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Putting the Listening Brain in Context

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Abstract

Speech provides a fleeting signal to the human brain. However, we rarely encounter speech without being provided some form of context. This article is conceived as a primer on forms and levels of context that can benefit the listener in comprehending speech. In an attempt to integrate psychological, audiological, and neuroscientific knowledge with more linguistic views, the neural functional organisation of facilitated speech comprehension particularly from semantic context is reviewed. The limits of contextual benefit as well as its (mal-)adaptive implications for ageing or hearing-impaired listeners are discussed.

Speech is a fleeting signal, and it has no single physical correlate. In my native language, German, there is not even a word for it, only complicated qualifications (*gesprochene Sprache*). Yet, we certainly know a speech signal when we hear one, and sometimes we even hear one when there wasn't one to start with (and instead it was only the howling wind, or a few sine waves summed together by an intrepid researcher). Thus, humans can make sense from speech; our ears and our brains know how to process it, and we are astonishingly good at comprehending the messages conveyed, even in what sometimes turn out to be most challenging acoustic conditions.

So how does the human neural system make sense from degraded speech signals? The new *Oxford American Dictionary* gives a definition of *to comprehend* as to 'to grasp the nature, significance, or meaning of [something]' (McKean 2005). That is, a certain element of inference is already palpable in this definition. 'To comprehend' does not simply mean 'to sensate' (e.g., a sound pressure change at the ear drum), and it may also entail more than 'to perceive' (e.g., a certain pitch or an acquired vowel category). Neural correlates of the speech comprehension process are very likely to transcend processes that could be termed sensory or perceptual – those processes that we hold accountable for 'decoding' (or neurally encoding) the sound of speech. Also, a full account on the functional organisation of speech comprehension in the human brain is likely to trespass outside the anatomical confines of the auditory pathway. Thus, there must be more to comprehension, in cognitive terms as well as in terms of its neural correlates.

But first, what are the lines of research on which our knowledge on the neural processing of speech comprehension will critically depend? Unfortunately, the so-called bottom-up flow of information in the auditory domain (i.e,, the transduction of acoustic into neural signals) is not as well understood as comparable processes in the visual domain. While the psychoacoustic phenomena of speech perception have been well described (e.g., Kollmeier et al. 2008), a truly mechanistic understanding of all peripheral and central neural operations on the acoustics of speech has not been achieved yet. Nevertheless, substantial progress has been made over the last decades in describing the functional organisational principles of the auditory system (e.g., Fritz et al. 2003; Merzenich and Brugge 1973; Schreiner and Winer 2007; Tian et al. 2001; Wang 2000) as well as the most relevant central anatomical pathways (e.g., Hackett 2008; Rauschecker and Scott 2009).

With respect to more cognitive neuroscientist views, there have been important empirical and conceptual advances in the last 15 years, co-occurring with the advent of functional neuroimaging for speech and language comprehension networks in the human brain (e.g., Binder et al. 2000; Davis and Johnsrude 2003; Friederici 2002; Hickok and Poeppel 2007; Scott et al. 2000).

In parallel but approaching from a different, more audiological line of research, the processes of listening comprehension and the interaction of acoustic constraints and cognitive capabilities have been subject to extensive behavioural study for a very long time (e.g., Boothroyd and Nittrouer 1988; Lunner et al. 2012; Miller et al. 1951; Pichora-Fuller et al. 1995; Rosen 1992; Wingfield et al. 2005, to cite a select, if canonical, few).

Note that it have been these more acoustic approaches to speech and language that also brought us the parametric manipulation of speech intelligibility – that is, thorough experimental control over how much acoustic detail is made available to the listener. Parametric variations in signal (i.e., speech) to noise (e.g., white noise, speech-filtered noise, competing talkers) or parametric variations in spectral detail ('noise-vocoding'; Shannon et al. 1995) have been used most often. We will re-encounter these parametric intelligibility manipulations throughout the remainder of the text.

Building from this diverse array of previous research, a central tenet here will be that one aspect that helps the listener comprehend speech is *contextual information*. The underlying research agenda put forward is to move on towards levels of description that do not aim at describing the isolated perception and comprehension of words or sentences. Instead, we can learn more and potentially generalise better about the realistic neural processes of comprehension when we study comprehension occurring in its more natural 'habitat': within the sub-optimal acoustics of howling winds and crowded bars, or in the compromised hearing system of older listeners or cochlear implant users – but usually surrounded by other meaningful bits of speech, that is, context.

