**Entrainment in Disguise: the Exogenous and Endogenous Cortical Rhythms
of Speech and Language Processing**

Lars Meyer^{1,*} lmeyer@cbs.mpg.de

Yue Sun² yue.sun@aesthetics.mpg.de

Andrea E. Martin³ andrea.martin@mpi.nl

¹Department of Neuropsychology,
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

²Department of Neuroscience,
Max Planck Institute for Empirical Aesthetics, Frankfurt am Main, Germany

³Psychology of Language Department,
Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands

*Corresponding author

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Summary

How neural systems represent information beyond the contents of sensory stimuli is a recurrent theme for models of perception and cognition—in particular in speech and language research: Speech is arrhythmic, yet steady oscillatory coupling to speech, so-called entrainment, still occurs. In addition, oscillatory coupling to linguistic information that does not have any physical counterpart has recently been described. We propose here that oscillatory responses to speech are not always entrained by exogenous sensory signals, but may also reflect endogenous rhythms that subserve the internal generation of linguistic representations. While acoustic information in speech provides punctate opportunities for exogenous entrainment proper, endogenous cortical rhythms may segment speech into semantic and syntactic structures in a form of perceptual inference. The proposed synthesis of endogenous and exogenous information can account for one of the hardest inference problems the human brain faces: the comprehension of language.

Perspective

The functional interpretation of cortical rhythms remains an issue of great theoretical importance in the neurosciences. This is especially pertinent in current research on speech perception and language comprehension (Friederici and Singer, 2015; Giraud and Poeppel, 2012; Lewis et al., 2016; Meyer, 2017). Given the fact that language comprehension is essentially the reconstruction of meaning from vibrations of air, comprehension must require the synthesis of top-down knowledge in the form of endogenous signals (e.g., a network's intrinsic activation state at stimulus onset) with bottom-up sensory information in the form of exogenous acoustic input (Bever and Poeppel, 2010; Halle and Stevens, 1962; Poeppel and Monahan, 2011). Yet, in the past years, the auditory neuroscience and speech processing fields have focused mainly on the entrainment of cortical rhythms during bottom-up processing, neglecting for a large part, their potential top-down functionality.

Entrainment describes the phase-locking of a neural oscillation, presumed to emanate from a population of neurons that fire in synchrony, to the phase of an acoustic stimulus, such as speech (Giraud and Poeppel, 2012; Pikovsky et al., 2003). Entrainment to amplitude rhythms in speech is attested at the gamma (Di Liberto et al., 2015), theta (Peelle et al., 2013), and delta (Bourguignon et al., 2013) frequencies (Gross et al., 2013), roughly corresponding to the occurrence frequencies of amplitude edges or peaks that accompany phonemes and syllables; while entrainment is also attested for intonation phrases (Meyer, 2017), these have a comparably weak rhythmicity. The general assumption that acoustic edges or peaks can indeed entrain a neural oscillation is supported by rodent work, where the phase of local field potentials in the auditory cortex was observed to be reset by high-amplitude neuronal discharges to complex acoustic stimuli (Szymanski et al., 2011).

It has often been proposed that entrainment of neural oscillations plays a mechanistic role in speech and language processing. Yet, convincing evidence for this role is mostly confined to the entrainment of theta-band oscillations to speech amplitude modulations at the

syllabic rate, which is emphasized in recent neurophysiological and computational models (Ghitza, 2011; Giraud and Poeppel, 2012). These models conceptualize theta-band entrainment as a mechanism to segment continuous speech signals into syllable-size acoustic chunks, based on exogenous acoustic landmarks, guiding follow-up auditory decoding on shorter time scales, such as phonemes. This view is supported by a close correlation between amplitude modulations at the theta-band frequency in speech (Ding et al., 2015) and average syllable duration in speech corpora (Greenberg, 2001; Pellegrino et al., 2011); further support comes from psychophysical studies (Ghitza and Greenberg, 2009).

There is reason to doubt such a mechanistic role of entrainment to exogenous acoustic information for the processing of higher-level linguistic representations, namely semantics and syntax. For example, language comprehension is largely intact when prosodic cues, which occur within the modulation frequency range of the delta band, are removed from the speech signal (Ding et al., 2015)—while removal of theta-range amplitude modulations results in a substantial loss of intelligibility (Doelling et al., 2014; Ghitza and Greenberg, 2009). In addition, phase-locking to high-level linguistic information occurs even when the speech stimulus contains distracting exogenous acoustic information (Meyer et al., 2016). It is intensively debated (and still requires future corpus analyses) whether amplitude cues provided by pauses, duration information, and pitch modulations that occur in frequency ranges slower than theta are rhythmic enough to entrain oscillations in the first place; it is also unclear whether these cues are reliable enough to infer lexical or phrasal boundaries (Cummins, 2012; Fernald and McRoberts, 1996; Goswami and Leong, 2013; Jusczyk, 1997; Kelso et al., 1986; Martin, 2016; Seidl, 2007; Soderstrom et al., 2003).

