

1 **Neural Dynamics in Speech Processing: Properties, Specificity and Open Questions**

2 **Running title:** Neural Dynamics in Speech Processing

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12 **The authors report no conflict of interest.**

13 **Acknowledgements:** This work was supported by the Agence Nationale de la Recherche
14 (grant numbers ANR-21-CE37-0002 and ANR-21-CE37-0003) and the Fondation pour
15 l'Audition (grant number FPA-RD-2021-10).

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19

20 **Abstract**

21

22 Human speech is a particularly relevant acoustic stimulus for our species, due to its role of
23 information transmission during communication. Speech is inherently a dynamic signal, and a
24 recent line of research focused on neural activity following the temporal structure of speech.
25 We review findings that characterise neural dynamics in speech processing and compare them
26 with temporal aspects in human speech. We highlight properties and constraints that both neural
27 and speech dynamics have, suggesting that auditory neural systems are optimised to process
28 human speech. We then discuss the speech-specificity of neural dynamics and their potential
29 mechanistic origins, and summarise open questions in the field.

30

31 Neural Dynamics in Speech Processing: Properties, Specificity and Open Questions

32

33 Human speech is possibly the most relevant acoustic stimulus for our species, at least one we
34 are continuously exposed to since birth. The fact that humans use speech to communicate
35 assigns it a distinct role among the multitude of sounds we are confronted with. Naturally, the
36 question how speech is processed in the brain has a long tradition in research (Moore, 2000;
37 Galantucci *et al.*, 2006; Steinschneider *et al.*, 2013; Carbonell & Lotto, 2014) and produced
38 important results. Studies on brain-function mapping have revealed a complex functional
39 neuroanatomy of speech that comprises temporal, parietal, and frontal regions of the cortex
40 (Hickok & Poeppel, 2007, 2016) as well as subcortical contributions (Kotz & Schwartz, 2010).
41 Speech, however, is a dynamic signal and carries relevant acoustic and linguistic information
42 in the temporal domain. Neural analysis of speech therefore requires information processing at
43 different time scales in parallel, from relatively brief phonemes to slower sentential information.
44 Research in the neurobiology of speech has started to address this facet of speech processing
45 by putting focus on the temporal aspect of neural activity. As we describe in this review, the
46 role of such *neural dynamics* for speech processing and the challenges that go along with such
47 a dynamic signal begin to be understood. In particular, neural dynamics have been shown to
48 follow the temporal structure of spoken utterances at distinct times scales. This phenomenon is
49 sometimes described as “neural tracking” or “neural entrainment in the broad sense” (Obleser
50 & Kayser, 2019). Although neural dynamics track a large variety of acoustic inputs, including
51 simple tone sequences (Lakatos *et al.*, 2008), beats (Nozaradan *et al.*, 2012), and music
52 (Doelling & Poeppel, 2015), they are thought to be necessary for successful speech
53 comprehension, and to contribute to the parsing of continuous speech into relevant linguistic
54 units (Giraud & Poeppel, 2012).

55

56 A long-standing question revolves around the mechanistic origins of neural tracking and, in
57 particular, whether it involves endogenous brain rhythms (Haegens & Zion Golumbic, 2018;
58 Zoefel, ten Oever, *et al.*, 2018; Lakatos *et al.*, 2019; Obleser & Kayser, 2019). In this review,
59 we first step away from this debate and focus, with no assumption on the underlying neural
60 implementation, on dynamic properties of neural activity that are relevant for speech
61 processing. In a first part, we describe these properties and their constraints, and discuss in how
62 far they might relate to challenges and demands that the dynamic complexity of speech imposes
63 onto the neural system. In a second part, we summarise to what extent these dynamic constraints
64 and properties are more pronounced or different during the processing of speech as compared

65 to that of other auditory signals. In the last part of the review, we consider how far neural
66 oscillatory models of speech processing can explain the described effects, and propose testable
67 hypotheses that result from this assumption. We conclude with open questions for research on
68 neural dynamics and speech processing.

69

70 **1. Properties of neural dynamics in the auditory system (and beyond) and how they**
71 **relate to those of human speech**

72

73 Human speech has rapid and complex temporal dynamics and therefore requires fast and
74 efficient temporal processing. In this chapter, we focus on properties of neural dynamics,
75 particularly in the auditory system, that seem ideal for this purpose. We also discuss how these
76 properties, along with their limits and constraints, might relate to the temporal characteristics
77 of speech.

78

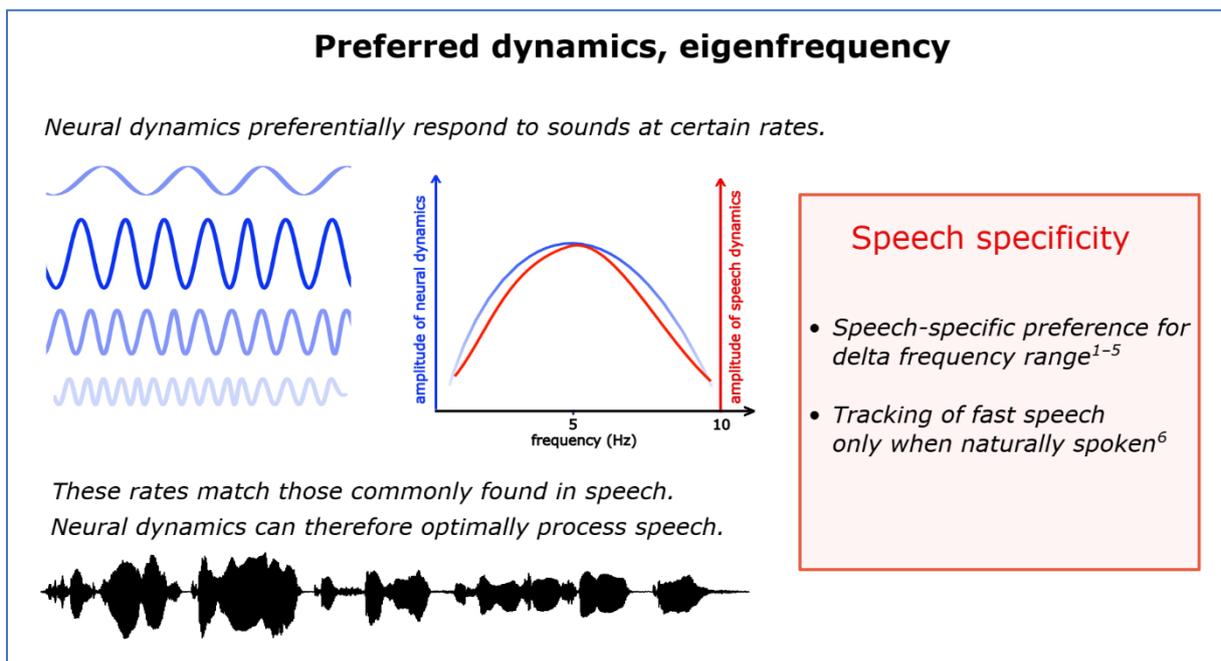
79 ***1.a. Preferred dynamics, eigenfrequency (Fig. 1)***