1. *What we Talk about When we Talk about Context*

Context in and by itself can come in many forms and shapes. Without further constraining what we mean by 'context', it would be too big a concept to be useful in guiding the study of speech and language comprehension. For our purposes, let me first approach the notion of context by reminding us of work published more than 60 years ago (see also Figure 1A): George Miller, one of the eminent psychologists of the 20th century and most recognised for his contributions to the limits of short-term memory, was probably the first to demonstrate with experimental precision that humans understand speech in noise better, to quantifiable degrees, when the conveyed speech content itself provides a certain amount of context (Miller et al. 1951; Figure 1A). Specifically, they demonstrated an increased tolerance towards worse signal-to-noise ratios for speech in noise when the speech signal offered more contextual constraints, in form of a sentential context (i.e., words in sentences better understood than words in isolation) or in form of a small, closed set of test items (i.e, a set of digits better understood than sentences).

Table 1 exemplifies a (potentially non-comprehensive) list of possible sources of context that listeners can draw on when listening to and trying to comprehend speech and that researchers should keep in mind when approaching their experiments on speech comprehension.

As shown in Table 1, I suggest ordering the various potential sources of context according to their 'remoteness' from the speech signal itself. To illustrate, a body gesture of menace can surely provide important, disambiguating context to an utterance (e.g., Jessen et al. 2012), but it is at least initially processed in very different neural pathways than the auditory signal itself and would thus classify as a comparably 'remote' source.

In contrast, the benefit in recovering an acoustically masked or ambiguous word-initial phoneme [k] from a word context (i.e,, the famous Ganong effect and its various derivates;

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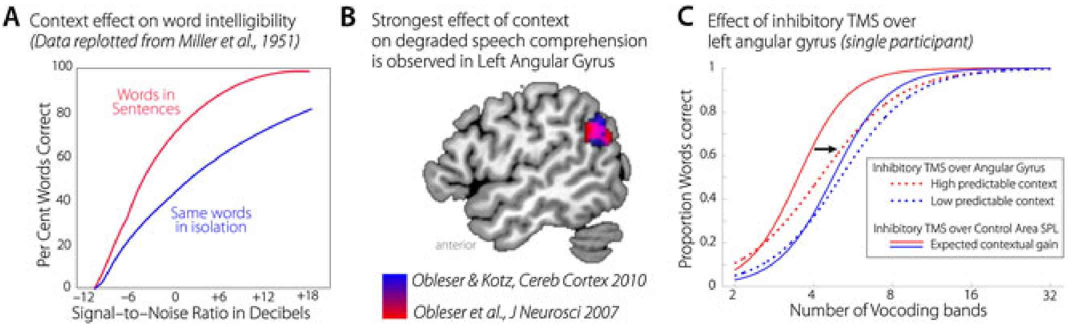

Fig. 1. The effect of context on speech comprehension and the role of the angular gyrus. (A) Result from Miller et al. (1951) first demonstrating persuasively the effect of linguistic context on word comprehension under various levels of acoustic degradation (labelled here ‘contextual gain’). (B) Two related functional MRI studies reviewed here show relatively enhanced left angular gyrus activation to be correlated with this contextual gain listeners draw from semantic context in simple sentence comprehension at intermediate levels of speech degradation. (C) Pilot data from a single participant (unpublished observation) indicates that disrupting normal angular gyrus function with inhibitory TMS can abolish the contextual gain (red-dashed psychometric curve is shifted to the right, indicating required better signal quality for equal comprehension). Note that TMS over a control site, superior parietal cortex, SPL, does not (red vs. blue solid lines).

Table 1. Typical forms and levels of context that affect speech comprehension.

Domain	Exemplary recent citations
Acoustic – derived or inferred *directly* from the acoustic signal	
Signal familiarity	Johnsrude et al. 2013
Signal predictability	Bendixen et al. 2009; Rimmele et al. 2012 [a] Scharinger et al. 2012
Linguistic – derived or inferred *indirectly* from the acoustic signal	
Lexicality	Eisner and McQueen 2005, 2006; Eulitz and Hannemann 2010; Gow et al. 2008
Prosody	Eckstein and Friederici 2006; Sammler et al. 2010
Syntax [b]	Obleser et al. 2011a; Peelle et al. 2010; Wingfield et al. 2006
Semantics	Bendixen et al. 2014; Davis et al. 2011; Lash et al. 2013; Obleser and Kotz 2010, 2011; Obleser et al. 2007; Rodd et al. 2005; Stickney and Assmann 2001
Pragmatics	van Berkum et al. 2003
Multisensory – conveyed *in parallel to but remotely from* the acoustic signal	
Written text	Sohoglu et al. 2012
Lip movements/(‘visems’)	Keil et al. 2012; McGettigan et al. 2012; Tye-Murray et al. 2007
Facial expressions	McGettigan et al. 2012
Gestures	Holle et al. 2008; Obermeier et al. 2012
Bodily expressions	Jessen et al. 2012 [a]

The different domains have been ordered by increasing degree of ‘remoteness’ to the acoustic signal itself.

