investigation.

567

568 Based on the available findings across primate species, endogenous content (re-)activation
569 can include modulations of beta activity both locally and in terms of long-range
570 synchronization between distant regions (see Figure 1B). Modulations of local beta power
571 have mostly been observed for low-dimensional information, such as scalar stimulus
572 attributes (e.g., Spitzer et al., 2010; Haegens et al., 2011b; Wimmer et al., 2016). Higher-
573 dimensional contents, such as object identity or task rules, have been associated with
574 sophisticated patterns of beta synchronization between multiple recording sites, potentially
575 reflecting the activation of more distributed cortical representations (e.g., Buschman et al.,
576 2012; Salazar et al., 2012; Antzoulatos and Miller, 2016). In all of these cases, beta seems to
577 provide a flexible scaffolding that sets up functional neuronal ensembles through temporary
578 synchronization of content-coding cell populations. The demand for flexibility in ensemble
579 formation may be particularly high in regions with “mixed selectivity” cells (Rigotti et al.,
580 2013), such as the prefrontal and parietal cortices, where single neurons respond to a
581 multiplicity of task variables (for review, see Fusi et al., 2016). It might be especially in
582 communication within and with these regions that frequency-specific synchronization
583 finesses the active representation of internally stored information alongside current input, in
584 potentially overlapping functional networks.

585

586 *Future perspectives*

587 An open question remains whether transient content-specificity of beta emerges from a
588 modification of ongoing beta rhythmicity (cf. Engel and Fries, 2010; Lundqvist et al., 2016),
589 or whether the two reflect functionally dissociable phenomena in overlapping frequency
590 ranges. It is possible that the beta band encompasses several rhythms, including a
591 potentially “inhibitory” rhythm that is functionally more similar to alpha and which seems

592 especially prevalent in somatomotor context (for review, see Kilavik et al., 2013). Indeed, the
593 possibility that beta is not a unitary phenomenon but covers several roles may help to
594 reconcile seemingly disparate observations, such as WM-load related beta-power increases
595 in some studies (e.g., Deiber et al., 2007; Kornblith et al., 2016), but decreases in others (cf.
596 e.g., Siegel et al., 2009; Lundqvist et al., 2011). Relatedly, several authors divide the beta-
597 band into a lower (<20 Hz) and a higher (>20 Hz) sub-range (Roopun et al., 2006; Kopell et
598 al., 2011), with potentially distinct functional roles (see Introduction). In the literature
599 reviewed here, however, we found only a weak—if any—tendency for content-specific
600 effects (Figure 1A, right) to occur in a higher beta frequency than overall, task-related
601 modulations (Figure 1A, left), with considerable variability across experiments, leaving the
602 question of potentially distinct beta rhythms (and the determinants of their precise
603 frequencies across cortical areas) to future targeted study.

604

605 A more general open question is the very nature of “latent” representations that are
606 amenable to beta-mediated re-activation. As one possibility, content-specific beta activity
607 might reflect a direct drive to reactivate activity-silent (e.g., synaptic) representations, as
608 schematically illustrated in Figure 4A. In an alternative scenario, dormant memory
609 representations are kept “silent” by actively inhibitory mechanisms, for instance, by content-
610 matching “inhibitory engrams” (Ramaswami, 2014; Barron et al., 2017). Under this view,
611 cortical reactivation may result from a release from inhibition, by suppression of inhibitory
612 engrams, a scenario in which beta-mediated reactivation might indeed operate via inhibitory
613 processes (“inhibition of inhibition”; Pfeffer et al., 2013). A related issue is the extent to
614 which beta-mediated reactivation relies on the contents or concepts in question being
615 familiar and consolidated in long(er)-term memory (which we assumed to be the case in

616 most of the above reviewed studies). It remains to be shown empirically whether content-
617 specific synchronization plays a role also in reactivating representations of entirely novel,
618 just encountered information, a “silent” memory of which may persist only in transient
619 patterns of short-term synaptic plasticity (Mongillo et al., 2008; Stokes, 2015).