80 Dynamic systems, including neural ones, often have an *eigenfrequency*, i.e. a frequency they
81 operate at in the absence of input, or a stimulus rate they most strongly respond to. Most studies
82 point to two distinct *eigenfrequency* ranges for the auditory system: The delta-theta range (~2-
83 8 Hz) and the gamma range (~30-40 Hz) (Boemio *et al.*, 2005; Giraud *et al.*, 2007). Human
84 perceptual sensitivity to acoustic spectro-temporal modulations is highest between 2 and 5 Hz
85 (Chi *et al.*, 1999; Edwards & Chang, 2013). Brain imaging revealed that BOLD responses to
86 amplitude modulated (AM) sounds are strongest if these are presented at 4-5 Hz (Giraud *et al.*,
87 2000; Tanaka *et al.*, 2000). Rhythmic AM sounds also give rise to rhythmic fluctuations in
88 auditory sensitivity that outlast the stimulus, but only at rates between ~2 and 8 Hz (Hickok *et*
89 *al.*, 2015; Farahbod *et al.*, 2020; L’Hermite & Zoefel, 2022). Non-rhythmic acoustic stimuli,
90 such as the onset of broadband noise, produce similar fluctuations in neural dynamics and
91 auditory sensitivity in the delta-theta range, although the exact frequency remains unclear (~1-
92 2 Hz in Kayser, 2019; ~5 Hz in Teng *et al.*, 2018; ~6-8 Hz in Ho *et al.*, 2017). Neural dynamics
93 follow acoustic rhythms most reliably when these are presented at theta and gamma rates, while
94 rates in-between do not generate reliable tracking responses (Galambos *et al.*, 1981; Zaehle *et*
95 *al.*, 2010; Teng *et al.*, 2017; Giroud *et al.*, 2020; Teng & Poeppel, 2020). Together, there is
96 converging evidence that auditory dynamics “prefer” certain stimulus rates and respond most
97 readily to them.

98

99 Speech is a dynamic signal that has its own “*eigenfrequencies*”, that is, it conveys information
 100 over distinct time scales. This leads to linguistic “building blocks” of speech, such as phonemes,
 101 syllables and words. Within each of these elements, the rate of information transmission is
 102 relatively stable. For example, phonemic features are typically of 20-50 ms duration, thus
 103 fluctuating at an average rate of ~35 Hz (Ghitza, 2011). Phonemes compose the syllables, which
 104 have a mean duration of 200-250 ms, corresponding to an average rate of 4-5 Hz (Greenberg,
 105 1999; Strauß & Schwartz, 2017). Words are usually spoken at a rate of 100-200 words per
 106 minute, i.e. at 1.5-3 Hz (Carver, 1973). The acoustic speech signal also entails regular temporal
 107 structure at distinct time scales. Across languages, human speech contains broadband amplitude
 108 modulations that are strongest around 3-5 Hz (Ding *et al.*, 2017; Varnet *et al.*, 2017), roughly
 109 corresponding to the spoken syllabic rate (Greenberg, 1999). Stress patterns or intonational
 110 units, carrying prosodic information, also show consistent rhythmic structure across languages,
 111 fluctuating at ~1 Hz (Inbar *et al.*, 2020).

112



113

114 *Figure 1. Preferred dynamics, eigenfrequency. References in speech-specificity box refer to: 1. Ding*
 115 *and Simon, 2014; 2. Etard and Reichenbach, 2019; 3. Keitel et al., 2018; 4. Molinaro and Lizarazu,*
 116 *2018; 5. Zuk et al., 2021; 6. Hincapié Casas et al., 2021.*

117

118 This match between neural auditory eigenfrequencies and those of speech might explain some
 119 perceptual effects. Sounds that are amplitude-modulated at the delta/theta rate produce a distinct
 120 perceptual category (termed “fluctuations”) that disappears at faster or slower rates (Edwards

121 & Chang, 2013). This observation suggests that the tuning to delta-theta rates, common to both
122 speech and auditory neural dynamics, also has a categorical impact on auditory perception. This
123 link between speech and neural dynamics is also supported by studies reporting that blind
124 listeners can understand speech at higher syllabic rates than a sighted population (Hertrich *et*
125 *al.*, 2013). This effect has been suggested to originate from a neural “recycling” of visual areas
126 for auditory processes (Van Ackeren *et al.*, 2018). The *eigenfrequency* of primary visual regions
127 (~ 10 Hz; Herrmann, 2001) is higher than the typical syllabic rate; if visual cortex is recruited
128 during speech processing in the blind, then this might also lead to faster auditory
129 eigenfrequencies and explain why blind people can understand faster speech.

130

131 ***1.b. Constrained temporal flexibility (Fig. 2)***

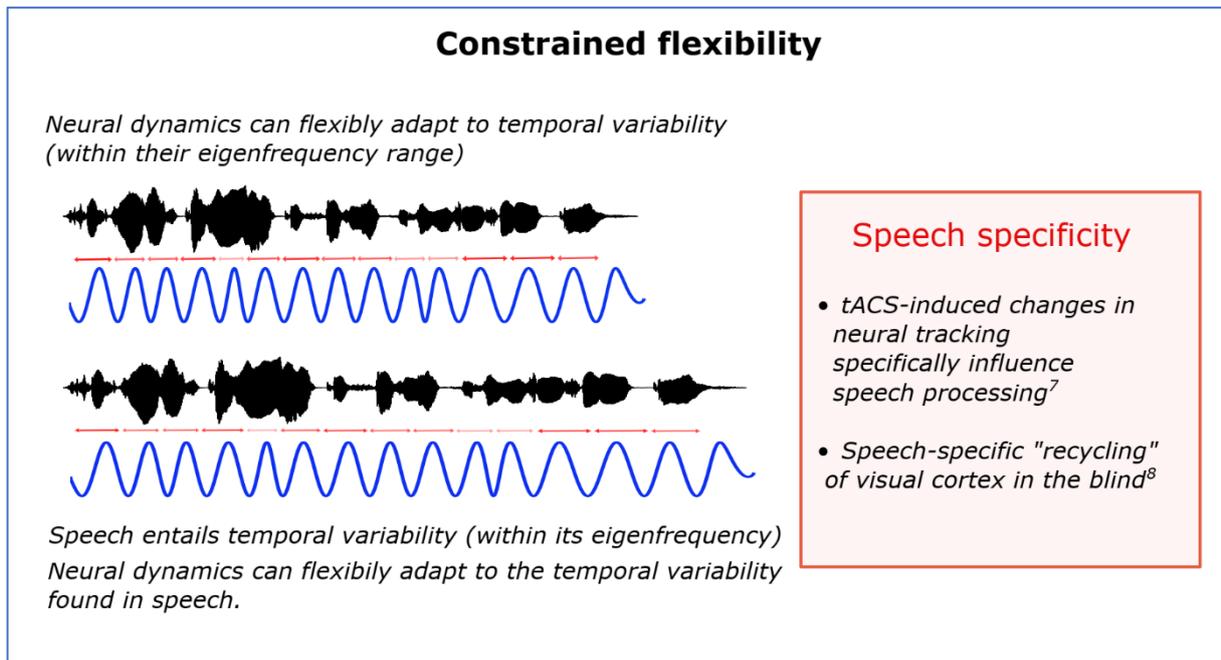
132 Despite having “preferred” frequencies, neural dynamics are not rigid and “track” different
133 acoustic rates in both non-speech (Lakatos *et al.*, 2008; Doelling & Poeppel, 2015) and speech
134 stimuli (Ahissar *et al.*, 2001; Kösem *et al.*, 2018), even when the stimulus is not perfectly
135 isochronous (Doelling *et al.*, 2022; Doelling & Assaneo, 2021; Kayser *et al.*, 2015). Studies
136 using transcranial brain stimulation to manipulate how neural dynamics adapt to acoustic
137 rhythms showed that neural tracking causally modulates auditory and speech perception, an
138 effect that has also been observed at various stimulation rates (Riecke *et al.*, 2015, 2018; Wilsch
139 *et al.*, 2018; Zoefel, Archer-Boyd, *et al.*, 2018; Keshavarzi *et al.*, 2020, 2021; Kösem *et al.*,
140 2020; Zoefel *et al.*, 2020; van Bree *et al.*, 2021). Importantly however, neural tracking has its
141 limits: Neural dynamics fail to track the acoustic rhythm if it is too slow or too fast. These limits
142 are defined by the system’s *eigenfrequency* range: Most of the neural effects described in the
143 previous section were observed for the delta/theta range but disappear if the stimulus is too fast
144 or slow (Galambos *et al.*, 1981; Zaehle *et al.*, 2010; Teng *et al.*, 2017; Farahbod *et al.*, 2020;
145 Teng & Poeppel, 2020; L’Hermite & Zoefel, 2022; but see Hertrich *et al.*, 2012; Nourski *et al.*,
146 2009, for neural responses that persist beyond the theta range). This suggests that neural
147 dynamics are flexible but constrained by their *eigenfrequency*.

