

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

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## **Abstract**

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

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

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

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

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

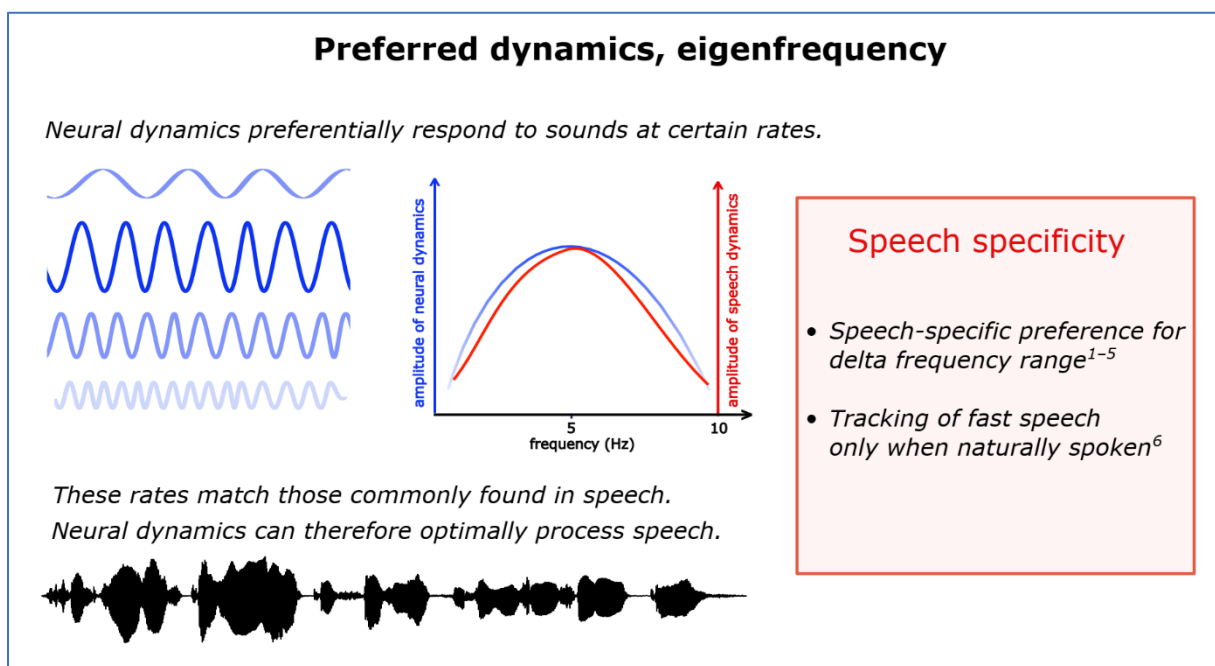
## **1. Properties of neural dynamics in the auditory system (and beyond) and how they relate to those of human speech**

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

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

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

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



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

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

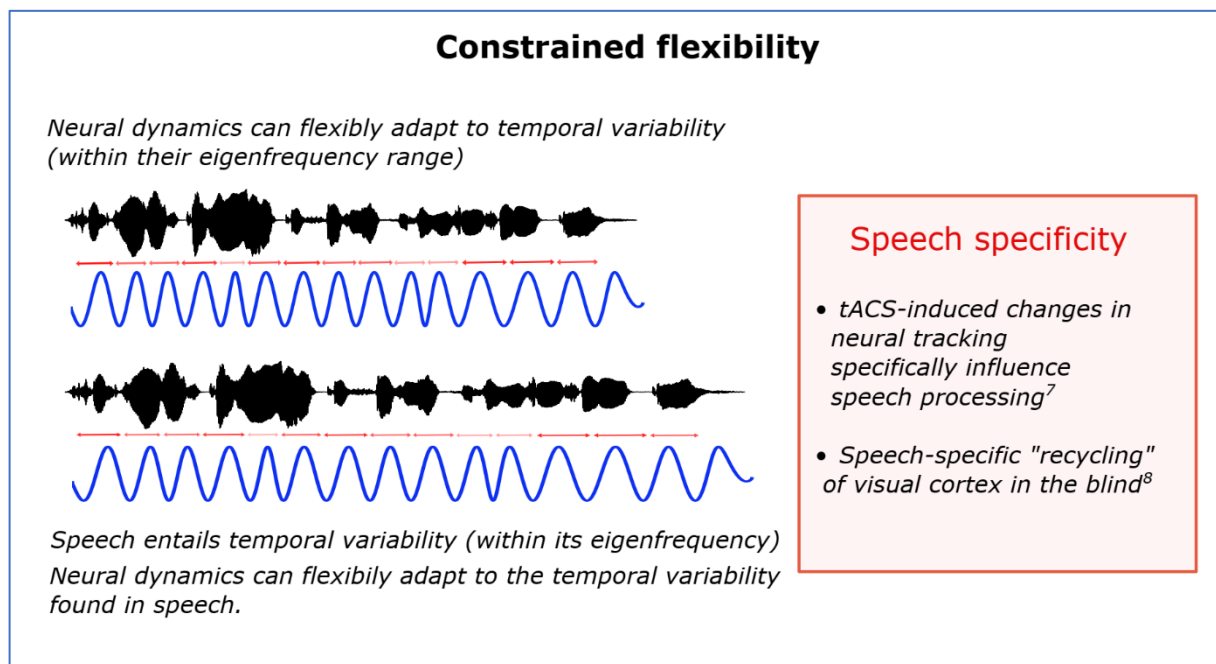
& Chang, 2013). This observation suggests that the tuning to delta-theta rates, common to both speech and auditory neural dynamics, also has a categorical impact on auditory perception. This link between speech and neural dynamics is also supported by studies reporting that blind listeners can understand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