Here, we propose that oscillatory rhythmicity during speech processing and language comprehension is not entrainment proper, but entrainment ‘in disguise’: The paucity of invariant amplitude cues below the syllabic rate implies that oscillatory rhythmicity at corresponding frequencies is really the result of the perceptual inference of higher-level

linguistic meaning, and thus endogenous information (Marslen-Wilson and Welsh, 1978; Martin, 2016; Martin and Doumas, 2017)—in line with major theories of the cortical representations of external stimuli during perception (Friston, 2005). For example, recent electrocorticographic data revealed how the classic phoneme restoration effect is manifest in neuronal populations in auditory cortex (Leonard et al., 2016); namely, a phoneme is inferred from activation spread across neuronal assemblies that code related phonological features in auditory cortex. Likewise, entrainment to acoustic and temporal information that is not diagnostic of a unique linguistic unit can still result in the stable perception of a lexically ambiguous stimulus when task instructions are to detect either one or the other of the possible percepts (Kösem et al., 2016). A similar effect has been found during the processing of syntactically ambiguous sentences, where sentence interpretations that contradict acoustic cues are associated with a decreased entrainment to these cues, but a consistent phase shift towards the syntactic structure that is actually perceived (Meyer et al., 2016). These types of effects strongly suggest that deployment of endogenous signals in the form of cortical rhythms can shape both stimulus perception and entrainment.

We propose that such endogenous mechanisms, fed by complex multi-dimensional linguistic cues, underlie the activation of higher-level linguistic representations (e.g., morphemes, lexical representations, syntactic and semantic structures, discourse and event structures, pragmatics) from speech (Martin, 2016). The amount of entrainment proper by the sensory stimulus that is required for the activation of a certain linguistic representation may be very minimal; once the linguistic representation is active, it may provide perceptual stabilization of the sensory signal via phase–amplitude coupling from slower to faster frequencies (Giraud and Poeppel, 2012; Gross et al., 2013; Kayser et al., 2015; Lakatos et al., 2005; Morillon et al., 2012; Riecke et al., 2015); rhythmicity resulting from phase–amplitude coupling might appear as entrainment to an exogenous stimulus, yet in reality would stem from entrainment ‘in disguise’, that is, the punctate endogenous activation of higher-level

information (e.g., via a local field or event-related potential) that is only active for a fraction of the phase cycle of the observed oscillation. For a continued, rhythmic train of oscillatory cycles, either an exogenous cue in the form of a new sensory signal or a strongly active endogenous candidate of an inferred higher-level linguistic representation is required. A line of results that are problematic for the exogenous-only account of rhythmic neural oscillations in response to speech stimuli are compatible with our new proposal: First, rhythmicity of neural oscillations can occur when the rhythmicity of external amplitude modulations is experimentally reduced (Calderone et al., 2014; Mathewson et al., 2012). Second, rhythmicity of slower-frequency oscillations is relatively more robust to environmental noise than entrainment of higher-frequency oscillations (Obleser et al., 2008; Peelle et al., 2013). Third and more generally, our proposal may help to address the recurring concern that amplitude modulations in speech are too arrhythmic to allow for exogenous entrainment (Cummins, 2012; Goswami and Leong, 2013; Kelso et al., 1986), yet entrainment can still occur (Kayser et al., 2009).

Figure 1 here

In the data that are recorded during speech perception with electrophysiological techniques, the ongoing labor of inferential linguistic processes would consistently result in cortical rhythms appearing as being exogenously entrained to acoustic events in the sensory input that are superficially associated with higher-level linguistic structures for the duration of the inferred structural unit. Functionally, such inferential mechanisms also provide a mechanism for the prediction of upcoming sensory input that can be verified or falsified in a form of predictive coding (Friston, 2005). This state of affairs implies that during speech processing and language comprehension, the relationship between bottom-up (i.e., exogenous) and top-down (i.e., endogenous) information in cortical networks is highly dynamic over time (Arnal