148

149 Human speech, despite having distinct temporal structure, also entails temporal variability in
150 each of its constituents (Ramus *et al.*, 1999). First, the rate of syllables and sentential phrases
151 can vary as function of language (Tilsen & Arvaniti, 2013; Varnet *et al.*, 2017; Coupé *et al.*,
152 2019), speaker (Tilsen & Arvaniti, 2013), emotional state (Sobin & Alpert, 1999), and other
153 factors. The mean syllabic rate of 4-5 Hz, common to most (if not all) languages (Ding *et al.*,
154 2017), can result from averaging faster and slower syllables, especially in stress-timed

155 languages (Strauß & Schwartz, 2017). However, variability in speech dynamics is structured
 156 and constrained by the time scales described above (Section 1.a). For example, although the
 157 syllabic rate is variable, it is rarely slower than 2 Hz or faster than 8 Hz. Thus, similar to neural
 158 dynamics, the temporal variability of each building block of speech (e.g., phrase, syllable,
 159 phoneme) is constrained to its typical (*eigenfrequency*) range. Indeed, speech understanding
 160 drops if word rate exceeds 4-5 Hz (Carver, 1973), or when the syllabic rate is above ~8-10 Hz
 161 (Ahissar *et al.*, 2001; Ghitza & Greenberg, 2009; Hincapié Casas *et al.*, 2021). Interestingly,
 162 comprehension of time-compressed, unintelligible speech is recovered if silent gaps are
 163 introduced between syllables (without slowing the time-compressed syllables themselves),
 164 suggesting that the restoration of a typical syllabic rate is key to successful speech perception
 165 (Ghitza & Greenberg, 2009).

166



167

168 **Figure 2. Constrained temporal flexibility. References in speech-specificity box refer to: 7. Zoefel,**
 169 **Archer-Boyd, et al., 2018; 8. Van Ackeren et al., 2018.**

170

171 Together, auditory neural dynamics show flexibility when it is most useful (within the
 172 *eigenfrequencies* of speech) but necessarily otherwise (outside of those ranges). This
 173 observation suggests that neural dynamics, particularly in the auditory system, are designed to
 174 cope with the temporal variability in the information they are exposed to.

175

176

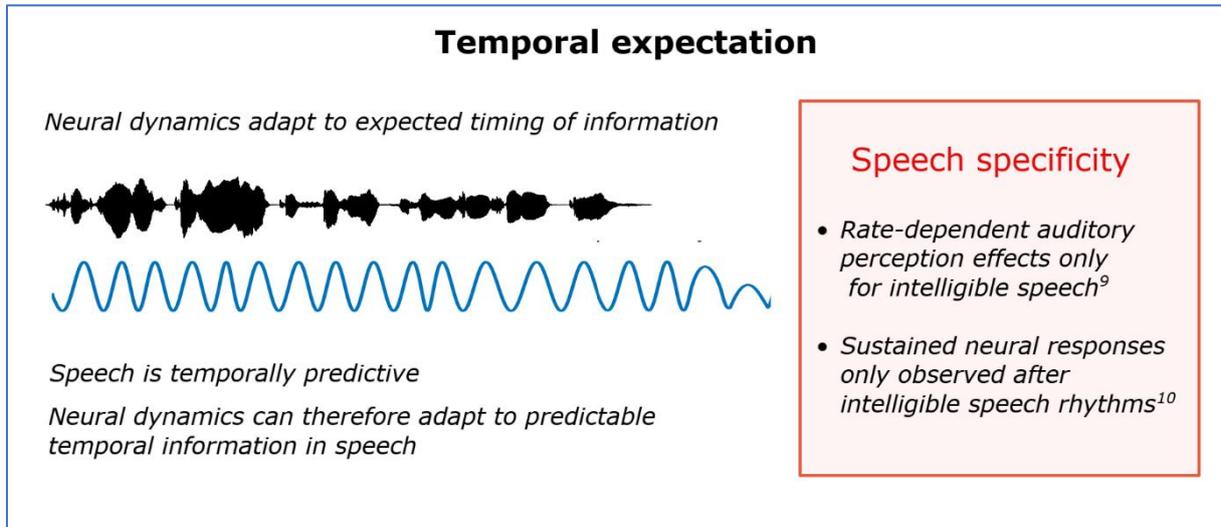
177 ***1.c. Temporal expectation (Fig. 3)***

178 To make sense of the world, the brain generates temporal predictions to anticipate future events
179 (Friston, 2019). This function is of particular relevance for a modality confronted with a rapid
180 stream of incoming information, such as the auditory one. Indeed, it has been shown that
181 auditory perception is modulated by the temporal predictability of its target, in particular in the
182 context of rhythmic scenarios. Sounds are more likely to be detected or more accurately
183 perceived when they are presented at the beat of a preceding rhythm (Jones *et al.*, 2002;
184 Lawrance *et al.*, 2014; ten Oever *et al.*, 2014), a finding that is fundamental for the theory of
185 “auditory dynamic attending” (Large & Jones, 1999; Bauer *et al.*, 2015). In line with these
186 perceptual effects, an anticipatory adjustment of neural dynamics to expected information has
187 been hypothesized and described in rhythmic (Lakatos *et al.*, 2013; Kösem & van Wassenhove,
188 2017) and non-rhythmic scenarios (Bonnefond & Jensen, 2012; Breska & Deouell, 2017;
189 Herbst & Obleser, 2017). This adjustment is often seen as a mechanism that aligns neural
190 resources to expected upcoming events so that these are optimally processed (Schroeder &
191 Lakatos, 2009). In line with this assumption, other studies have shown that the neural dynamics
192 that track auditory rhythms are sustained, i.e. neural dynamics keep fluctuating at the rhythm
193 of the stimulus even when it stops (Lakatos *et al.*, 2013; van Bree *et al.*, 2021; Bouwer *et al.*,
194 2022) or despite a change of temporal properties of the acoustic stimulus (Kösem *et al.*, 2018;
195 Lenc *et al.*, 2020). These neural “echoes” are also seen in corresponding perceptual data,
196 changing rhythmically after a rhythmic acoustic stimulus (Saberri & Hickok, 2021). This effect
197 is only observed for acoustic rhythms between 2 and 8 Hz (Farahbod *et al.*, 2020; L’Hermite &
198 Zoefel, 2022), suggesting an involvement of neural dynamics with similar constrained temporal
199 flexibility as described above. Together, neural echoes can be assumed to reflect anticipation
200 that was induced by the rhythmicity of the stimulus and demonstrate temporal expectation in
201 neural and perceptual dynamics.