620

621 Lastly, a key question for future work is how burst-like, transient beta events are temporally
622 organized. One possibility is that temporal context is provided by other (lower) frequency
623 rhythms that modulate beta via cross-frequency interactions. For instance, delta oscillations
624 (1–3 Hz) are thought to tap into the temporal structure of behaviorally relevant events
625 (reviewed in Merchant et al., 2015; cf. Lakatos et al., 2008; Schroeder and Lakatos, 2009),
626 with faster oscillations “nested” in these slower rhythms. Such interactions might manifest in
627 phase-amplitude coupling, where the phase of delta provides “windows-of-opportunity” for
628 beta to burst. Indeed, there are indications that beta power can be modulated by delta
629 oscillations in the context of WM (Siegel et al., 2009) and temporal prediction (Arnal et al.,
630 2015; Herrmann et al., 2016). Such temporal structuring could be implemented via
631 corticothalamocortical, and/or cortico-basal ganglia loops (cf. Merchant et al., 2015). For
632 example, beta could be timed by bursting thalamic inputs (cf. Sherman et al., 2016), which in
633 turn could be gated via the basal ganglia. Albeit speculative, these ideas are in line with
634 studies showing that beta oscillations in the basal ganglia are associated with interval timing
635 (e.g., Bartolo et al., 2014), providing promising avenues for future research.

636

637 *Conclusion*

638 To summarize, we propose that content-specific beta synchronization provides a mechanism
639 for the formation of functional neuronal ensembles during endogenous (re-)activation of

640 cortical representations. This framework is in line with the emerging view that beta
641 facilitates network-level communication (Kopell et al., 2000; Varela et al., 2001; Siegel et al.,
642 2011) and specifically endogenous, top-down driven interactions (Engel and Fries, 2010;
643 Wang, 2010; Arnal and Giraud, 2012; Bastos et al., 2012; Sherman et al., 2016). However,
644 beyond a static role in maintaining the “status quo” (cf. Engel and Fries, 2010), we
645 characterize content-specific beta synchronization as a dynamic and highly flexible
646 mechanism, one that can “wake up” (see also Fries, 2015)—rather than merely preserve—an
647 endogenous cognitive set. This proposal accommodates accumulating findings in animals
648 and humans and outlines a functional role for beta that may fit its “burst-like” temporal
649 characteristics (Jones, 2016). An intriguing question for future research is whether and how
650 the beta-band dynamics discussed here interact with sensorimotor rhythms when (re-
651)activated content representations are translated into concrete action plans.

652

653

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655

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1042 **Figure Legends**

1043

1044 **Figure 1. Beyond motor control: Schematic overview of oscillatory beta-band effects across**
1045 **cortex. A.** Overall beta activity changes (in-/decreases) associated with different cognitive
1046 functions (NB: non-exhaustive). **B.** Content-specific modulations of beta-band activity; see
1047 text for details. For convenience, findings from human- and non-human primate studies are
1048 rendered on a common template. Unless specified (L: left, R: right; C: contralateral), effects
1049 were not systematically lateralized.

1050

1051 **Figure 2. Content-specific beta activity during WM processing. A.** During WM maintenance
1052 of vibrotactile frequency information, prefrontal EEG beta power is parametrically modulated
1053 by the frequency of the to-be-maintained stimulus (f_1). Adapted with permission from
1054 Spitzer et al. (2010). **B.** Similar beta power modulations were found in LFP recordings in
1055 monkey prefrontal cortex during WM maintenance of visual motion information. Adapted
1056 with permission from Wimmer et al. (2016). Note that in the standard delay tasks in A-B,
1057 beta modulations occurred mostly late in the WM delay period. **C.** In contrast, when
1058 participants were retro-cued to focus on a given WM content for further maintenance, beta
1059 was modulated early after the cue. Adapted with permission from Spitzer and Blankenburg
1060 (2011). **D.** Similar early modulations were observed during WM processing of the
1061 approximate number of previously presented inputs (3–8 pulses in rapid sequence,
1062 illustrated in purple). Adapted with permission from Spitzer et al. (2014a). **E.** Content-specific
1063 fronto-parietal beta synchronization during WM maintenance of visual object information in
1064 monkeys. As in A-D, these effects were absent during stimulus encoding. Adapted with
1065 permission from Salazar et al. (2012). Reprinted with permission from AAAS. **F.** Rule-