and Giraud, 2012; Herrmann et al., 2004; Marslen-Wilson and Welsh, 1978; Martin, 2016; Sherman et al., 2016). Behaviorally, speech perception and language comprehension might even stay equally good under dynamically changing environmental conditions, due to dynamic fluctuations in the exogenous–endogenous imbalance over time: When the speech signal is clear and environmental conditions are excellent, entrainment can dominate speech perception; in turn, any representation that has been identified from the speech stream allows for the generation of predictions across the various linguistic levels (Hale, 2001; Levy, 2008; Martin, 2016), which can result from the same inferential process that structure building would, without the invocation of an additional predictive mechanism (Marslen-Wilson and Welsh, 1978; Martin, 2016). Endogenously generated linguistic information can thus keep neural oscillations in the auditory system in a rhythmic state through phase–amplitude coupling from slower to faster frequencies, stabilizing phase-locking to the speech stimulus even when exogenous cues at these faster frequencies are arrhythmic or temporarily lacking (see Figure 1). Indeed, the processing of clear speech, relative to the processing of acoustically degraded speech, is not only associated with reliable entrainment to sensory input, but also with an increase in endogenous modulation of sensory entrainment (Herrmann et al., 2004; Park et al., 2015; Sherman et al., 2016)—endogenous neural oscillations that provide inferred linguistic information may thus provide human language with a powerful degree of redundancy, potentially compensating for the transient non-rhythmicity of acoustic information throughout speech. Furthermore, such a state of affairs would be consistent with data from auditory perception research that indicates that behavioral performance is entrained by rhythmic stimuli, yet exhibits continued rhythmicity even when a prior rhythmic stimulus is experimentally extinguished (Hickok et al., 2015; Neuling et al., 2012). An analogy for the interplay of endogenous and exogenous signals would be riding a bicycle, where you might achieve the same overall speed with strong pedaling of the left leg, but weaker pedaling of the right leg, or vice versa.

In addition to providing a novel explanation for oscillatory phenomena in speech processing and language comprehension, our proposal also allows for a new view on language acquisition—as a case in principle for a progression from exogenously-driven entrainment proper to endogenously-driven entrainment ‘in disguise’: Late in the womb and up to six months after birth, fetuses and neonates are able to distinguish both native and non-native phonemes (Gervain, 2015; Mahmoudzadeh et al., 2013); six months after birth and possibly earlier⁵³, this perceptual ability narrows selectively towards native phonemes (Kuhl, 2000; Kuhl et al., 2014). Such perceptual specialization occurs both on the phonemic and syllabic level; strikingly, for phonemes, specialization is associated with an enhancement of gamma-band entrainment (Ortiz-Mantilla et al., 2016), whereas for syllables, it is associated with an amplification of theta-band entrainment (Bosseler et al., 2013; Ortiz-Mantilla et al., 2016). Both examples offer support for the idea that the accumulation of linguistic knowledge leads to the deployment of endogenous signals that give rise to entrainment ‘in disguise’. A similar trajectory might be observable for higher-level linguistic information: In the developing ability to parse words into syntactic phrases, infants start out with the ability to perceive—and later infer—these phrases’ boundaries through exogenous amplitude cues (Isobe, 2007; Männel and Friederici, 2009; Wiedmann and Winkler, 2015); yet, after six years of age, amplitude cues are not necessary for syntactic phrasing anymore (Männel et al., 2013) and perhaps become overridden by information that manifests as endogenous syntactic preferences in adults—in association with a decreased entrainment to amplitude cues that contradict these endogenous preferences (Meyer et al., 2016).

We have argued that segmenting speech into representations with structure and meaning calls on two forms of entrainment—entrainment to the exogenous stimulus that is phase-locked to the speech envelope (and likely to other acoustic features of speech), and entrainment ‘in disguise’ of a cortical network that is generating linguistic meaning based on

the synthesis of the exogenous acoustic signal with (pre-)activated endogenous representations through perceptual inference.

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Figure caption

Figure 1: A: Entrainment of neural oscillations to a rhythmic exogenous acoustic stimulus (e.g., a regular tone sequence). Rhythmic edges or peaks in the amplitude envelope of the stimulus synchronize neural oscillation at stimulation frequency; B: Entrainment impossible in cases of non-rhythmic amplitude cues in speech stimulus; C: Entrainment-in-disguise of neural oscillations to a non-rhythmic acoustic stimulus (e.g., speech). Predictive linguistic knowledge (e.g., of upcoming syllables, words, or syntactic structure) deployed by endogenous signals (i.e., local-field potentials or slower-frequency neural oscillations) establishes continued oscillatory rhythmicity in spite of lacking acoustic cues for entrainment.