202

203 Despite temporal variability, human speech is a predictable stimulus. The average timing of its
204 constituents is predictable, as each of them possesses a typical rate (an *eigenfrequency*). Beyond
205 these average rates, the temporal variability itself is also predictable. Across languages, a
206 slowdown in rate is a robust predictor of a noun to be spoken (Seifart *et al.*, 2018). The duration
207 of a syllable can also predict that of neighboring ones (Greenberg, 1999; Greenberg *et al.*, 2003;
208 Strauß & Schwartz, 2017; but see Jadoul *et al.*, 2016). Moreover, the variability of durational
209 cues in speech can influence speech understanding throughout language development. Adults
210 and babies are able to distinguish languages only based on contrastive durational phonemic

211 cues (Nazzi *et al.*, 1998; White *et al.*, 2012). These variations in timing are therefore an acoustic
212 feature that can be used for temporal predictions.



213
214 **Figure 3. Temporal expectation. References in speech-specificity box refer to: 9. Pitt et al., 2016;**
215 **10. van Bree et al., 2021.**

216
217 The fact that speech is predictable is nicely illustrated by various perceptual effects that link
218 speech properties with neural ones. For example, speech perception is influenced by preceding
219 speech rate so that some words are not perceived if the surrounding speech is pronounced at a
220 fast or slow rate (Dilley & Pitt, 2010). Vowels can be perceived as short or long, depending on
221 the rate of preceding speech, and this can alter the meaning of words in certain contexts (Bosker,
222 2017; Kösem *et al.*, 2018). Interestingly, this effect is correlated with the neural echoes
223 described in the previous paragraph: Kösem and colleagues (2018) showed that neural
224 dynamics at a frequency that corresponds to the rate of a presented speech stimulus persists
225 when the latter changes its rate, and that this “echo” biases the perception of an ambiguous
226 syllable. Humans are also strikingly efficient in anticipating their turn in a conversation
227 (Levinson, 2016). This anticipatory effect might involve a network of brain regions specialised
228 for turn-taking in speech (Castellucci *et al.*, 2022) and indicates that we continuously predict
229 the end of the turn of our conversation partner.

230
231 Finally, the duration of spoken words is linked to their semantic predictability: the more
232 predictable the word, the shorter it is (Ten Oever *et al.*, 2022). Perhaps as a consequence, speech
233 can be processed better when spoken naturally. Adults understand speech in noise better when
234 spoken at a natural rate, as compared to when it is made artificially rhythmic or spoken at an

235 unnatural rhythm (Aubanel & Schwartz, 2020); neural tracking is stronger in response to
236 naturally spoken fast speech, as compared to normal speech that has been accelerated (i.e. to a
237 signal has a temporal structure that is unnatural for a fast speaking rate) (Hincapié Casas *et al.*,
238 2021).

239

240 Human speech is not the only stimulus that is temporarily predictable. But given the rapid and
241 complex temporal dynamics of the speech signal, it can only be processed efficiently with
242 neural dynamics that can rapidly adapt to the expected timing of information. The fact that we
243 seem to possess such adaptable neural dynamics again suggests that these meet the requirements
244 imposed by dynamics of speech.

245

246 ***1.d. Hierarchical structure (Fig. 4)***

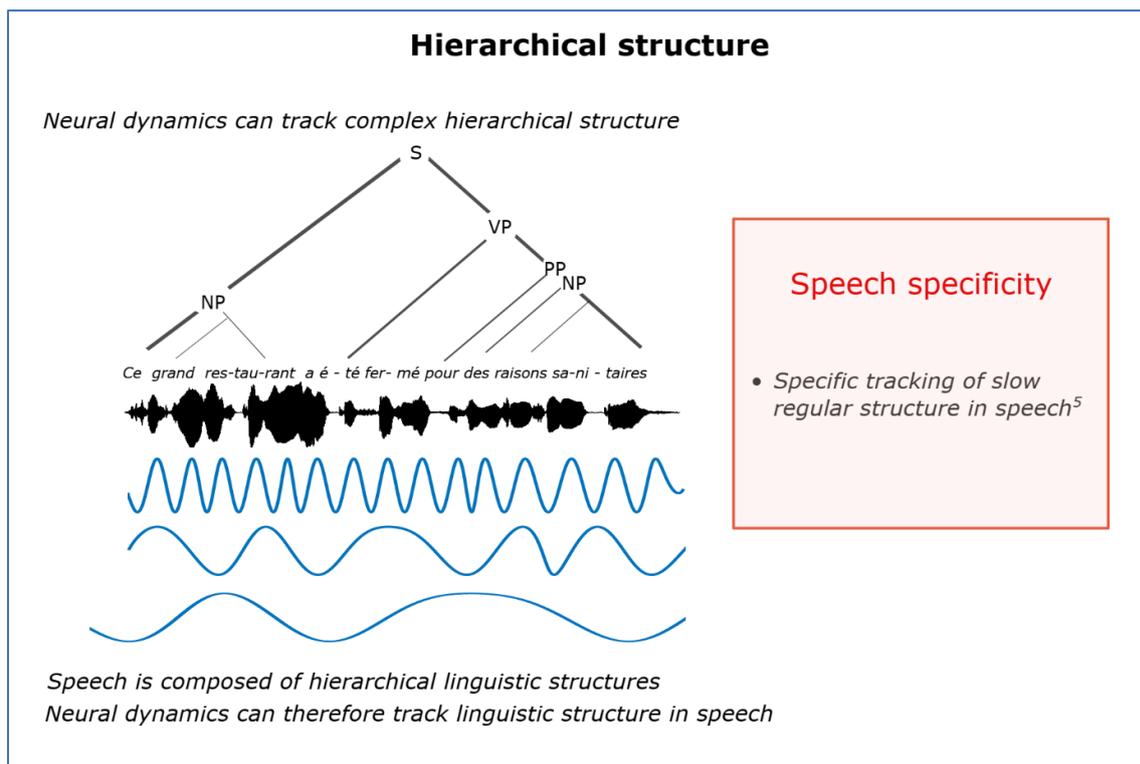
247 Neural dynamics can track abstract, structural features of an acoustic stimulus. Dynamics in A1
248 of non-human primates delineate the perceived parsing of repetitive patterns in sounds (Barczak
249 *et al.*, 2018). In humans, neural activity aligns to higher-level structure in musical stimuli, such
250 as when participants are asked to imagine a beat (Nozaradan *et al.*, 2012), or when they detect
251 changes in melodic sequences (Baltzell *et al.*, 2019). Moreover, neural dynamics can track
252 various structural or “higher-level” features of speech (for reviews, see Ding & Simon, 2014;
253 Zoefel & VanRullen, 2015a). Ding *et al.* (2016) showed that, only when participants
254 comprehend speech and are therefore able to parse it into various linguistic elements (e.g.,
255 phrases), brain responses follow the rate of these higher-level structures. The identity of
256 symbolic linguistic information, such as phonemes (Di Liberto *et al.*, 2015), semantic surprisal
257 (Brodbeck *et al.*, 2018; Weissbart *et al.*, 2020), or word entropy (Armeni *et al.*, 2019), can be
258 decoded from neural dynamics tracking human speech at delta/theta frequencies.