1066 dependent beta-synchronization in monkey prefrontal cortex at the time of the to-be-
1067 evaluated stimulus (see also Figure 4C). Adapted with permission from Buschman et al.
1068 (2012). Reprinted with permission from Elsevier.

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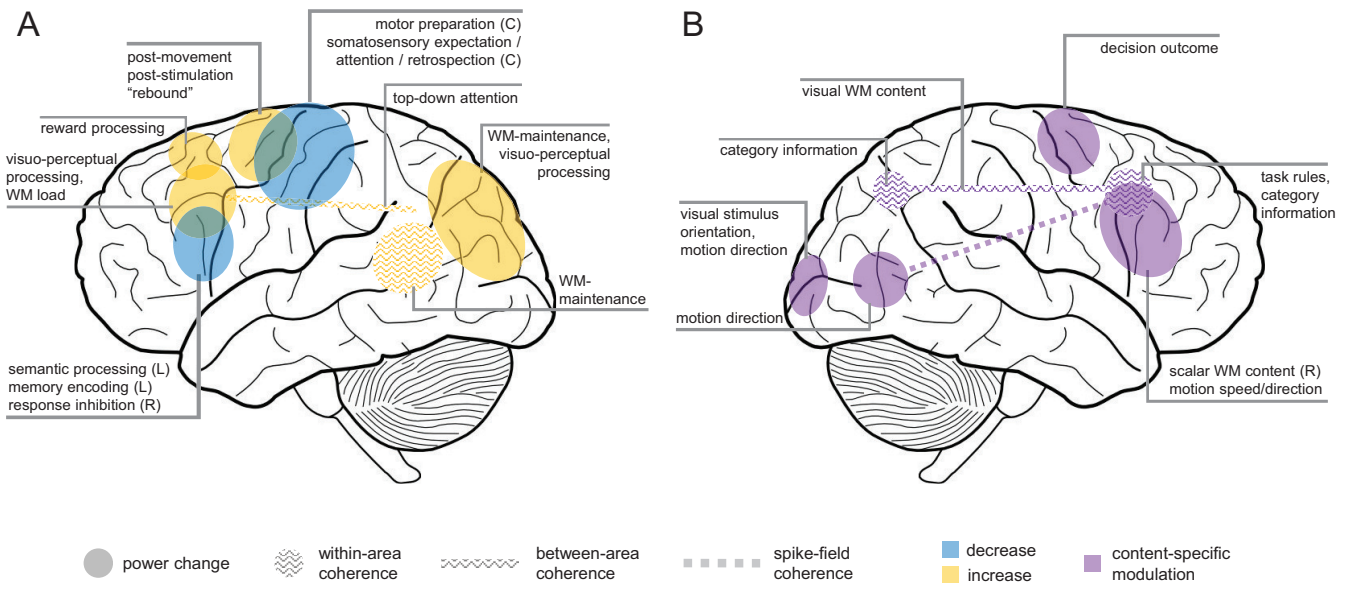
1070 **Figure 3. Content-specific beta activity during decision-making. A.** Source reconstruction
1071 showing lateralized, effector-selective beta activity (left- versus right-hand response) prior to
1072 button press, in human subjects performing a visual motion detection task (left panel). Time
1073 courses of lateralized beta activity in motor cortex indicate accumulative updating of the
1074 motor plan as a decision evolves (right panel). Adapted with permission from Donner et al.
1075 (2009). Reprinted with permission from Elsevier. **B.** Beta power modulation in monkey medial
1076 premotor cortex prior to motor response in vibrotactile discrimination task reflects binary
1077 decision outcome, also on error trials. Spectra on the right are averaged over the time
1078 window indicated by dashed box in the left panel, per stimulus class (sorted by f2-f1
1079 difference), for correct and incorrect trials separately. Adapted with permission from
1080 Haegens et al. (2011b). **C.** Remarkably similar observation as in B, in human EEG recordings
1081 using the same paradigm. Adapted with permission from Herding et al. (2016). © 2016 by
1082 the Massachusetts Institute of Technology, published by the MIT Press.