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

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

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

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



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

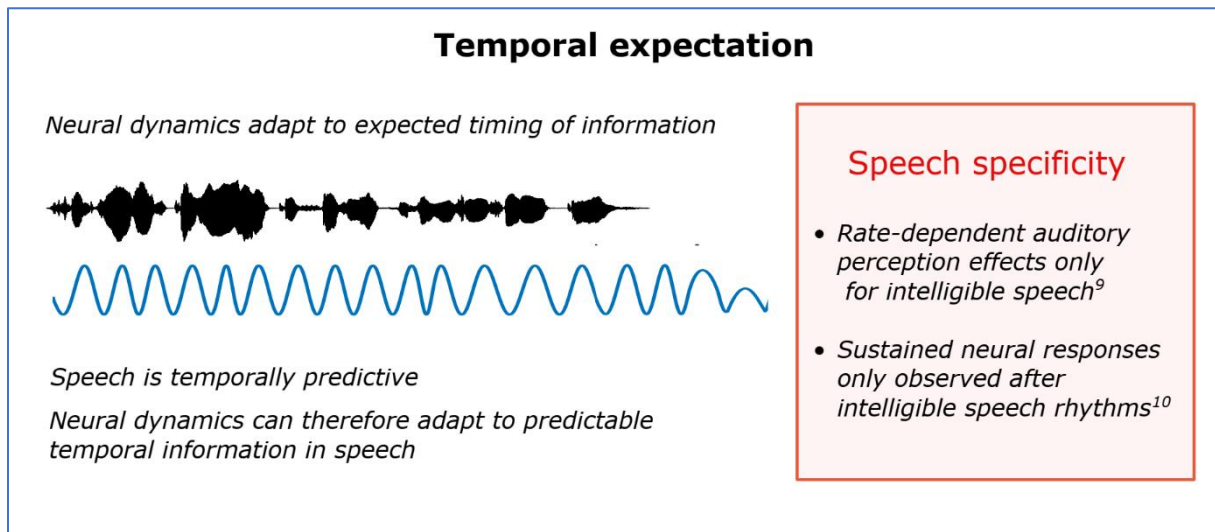
Together, auditory neural dynamics show flexibility when it is most useful (within the *eigenfrequencies* of speech) but necessarily otherwise (outside of those ranges). This observation suggests that neural dynamics, particularly in the auditory system, are designed to cope with the temporal variability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

### 1.c. Temporal expectation (Fig. 3)

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

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

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



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

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

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

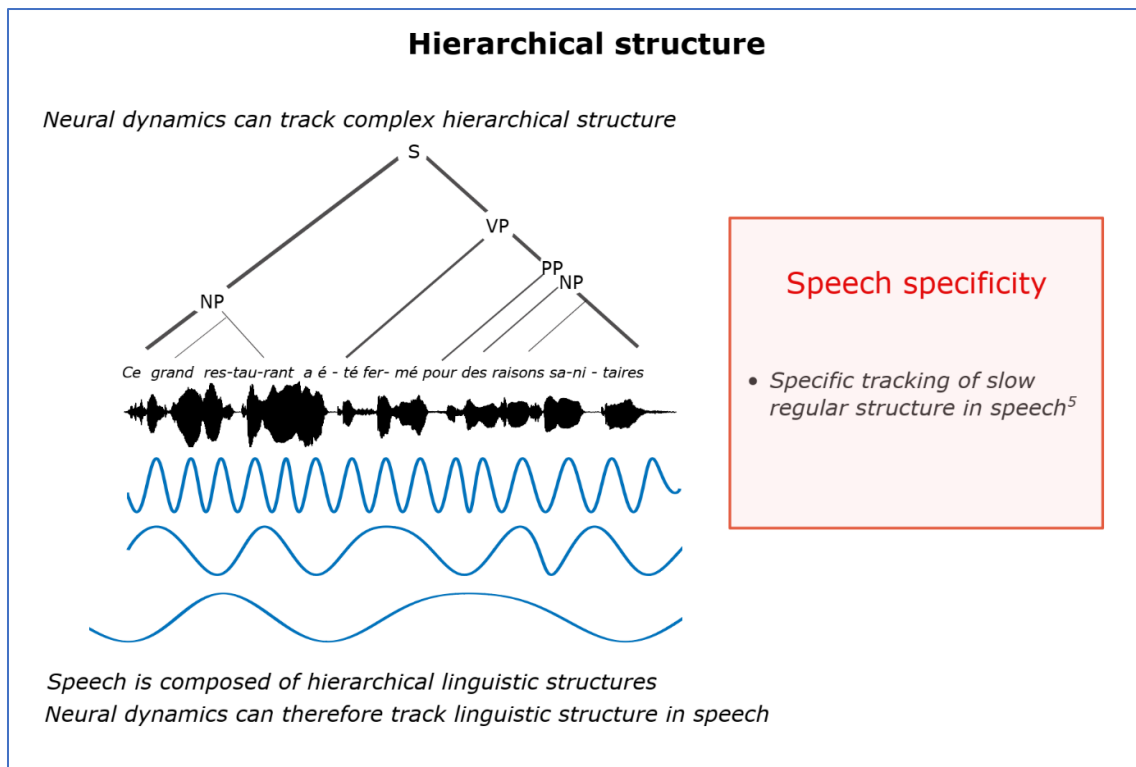
unnatural rhythm (Aubanel & Schwartz, 2020); neural tracking is stronger in response to naturally spoken fast speech, as compared to normal speech that has been accelerated (i.e. to a signal has a temporal structure that is unnatural for a fast speaking rate) (Hincapié Casas *et al.*, 2021).