259

260 Structure is omnipresent in human speech which combines smaller units, such as syllables or
261 words, into higher-level structures such as phrases or sentences. The ability of neural dynamics
262 to follow the hierarchical structure of a stimulus might therefore have evolved from the
263 necessity to do so in order to successfully comprehend speech. Several theoretical frameworks
264 assume such a link, considering neural dynamics a “tool” to parse speech into its various
265 building blocks (e.g., Giraud & Poeppel, 2012; Ghitza, 2013; see also Kazanina & Tavano,
266 2023).

267

268



269

270 **Figure 4. Hierarchical structure. References in speech-specificity box refer to: 5. Zuk et al., 2021.**

271

272 ***1.e. Cross-modality and sensory-motor interactions***

273 Most neural dynamics can be influenced by more than one (sensory-motor) modality
 274 (Ghazanfar & Schroeder, 2006). Activity in auditory regions does not only adapt to acoustic
 275 stimuli but to input from other modalities as well, including simple visual rhythms (Lakatos *et*
 276 *al.*, 2008; Besle *et al.*, 2011; Kösem *et al.*, 2014) or input from the motor system (Morillon *et*
 277 *al.*, 2014; Assaneo & Poeppel, 2018).

278

279 Human speech is in most situations a cross-modal phenomenon. In face-to-face interactions,
 280 we see the other person move their lips when they talk. These visual speech cues usually precede
 281 acoustic information by tens to a hundred milliseconds, depending on the spoken utterance
 282 (Schwartz & Savario, 2014). Facial expressions, as well as beat gestures and semantic gestures,
 283 emphasize content and further contribute to speech understanding. For instance, congruent
 284 facial movements and gesture improve speech comprehension in noisy environments (Helfer,
 285 1997; Drijvers & Özyürek, 2017).

286

287 The similar cross-modal organisation of neural dynamics and speech can lead to various
 288 perceptual phenomena. Most notably, the fact that visual speech cues precede acoustic

289 information in speech makes the former a reliable cue to anticipate the latter, and visual
290 information therefore influences the processing and interpretation of speech. In line with this
291 assumption, neural dynamics in both visual and auditory regions track lip movements, even
292 when presented without the accompanying sounds (Park *et al.*, 2016, 2018; Giordano *et al.*,
293 2017; Bourguignon *et al.*, 2020). It has been proposed that visual cues reset auditory delta/theta
294 dynamics to prepare them for upcoming acoustic information (Thorne & Debener, 2014;
295 Mégevand *et al.*, 2020; Biau *et al.*, 2021). Audio-visual speech produces shorter latencies in
296 neural responses than auditory-only speech (van Wassenhove *et al.*, 2005), and the presentation
297 of distinct acoustic and visual consonantal information can lead to the percept of a third
298 consonant (Mcgurk & Macdonald, 1976). There is also evidence that we perceive acoustic and
299 visual information to be synchronous when the latter *precedes* the former, an effect that might
300 reflect the system's tuning to temporal statistics of human speech (van Wassenhove *et al.*, 2007;
301 Freeman *et al.*, 2013). Finally, we highlight a recent study reporting that coupling between
302 auditory and motor regions is most reliable when words are spoken at 4.5 Hz (Assaneo &
303 Poeppel, 2018). This result does not only illustrate cross-modality of neural dynamics but
304 reveals an *eigenfrequency* of auditory-motor synchronisation that suggests once more an
305 optimisation to process human speech.

306

307 **2. Speech-specificity of neural dynamics**

308

309 Some brain regions respond more readily to human speech than to other sounds, and
310 increasingly so at higher levels of the auditory hierarchy (Scott *et al.*, 2000; Mesgarani *et al.*,
311 2014; Landemard *et al.*, 2021). The existence of this speech-specific pathway (Scott *et al.*,
312 2000; Saur *et al.*, 2008), together with the close match between temporal properties of speech
313 and neural dynamics, might lead to the assumption that neural dynamics during speech differ
314 from those observed during other sounds. In this section, we summarize findings that certain
315 properties of neural dynamics only appear – or at least, they are particularly prominent – when
316 confronted with intelligible speech, but not with other sounds.

317

318 ***2.a. Intelligible speech produces stronger neural tracking responses than other sounds***

319 As described above, neural dynamics follow the temporal evolution of auditory input
320 irrespective of its complexity, and have been shown to track speech, pure tones, and various
321 other non-speech stimuli (Nozaradan *et al.*, 2012; Doelling & Poeppel, 2015; Barczak *et al.*,
322 2018; Lakatos *et al.*, 2019; Obleser & Kayser, 2019). Tracking of human speech is not restricted

323 to human listeners and can also be observed in non-human primates (Zoefel *et al.*, 2017). The
324 magnitude of neural tracking (or entrainment) varies with certain properties of the auditory
325 stimulus. Several studies have reported that a reduction in spectral detail of a speech stimulus
326 – to a degree that makes it unintelligible – also reduces neural tracking, even if the broadband
327 amplitude envelope remains unchanged (Peelle *et al.*, 2013; Molinaro & Lizarazu, 2018; Meng
328 *et al.*, 2021). Temporal reversal does not only make speech unintelligible, it also attenuates
329 neural dynamics aligned to it (Gross *et al.*, 2013; Park *et al.*, 2015). Reduced neural tracking of
330 speech is also observed when acoustic edges in speech are removed (Doelling *et al.*, 2014;
331 Oganian & Chang, 2019), or when background noise or distracting speech signals are added
332 (Ding & Simon, 2013; Zion Golumbic *et al.*, 2013; Rimmele *et al.*, 2015; Zoefel & VanRullen,
333 2015b).

334

335 Van Ackeren *et al.* (2018) contrasted magnetoencephalography (MEG) responses to intelligible
336 and unintelligible noise-vocoded speech in blind and sighted participants. Unsurprisingly, both
337 groups showed speech tracking in auditory regions. However, speech-aligned responses were
338 also observed in primary visual cortex. Although this was the case for both participant groups,
339 stronger tracking for intelligible speech in visual cortex was observed *only* in blind participants.
340 Thus, the well-established reorganization of visual cortex for auditory dynamics in the blind
341 (Voss & Zatorre, 2012; Collignon *et al.*, 2015) seems to entail specific processing of intelligible
342 speech.

343

344 In all of these cases, the simultaneous reduction in neural tracking and speech comprehension
345 was produced by changes in the acoustic signal, making it difficult to disentangle acoustic and
346 linguistic effects on neural dynamics (Kösem & van Wassenhove, 2017). Some studies have
347 failed to find a correlation between neural tracking and comprehension, including studies that
348 manipulated intelligibility of speech independently of its acoustics (e.g., through training)
349 (Millman *et al.*, 2015; Zoefel & VanRullen, 2016; Dai *et al.*, 2022; Kösem *et al.*, 2023). Other
350 studies found differences in neural tracking when contrasting participants presented with the
351 identical physical stimulus, but who differ in their proficiency of a given language and its
352 linguistic structure (Ding *et al.*, 2016; Lizarazu *et al.*, 2021), or their expectation about linguistic
353 content (Di Liberto *et al.*, 2018). In addition, brain stimulation studies showed that the
354 manipulation of speech-aligned neural dynamics results in a change in speech perception, even
355 if the speech stimulus itself remains unchanged (Riecke *et al.*, 2018; Wilsch *et al.*, 2018; Zoefel,

356 Archer-Boyd, *et al.*, 2018; Keshavarzi *et al.*, 2020, 2021; Zoefel *et al.*, 2020; van Bree *et al.*,
357 2021).

358

359 These findings support the notion that the intelligibility of speech *per se* can influence neural
360 dynamics. Nevertheless, caution is warranted when manipulation of speech intelligibility goes
361 along with acoustic changes, considering that a small change in acoustic parameters can have
362 strong effects on the neural tracking response (Dai *et al.*, 2022; Kösem *et al.*, 2022). Although
363 stronger tracking is observed for intelligible speech, it may reflect acoustic processing, and not
364 necessarily language-related brain mechanisms. In addition, intelligible speech is a particularly
365 relevant acoustic stimulus and thus prone to capture listeners' attention. Neural dynamics,
366 including tracking of auditory rhythmic stimuli are modulated by attention (Lakatos *et al.*,
367 2013), and so is their alignment to both acoustic and symbolic information in speech (Ding *et*
368 *al.*, 2018; Dai *et al.*, 2022). Therefore, stronger brain responses to intelligible speech might
369 reflect stronger, attention-related neural activity that are not specific to speech.