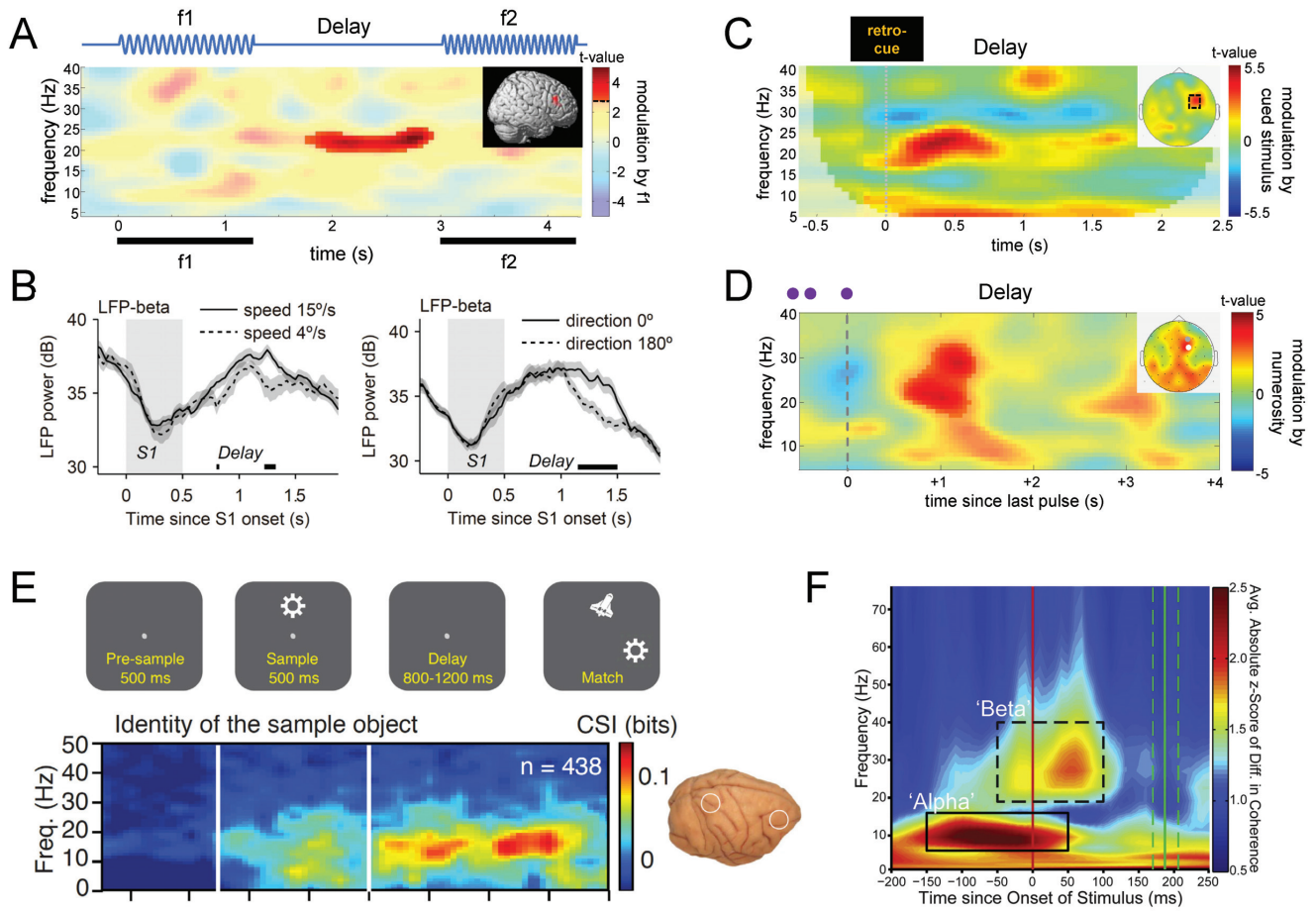
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1084 **Figure 4. A framework for content-specific beta activity. A.** Content-specific beta
1085 synchronization as endogenously driven transition from latent to active cortical
1086 representation. Left: *active* cortical representations (e.g., of currently perceived, task-
1087 relevant information) are characterized by spiking activity (symbolized in red) in content-
1088 specific neuronal ensembles. Second from left: In the absence of perceptual input and/or
1089 attentional prioritization, information can be retained in *latent* memory representations,