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

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

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

- While neural oscillators seem robust to a certain amount of external temporal variability (Doelling & Assaneo, 2021), it remains unclear how they adapt to the temporal variability in human speech. Unlike other relevant sounds like music, speech consists of frequent changes in rate and entails relatively irregular silent gaps between words or phrases. This leads to a temporal variability that is high in spoken speech (Tilsen & Arvaniti, 2013; Varnet *et al.*, 2017; Ten Oever *et al.*, 2022), and some researchers raised doubts about whether it is rhythmic at all (Nolan & Jeon, 2014; Jadoul *et al.*, 2016). Whereas dominant rates in speech do imply *some* rhythmicity, it is clear that a perfectly sinusoidal oscillation would struggle to align to this rhythm. Indeed, if speech perception relied on such an oscillation, regularly spoken speech should be easier to understand, which is not the case (Aubanel & Schwartz, 2020). This does not necessarily rule out an involvement of oscillations as they possess means to change their instantaneous frequency and phase. Acoustic “edges” might serve as a cue to “reset” oscillations (Doelling *et al.*, 2014) and visual cues might prepare oscillatory activity for upcoming acoustic information (Thorne & Debener, 2014; Mégevand *et al.*, 2020; Biau *et al.*, 2021). How exactly this is done remains to be investigated, as well as the question whether and why a rhythmic neural process (i.e. oscillation) that needs to be continuously adapted has an advantage over a non-rhythmic one (for a different perspective, see also Meyer *et al.*, 2020).
- Neural oscillations are difficult to identify during human speech as they need to be disentangled from evoked activity that is repeated regularly due to the rhythmicity of the stimulus (Haegens & Zion Golumbic, 2018; Zoefel, ten Oever, *et al.*, 2018). Although progress has been made recently (Doelling *et al.*, 2019), most of the evidence for their involvement is relatively indirect (such as “entrainment echoes”; Section 1.c) and we still lack methods to extract endogenous oscillations during rhythmic stimulation.
- Due to their relation to neural excitability (Buzsáki & Draguhn, 2004), incoming information is supposedly inhibited during the low-excitability part of the oscillation (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 • Neural oscillations at frequencies that do not match those of speech also seem to play a  
568 role for speech processing (such as alpha oscillations; Strauß et al., 2014). The precise  
569 role of these oscillations, and whether they are speech-specific, remains unclear.
- 570 • Preferred neural “time scales” seem to increase along the cortical hierarchy (Giraud et  
571 al., 2000; Kiebel et al., 2008; Murray et al., 2014; Wolff et al., 2022; see also summary  
572 of corresponding effects in the auditory system in Edwards & Chang, 2013).  
573 Corresponding analyses for oscillatory activity are sparse, but first results revealed an  
574 opposite pattern of decreasing time scales, with prefrontal areas showing fastest  
575 dynamics (> 20 Hz) (Capilla *et al.*, 2022). This seems to contradict the notion that  
576 endogenous oscillations track different hierarchical levels of human speech, and needs  
577 to be resolved in future work.

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

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

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

- How speech-specific are neural dynamics reflecting temporal expectation? These dynamics should disappear when it has become clear that the temporal expectation has been violated. This can be tested and compared with similar effects observed for non-speech stimuli in which temporal expectation is manipulated. For expectations on hierarchically higher levels of linguistic information, the effect should only be observed for participants proficient in the language spoken. Moreover, whereas speech is easier to understand when it contains natural temporal variability (Aubanel & Schwartz, 2020), it remains unclear whether equivalent effects exist for non-speech sounds.
- Given the tight temporal correspondence between lip movements and speech, are temporal expectations given by visual cues more relevant for speech processing than for other audiovisual stimuli? Speech-specific dynamics might particularly rely on visual cues to anticipate auditory events that might otherwise difficult to predict, like the onset of a new phrase (Zoefel, 2021).

- 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

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

## **5. Conclusion**

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

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