370

371 **2.b Speech-specific neural dynamics**

372 We use face-specific brain responses, observed in the human fusiform gyrus (McCarthy *et al.*,
373 1997), as an analogue to illustrate speech-specific neural dynamics. Neural activity in some
374 parts of this brain region is stronger during the presentation of human faces as compared to non-
375 face stimuli. To evoke face-specific activity, the face needs to be identified, and this is only
376 possible based on certain visual patterns. This means that faces and non-faces will necessarily
377 differ in visual properties and these differences can explain the observed neural results – just
378 like speech and non-speech sounds will always have some acoustic differences, and these can
379 produce differences in neural dynamics. It is interesting, however, that the identification of a
380 face activates certain neural populations that are otherwise not active and might respond in a
381 way that differs from other, more general populations. The same logic applies to speech-specific
382 neural dynamics, which might need to be activated by certain acoustic patterns but, once
383 activated, have distinct properties. As we explain in the following, these speech-specific circuits
384 and their properties might produce neural responses to speech that are not only stronger but also
385 different from those to other, non-verbal sounds.

386

387 In support of speech-specific neural dynamics, there is evidence that the lower range of
388 eigenfrequencies (Section 1.a; Fig. 1), is special for neural populations tuned to human speech.
389 Several studies reported that comprehension of natural speech is correlated with neural

390 dynamics in the delta, but not theta frequency range (Ding & Simon, 2014; Keitel *et al.*, 2018;
391 Molinaro & Lizarazu, 2018; Etard & Reichenbach, 2019). A recent study showed that this
392 “preference” for low frequencies is specific to speech and not found for other stimuli like music
393 (Zuk *et al.*, 2021). Indeed, the topographical pattern of delta activity in response to speech
394 seems distinct from more typical auditory processes (Bourguignon *et al.*, 2018) and involve
395 parietal sensors (Zuk *et al.*, 2021). In contrast, theta dynamics more closely resembles typical
396 auditory activity (Bourguignon *et al.*, 2018; Zuk *et al.*, 2021). A somewhat different result was
397 obtained by Hincapié Casas *et al.* (2021), who used MEG to measure neural activity aligned to
398 speech sentences spoken at a fast rate (9 syllables/s) and compared it with that to sentences
399 spoken at a slower rate, but time-compressed to the fast rate. This time-compressed speech was
400 not only significantly less intelligible than natural speech, it also did not entrain neural activity
401 – in contrast to naturally fast speech which produced a reliable alignment between MEG signal
402 and speech rhythm. More research is required to determine whether not only the lower, but also
403 the upper limit of the delta/theta range has a distinct role for the processing of human speech.

404

405 Additional results suggest that the neural tracking response to intelligible speech (section 1.b;
406 Fig. 2) differs from that to non-intelligible acoustic controls. Zoefel *et al.* (2018) manipulated
407 speech tracking by varying the timing of transcranial alternating current stimulation (tACS)
408 relative to rhythmic speech and measured consequences of this manipulation using brain
409 imaging (fMRI). They found that tACS-induced changes in tracking altered fMRI responses to
410 speech, but this effect was only observed when the speech was intelligible (16-channel noise-
411 vocoded speech) and not for an unintelligible, amplitude-matched control stimulus (1-channel
412 noise-vocoded speech). Van Bree *et al.* (2021) presented rhythmic noise-vocoded speech that
413 was either clearly intelligible or unintelligible and noise-like. They showed that intelligible
414 speech produces rhythmic fluctuations in the MEG that outlast the rhythmic stimulus, the
415 “neural echo” described above. Importantly, this sustained rhythmic response was not present
416 for unintelligible speech, and measured at parietal MEG sensors rather than those typically
417 capturing auditory responses. This finding implies that rhythmic echoes, possibly reflecting
418 temporal expectation of upcoming events (section 1.c; Fig. 3), might be particularly pronounced
419 in response to speech compared to other acoustic stimuli. It is of note that intelligible speech
420 does not only produce stronger neural echoes, but also stronger neural dynamics during its
421 presence. An interesting follow-up study would include the design of speech and non-speech
422 sounds that produce comparable neural dynamics during the sound, and the test whether
423 intelligible speech still produces stronger neural echoes in this case. Lastly, a recent study found

424 that rhythmic irregularities in noise-vocoded speech are easiest to detect if it is intelligible
425 (Zoefel *et al.*, 2022). Moreover, rhythm perception was more accurate in an experimental group
426 that perceived a (sine-wave) stimulus as speech, as compared to another group that did not. This
427 finding is additional evidence that temporal prediction mechanisms, putatively carried by neural
428 dynamic activity, are improved during speech processing as compared to non-verbal
429 processing.

430

431 The extraction of linguistic and other symbolic features of speech (section 1.d, Fig. 4) requires
432 speech-specific processing (by definition, linguistic features are specific to speech). However,
433 their tracking (Di Liberto *et al.*, 2015; Brodbeck *et al.*, 2018; Broderick *et al.*, 2019; Har-shai
434 Yahav & Zion Golumbic, 2021) could rely on an unspecific circuit that aligns neural processing
435 to stimulus properties (or structure) in the attentional focus. It has been proposed that neural
436 dynamics characterise the nested recursive structure of various stimuli, such as language, but
437 also music, spatial sequences, or mathematical structures (Dehaene *et al.*, 2022). For instance,
438 neural oscillatory activity can reflect the complexity of geometrical sequences, and parse
439 geometrical primitives (Al Roumi *et al.*, 2021) in the same way as it parses syntactic structures
440 in language (Ding *et al.*, 2016). Here, a demonstration of speech-specific tracking would require
441 the comparison with an unintelligible control stimulus that does not entrain neural dynamics.
442 One of the rare studies that used such a comparison is described above: Zuk *et al.* (2021)
443 demonstrated low-frequency tracking that is specific for human speech. Nevertheless, we
444 currently lack evidence whether a single higher-level circuit tracks rhythmic structure in a
445 stimulus, independently of the stimulus' identity, or whether speech is parsed differently from
446 other non-speech stimuli.

447

448 Although audio-visual neural dynamics and corresponding perceptual effects might reflect
449 optimisation to process speech (section 1.e), it remains unclear in how far these can be
450 generalised to other sounds. For example, visual speech cues reset auditory dynamics in general,
451 not only speech-specific ones (Biau *et al.*, 2021). Some evidence for speech-specific effects has
452 been reported for auditory-motor interactions. Delta activity that is associated with speech
453 comprehension seems to be coupled specifically to beta oscillations originating from the motor
454 system (Keitel *et al.*, 2018). Unlike delta, the frequency of beta oscillations (13-30 Hz) does not
455 match rates found in speech and might be due to characteristics found in the motor system. The
456 speech-specific role of beta oscillations from sensory-motor interactions has been confirmed by
457 Michaelis and colleagues (2021). They presented participants with speech and non-speech

458 sounds and found that only the former produced an amplitude decrease of such oscillations in
459 left sensorimotor clusters (indicating increased motor activity).