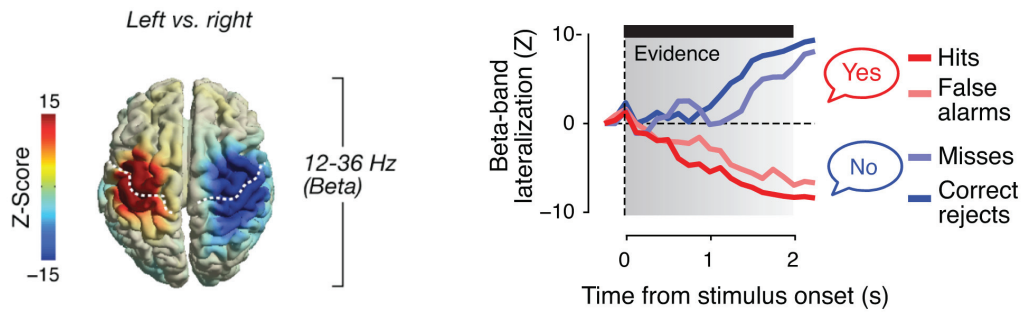
1090 without spiking activity in the content-specific ensemble, e.g., in patterns of synaptic
1091 weights. Second from right: Endogenously driven *(re-)activation* of a content-coding
1092 ensemble is characterized by a brief period of beta synchronization, involving both local and
1093 long-range (top-down) interactions (see text for details). Right: *(re-)activated* content
1094 representations may again be characterized by spiking ensemble activity, similar (but not
1095 necessarily exactly identical) to representations of just perceived information (cf. *left*). **B.**
1096 Local beta activity appears content-specific when population-level recordings register the
1097 synchronization of individual subpopulations (symbolized in blue and red) with differential
1098 sensitivity (e.g., red>blue, by spatial proximity to recording site). **C.** Transient network-level
1099 beta coherence in monkey prefrontal cortex during application of different task rules (see
1100 also Figure 2F, dashed rectangle). Adapted with permission from Buschman et al. (2012).
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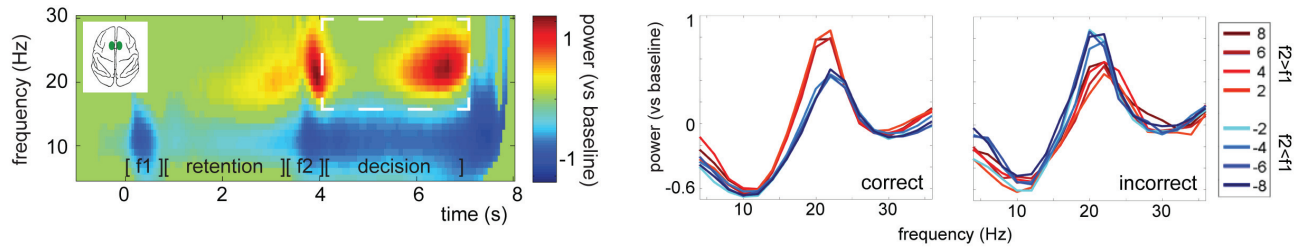




A



B



C