[a] Studies did not directly test speech.

[b] Syntax poses a particular case: The evidence cited here shows that syntactical complexity interacts with acoustic degradation and potentially draws on common neural resources; thus, only simple, as in direct contrast to complex syntax, should be assumed to ‘facilitate’ comprehension.

Ganong 1980; Gow et al. 2008) depends very much on accurately encoding the context-providing phonemes […iss], delivered from the same source to the same ear and neural fibres,

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and processed in high spectral and temporal proximity to the missing phoneme – an extreme case for a direct interdependence of contextual encoding and signal recovery.

The remainder of this short primer will mostly focus on a central yet particularly intricate source of context (Kalikow et al. 1977; Miller et al. 1951; Stickney and Assmann 2001): semantic context. This term is supposed to subsume the semantic richness that typical speech utterances offer to the listener and which the listening brain exploits in order to allow improved speech comprehension in particular under challenging listening situations. The studies discussed not only manipulated the speech signal acoustically (i.e,, its intelligibility), but they played with this additional variable of semantic context and its potency in supporting and facilitating speech comprehension when the listener is confronted with degraded speech. Note that the original studies reviewed in this section refer to this factor as *semantic context*, *semantic expectancy*, or *semantic predictability* almost interchangeably. For simplicity, I will here stick with the term *semantic context*.

2. Delineating the Impact of Semantic Context in Speech: Neuroimaging Evidence

The studies on semantic context I will now briefly recapitulate build logically and chronologically onto each other. First, a comparably broad approach onto the topic was chosen, as not many neuroimaging studies that tackle directly the interaction of acoustic quality and semantic context in speech comprehension had been performed up to that point (a notable exception being Davis et al. 2011, a study being presented first in 2005).

In a first functional MRI study on the role of semantic context in comprehending degraded speech (Obleser et al. 2007), we presented listeners with sentences from the speech in noise (SPIN) corpus (Kalikow et al. 1977) at various levels of spectral degradation (i.e., noise-vocoding, Drullman 1995; Shannon et al. 1995) to vary intelligibility. The important contextual constraint offered by the SPIN sentences is semantic in nature: All sentences end in a keyword (e.g., 'strap') which is preceded either by a semantically constraining sentence frame rendering the keyword highly predictable ('My sandal has a broken strap') or by a sentence frame without such constraints (low predictable, 'They were interested in the strap').

High compared with low semantic context resulted in considerable improvement in speech comprehension (see also Figure 1A,C). This manifested most clearly at intermediate levels of degradation (8-band vocoding), where comprehension of the last keyword benefitted from high semantic context by a factor of 1.8 compared to low semantic context.

However, this study also transcended the previous behavioural work: We found that the behavioural comprehension benefit at 8-bands was accompanied by increased activity in a wide left-hemispheric network comprising the left angular gyrus, the medial and left lateral prefrontal cortices, and the posterior cingulate cortex. Note that these areas are all situated remote from unimodal auditory cortex, in high-order heteromodal and amodal cortices.

Furthermore, the effective connectivity between these regions, as assessed by correlations amongst the activity time courses in these regions, was also increased for 8-band high-context compared to low-context sentences. This was particularly the case for effective connectivity between the left angular gyrus and the other areas under consideration (see above). Thus, we concluded that the beneficial influence of semantic context on speech comprehension is partly rooted in enhanced coupling of metabolic brain activity in an angular gyrus-centred network. This most likely reflects the additional conceptual and semantic computations (Binder et al. 2009; Seghier 2013) that are feasible because of the richer semantic context; a claim since backed by further empirical work (Bonner et al. 2013; Erb et al. 2013; Obleser and Kotz 2010; see also below).

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Using the SPIN sentence corpus helped us root this first fMRI study firmly in behavioural research performed in English before (e.g., Pichora-Fuller et al. 1995; see also Zust and Tschopp 1993 for an earlier attempt to replicate the contextual benefit in German listeners). However, the SPIN sentences trade in a desirable level of linguistic control for maximising the semantic context effect. For example, high- and low-context SPIN sentences are matched for average number of syllables and for occurrence frequency of phonetic features (Kalikow et al. 1977) but not for syntactic complexity, imageability, et cetera. This poses certain restrictions when interpreting brain activation differences observed between sets of these sentences in this first study.

Therefore, a follow-up study (Obleser and Kotz 2010) used a much more restricted set of sentences. Semantic context here was manipulated in the form of cloze probability (Taylor 1953), a measure of how strongly or consistently one word raises the expectation for another (for a recent elegant treatment of this effect, see Lash et al. 2013). Here, cloze probability was manipulated by a verb change in a pronoun–verb–determiner–noun sentence (e.g., low-cloze probability 'Er sieht das Haus' [he sees the house], high-cloze probability 'Er baut das Haus' [he builds the house]). Again, behavioural pilot experiments helped determine the most appropriate levels of speech degradation.