460

461 **3. Neural Oscillations: A mechanistic origin of speech-optimised neural dynamics?**

462

463 In this paper, we focus on neural dynamics, temporal patterns of neural activity that seem
464 optimised to process human speech. Neural oscillations are a distinct class of neural dynamics
465 (Buzsáki & Draguhn, 2004; Wang, 2010; van Bree *et al.*, 2022) and possess certain properties
466 that might underlie a specialisation to process speech.

467

468 ***3.a Properties of neural oscillations that suggest speech optimisation***

469 Neural oscillations have been put forward as a mechanism that structures and gates information
470 processing in time (Schroeder & Lakatos, 2009; Lisman & Jensen, 2013; VanRullen, 2016).
471 Oscillations are regular fluctuations in the excitability of neural ensembles that lead to a
472 rhythmic alternation between phases of stimulus amplification and suppression (Buzsáki &
473 Draguhn, 2004). The alignment of neural dynamics to periodic or quasi-periodic stimulus
474 features, described as “tracking” and “entrainment” above, is often assumed to involve such
475 oscillations (Lakatos *et al.*, 2008, 2019; Obleser & Kayser, 2019). According to initial theories
476 (Large & Jones, 1999; Schroeder & Lakatos, 2009), by adapting to the rhythm of speech,
477 endogenous oscillations can align their amplifying phases to important events in the speech
478 stream and their suppressive phases to irrelevant ones (e.g., a distracting, competing speaker),
479 thereby efficiently and elegantly allocating neural resources to when they are needed.
480 Consequently, neural oscillations and their entrainment are often considered instrumental in
481 speech processing (Giraud & Poeppel, 2012; Peelle & Davis, 2012; Meyer, 2018).

482

483 There is no doubt that neural dynamics can follow specific temporal features of speech and
484 other sounds. Evidence for an actual involvement of endogenous oscillations is trickier to
485 demonstrate and has been discussed in detail elsewhere (e.g., Zoefel, ten Oever, *et al.*, 2018).
486 We here ask whether the involvement of neural oscillations is a promising model to explain
487 speech-constrained neural dynamics, and focus on properties of oscillations that might support
488 such a model:

- 489 • Endogenous neural oscillations have an *eigenfrequency* (Hutcheon & Yarom, 2000) and
490 will respond more strongly to stimuli close to their preferred frequency (Fröhlich, 2015;

491 Herrmann *et al.*, 2016). This is in line with findings on auditory neural dynamics that
492 also possess an *eigenfrequency* (Section 1.a).

- 493 • Neural oscillations flexibly adapt to the rate of rhythmic stimulation if (and only if) it
494 falls into their *eigenfrequency* range (constrained flexibility) and can tolerate a certain
495 amount of jitter in the stimulus rhythm (Doelling & Assaneo, 2021), as observed for
496 neural dynamics processing speech (Section 1.b).
- 497 • Neural oscillations are apt to undergo inertia, a property that identifies oscillations in
498 ambiguous situations (Thut *et al.*, 2011). This leads to oscillatory activity outlasting
499 rhythmic sensory and electric stimulation (e.g., Kösem *et al.*, 2018; van Bree *et al.*,
500 2021). In simple scenarios (e.g., phrases with relatively constant syllable rate), this
501 neural echo is mechanistically relevant for temporal expectation (Section 1.c) as it aligns
502 neural dynamics with the expected timing of upcoming events.
- 503 • Similar to human speech (Section 1.d), neural oscillations can have nested structures,
504 where slower and faster rhythms are coupled. Oscillations might therefore be suitable
505 to process the hierarchical structures that speech has (Ghitza, 2011, 2013; Giraud &
506 Poeppel, 2012)
- 507 • Interactions between distinct oscillatory populations play an important role for many
508 basic neural and cognitive functions (Akam & Kullmann, 2014). An interaction between
509 distinct modalities (auditory, visual, motor; Section 1.e) is also necessary for successful
510 speech perception. Oscillatory networks might therefore support cross-modal speech
511 processing (Bauer *et al.*, 2020). The observation of a visually-induced reset of auditory
512 delta/theta oscillations (Biau *et al.*, 2021) is in line with this assumption.

513 Together, those properties that reveal a close match between neural dynamics and human
514 speech can also be found in neural oscillations (*eigenfrequency*, constrained flexibility,
515 temporal expectation, cross-modality). Some of these properties are unique to, others
516 characteristic for neural oscillations (van Bree *et al.*, 2022). This supports the notion of
517 neural oscillations being involved in the generation of the observed speech-constrained
518 neural dynamics.

519

520 ***3.b Neural oscillations underlying speech processing: Open questions***

521 Whereas the neural oscillation framework provides clear strengths, several open questions
522 remain that need to be answered in follow-up work. In the future, these answers might lead to

523 a model that explains neural dynamics during speech perception by complementing neural
524 oscillations with additional, not necessarily oscillatory, processes.

525

526 • While neural oscillators seem robust to a certain amount of external temporal variability
527 (Doelling & Assaneo, 2021), it remains unclear how they adapt to the temporal
528 variability in human speech. Unlike other relevant sounds like music, speech consists
529 of frequent changes in rate and entails relatively irregular silent gaps between words or
530 phrases. This leads to a temporal variability that is high in spoken speech (Tilsen &
531 Arvaniti, 2013; Varnet *et al.*, 2017; Ten Oever *et al.*, 2022), and some researchers raised
532 doubts about whether it is rhythmic at all (Nolan & Jeon, 2014; Jadoul *et al.*, 2016).
533 Whereas dominant rates in speech do imply *some* rhythmicity, it is clear that a perfectly
534 sinusoidal oscillation would struggle to align to this rhythm. Indeed, if speech
535 perception relied on such an oscillation, regularly spoken speech should be easier to
536 understand, which is not the case (Aubanel & Schwartz, 2020). This does not necessarily
537 rule out an involvement of oscillations as they possess means to change their
538 instantaneous frequency and phase. Acoustic “edges” might serve as a cue to “reset”
539 oscillations (Doelling *et al.*, 2014) and visual cues might prepare oscillatory activity for
540 upcoming acoustic information (Thorne & Debener, 2014; Mégevand *et al.*, 2020; Biau
541 *et al.*, 2021). How exactly this is done remains to be investigated, as well as the question
542 whether and why a rhythmic neural process (i.e. oscillation) that needs to be
543 continuously adapted has an advantage over a non-rhythmic one (for a different
544 perspective, see also Meyer *et al.*, 2020).

545

546 • Neural oscillations are difficult to identify during human speech as they need to be
547 disentangled from evoked activity that is repeated regularly due to the rhythmicity of
548 the stimulus (Haegens & Zion Golumbic, 2018; Zoefel, ten Oever, *et al.*, 2018).
549 Although progress has been made recently (Doelling *et al.*, 2019), most of the evidence
550 for their involvement is relatively indirect (such as “entrainment echoes”; Section 1.c)
551 and we still lack methods to extract endogenous oscillations during rhythmic
552 stimulation.

553

554 • Due to their relation to neural excitability (Buzsáki & Draguhn, 2004), incoming
555 information is supposedly inhibited during the low-excitability part of the oscillation
556 (Lakatos *et al.*, 2013). While this might be beneficial for speech perception if this

557 suppressive phase coincides with distracting information (e.g., a competing speaker;
558 Zion Golumbic et al., 2013), this might not always be the case, given considerable
559 temporal variability in speech. It is unclear how the system deals with potentially
560 important information coinciding with the low-excitability phase of the oscillation
561 (VanRullen *et al.*, 2014). A related prediction is that the perception of speech segments,
562 phonemes specifically, should depend on the phase of entrained neural oscillations.
563 However, several studies have failed to find such effects (Bosker & Kösem, 2017;
564 Kösem *et al.*, 2020): In these studies, only the rate but not the phase of a rhythmic
565 stimulus (speech or tACS), assumed to entrain oscillations, modulated the perception of
566 speech phonemes.

- 567
- 568 • Neural oscillations at frequencies that do not match those of speech also seem to play a
569 role for speech processing (such as alpha oscillations; Strauß et al., 2014). The precise
570 role of these oscillations, and whether they are speech-specific, remains unclear.
 - 571 • Preferred neural “time scales” seem to increase along the cortical hierarchy (Giraud et
572 al., 2000; Kiebel et al., 2008; Murray et al., 2014; Wolff et al., 2022; see also summary
573 of corresponding effects in the auditory system in Edwards & Chang, 2013).
574 Corresponding analyses for oscillatory activity are sparse, but first results revealed an
575 opposite pattern of decreasing time scales, with prefrontal areas showing fastest
576 dynamics (> 20 Hz) (Capilla *et al.*, 2022). This seems to contradict the notion that
577 endogenous oscillations track different hierarchical levels of human speech, and needs
578 to be resolved in future work.
- 579

580

581 **4. Outlook: Questions and hypotheses for research on speech-specific neural dynamics**

582

583 We conclude this article with a list of open question and testable hypotheses for the exciting
584 field of neural dynamics processing human speech.

585

- 586 • If face-specific neural activity requires the presence of certain features that are necessary
587 to identify faces and activate face-specific brain areas, then similar speech-specific
588 features might be necessary to activate speech-specific neural dynamics. It is likely that
589 such features exist, given that we perceive speech as categorically different from most
590 other sounds. It remains, however, an open question what these features are. In studies

591 reporting speech-specific dynamics, any difference between intelligible and
592 unintelligible (or non-) speech sounds might have produced them. For example, 16- and
593 1-channel noise-vocoded stimuli do not only differ in their intelligibility but also in their
594 spectral complexity (Shannon *et al.*, 1995). Time-compressed speech might have altered
595 various acoustic features in addition to reduced intelligibility. We here propose that
596 recognising human speech as such – based on (acoustic or linguistic) features that are
597 distinct for speech and allow the listener to identify it – is crucial to activate speech-
598 specific processing, a hypothesis that needs to be tested in the future and might reveal
599 insights into the question of what makes human speech such a characteristic stimulus.
600 A study by Overath *et al.* (2015) is important in this respect, demonstrating that parts of
601 the Superior Temporal Sulcus (STS) respond selectively to acoustic, temporal structure
602 of speech (but not other sounds).

603 In any case, if those characteristic features are not linguistic, then we should be able to
604 reproduce them in non-speech stimuli that then activate the same speech-specific
605 dynamics. As long as a non-speech stimulus mimics the critical properties of speech
606 (e.g., its typical rate, association with visual cues and temporal predictability) it should
607 produce neural dynamics that so far seem distinct for speech (Section 2.b).

608

- 609 • How speech-specific are neural dynamics reflecting temporal expectation? These
610 dynamics should disappear when it has become clear that the temporal expectation has
611 been violated. This can be tested and compared with similar effects observed for non-
612 speech stimuli in which temporal expectation is manipulated. For expectations on
613 hierarchically higher levels of linguistic information, the effect should only be observed
614 for participants proficient in the language spoken. Moreover, whereas speech is easier
615 to understand when it contains natural temporal variability (Aubanel & Schwartz, 2020),
616 it remains unclear whether equivalent effects exist for non-speech sounds.

- 617 • Given the tight temporal correspondence between lip movements and speech, are
618 temporal expectations given by visual cues more relevant for speech processing than for
619 other audiovisual stimuli? Speech-specific dynamics might particularly rely on visual
620 cues to anticipate auditory events that might otherwise difficult to predict, like the onset
621 of a new phrase (Zoefel, 2021).

623

- 624 • Did neural dynamics and speech production co-evolve (Assaneo and Poeppel, 2020), or
625 was one shaped by the other? On the one hand, temporal constants of neural dynamics
626 are conserved across species (Buzsáki *et al.*, 2013). If basic neural architecture
627 principles are indeed preserved throughout evolution, then dynamics of human speech
628 might have adapted according to corresponding temporal constraints. On the other hand,
629 neural dynamics are dependent on sensory experience (Kral, 2013). As one of the most
630 prominent acoustic stimuli an individual is exposed to since birth, exposure to speech
631 might have constrained auditory cortices to adapt to its temporal dynamics.
632
- 633 • If neural dynamics are shaped by the exposure to speech, do they develop in parallel
634 with language acquisition? Do listeners show differences in neural dynamics when
635 presented with their native language as compared to other ones?
636
- 637 • Does this potential co-evolution have an impact on the processing of other auditory
638 stimuli? Such a “spillover effect” might explain why we are attracted to music – a
639 stimulus that fluctuates at similar rates, is temporarily predictable but entails some
640 variability, and has therefore similar properties as human speech. Can the cross-modal
641 wiring of neural dynamics explain why we like to dance to music (audio-motor
642 interactions) or watch musicians during a concert (audio-visual interactions)? Related,
643 a recent study suggested that audition’s (delta/theta) *eigenfrequency* is indeed imposed
644 onto eye movements during reading (Gagl *et al.*, 2022).
645
- 646 • It seems to be a general property of the human brain that “intrinsic time scales” become
647 longer at higher levels of the cortical hierarchy (Giraud *et al.*, 2000; Kiebel *et al.*, 2008;
648 Edwards & Chang, 2013; Murray *et al.*, 2014; Wolff *et al.*, 2022). Not much is known
649 about how much of this phenomenon holds for speech processing. In particular,
650 *eigenfrequencies* should decrease along the speech processing hierarchy, as relevant
651 rates in speech also decrease.
652
- 653 • Do speech-specific neural dynamics localise to specific brain areas? It is of note that
654 most speech-specific effects reported above are measured in regions (or at sensors) that
655 do not show the strongest response to acoustic rhythms in general. Arguably, networks
656 responding more readily to human speech than to other sounds (Scott *et al.*, 2000; Saur

657 *et al.*, 2008) are likely to show such speech-specific neural dynamics, but this
658 assumption requires confirmation. Moreover, these networks are large and contain sub-
659 networks with distinct properties (e.g., *eigenfrequency*).

660

661 **5. Conclusion**

662

663 In this review, we address the role of neural dynamics in the processing of speech and other
664 sounds. We highlight that the brain can track various auditory signals and that this tracking has
665 specific properties and constraints. These resemble characteristics of human speech and might
666 therefore reflect the system's optimisation for speech processing. We also describe how neural
667 dynamics during speech seem to be both quantitatively and qualitatively different from
668 dynamics observed during other acoustic stimuli. More research is needed to understand the
669 mechanistic origins of speech-specific dynamics and their impact on speech analysis.

670

671

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673

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