In accordance with the rather limited variations across sentences, the comprehension benefit that arose from the semantic context was strongest at a slightly more degraded level (4-band vocoding vs. 8-band vocoding in the previous study). For this second fMRI study, we thus used 4-band vocoded speech in high- vs. low-context sentences as the key comparison but took a more wholesome approach: We looked at linear trends in brain activation with increasing (or decreasing) intelligibility and tested for the interaction with cloze probability (i.e., our refined operationalisation of what we here refer to as semantic context).

The key findings of Obleser and Kotz 2010 can be summarised as follows: The linear trends with increasing intelligibility along the superior temporal gyri (STG) and sulci (STS) appeared extended anteriorly and posteriorly in low-context sentences but were restricted to a mid-STG/STS area in more predictable high-cloze sentences. Thus, a richer context appears to be able to constrain the neural resources in auditory brain areas that are devoted to tracking or 'mapping' the changes in intelligibility.

Second, left angular gyrus activation again covaried with successful speech comprehension (see also Erb et al. 2013; Golestani et al. 2013; Pallier et al. 2011). Interestingly, this was true no matter whether comprehension success profited from increased signal quality (i.e., 16-band more than 4-band more than 1-band speech) or from semantic context (i.e., high-cloze probability).

Both fMRI studies together provide concordant evidence from English and German listeners and sentences of varied linguistic complexity that the angular gyrus appears critically involved in enabling the behavioural *benefit* listeners can draw from semantic context in an adverse listening situation (Figure 1B).

What so far has been lacking, however, is more direct evidence that the left angular gyrus is a critical node in facilitating speech comprehension by channelling and utilising contextual information in challenging listening conditions.

Figure 1C shows preliminary single-participant data from a repetitive transcranial magnetic stimulation (rTMS) paradigm (G. Hartwigsen, T. Golombek, & J. Obleser, personal communication) where exactly this was pursued: We putatively disrupted normal neural processing in the left angular gyrus precisely during the last keyword of simple (SPIN) sentences using rTMS (using a translated and calibrated German version of the SPIN corpus, termed G-SPIN; Erb et al. 2012, 2013).

From Figure 1C, it is apparent that the comprehension benefit this listener can normally draw under degraded conditions from highly predictable sentences (i.e.,, with rTMS administered at a

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control site, here over superior parietal lobule; SPL) is absent when rTMS disrupts normal angular gyrus function. Note how, at least in this participant, the typical psychometric function capturing degradation-gated comprehension of highly predictable sentences (red solid lines) is shifted to the right (i.e,, towards more favourable acoustic conditions) under disruptive left-angular gyrus rTMS (red-dashed line, assimilating to the curve obtained for low-predictable conditions; dashed and solid blue lines).

One further study to round up these examinations of context in degraded speech (Obleser and Kotz 2011) stayed very close to the core research question, namely, the neural interaction of speech degradation and contextual cues (i.e,, semantic context). However, it approached this question by exploiting the temporal fidelity of electroencephalography (EEG). We reasoned that with EEG we would be able to better track the *unfolding in time* of comprehension and study not only a singular neural measure of magnitude for the entire sentence (i.e,, the blood oxygenation level dependent (BOLD) response in functional MRI studies, particularly so in 'single-shot' sparse-imaging sequences often used in auditory paradigms, Hall et al. 1999) but various neural signatures and their occurrence at sentence onset, during, and after the sentence-final keyword.

On the one hand, we analysed the evoked (i.e,, precisely phase- and time-locked) responses N100 (elicited by the sentence onset) and N400 (in response to the final keyword, reflecting by common understanding the neural effort with which a word is integrated into the sentence context; e.g., Kutas and Hillyard 1984; Kutas and Federmeier 2000). Note that 'neural effort' is a contentious and ill-defined term. However, for the present purpose of understanding the effects of semantic context in comprehending degraded speech, it should suffice to say that the N400 effect quantifies how much more neural activity is evoked by a lack or ambiguity of such context.

On the other hand, we also considered the induced gamma-band response (i.e,, neural oscillations with a frequency >30 Hz that are time-locked but not precisely phase-locked to the stimulus; Tallon-Baudry and Bertrand 1999). Why the gamma-band response in this study of semantic facilitation in degraded speech comprehension? Many studies on the top-down formation of percepts have focussed on this electrophysiological signature in the visual domain (e.g., Gruber et al. 2002), in multisensory integration (e.g., Schneider et al. 2008) but also in the auditory (e.g., Lenz et al. 2007), and the speech domain (Hannemann et al. 2007; Shahin et al. 2009b). Jointly, these studies indicate that the facilitation in forming a percept ('gestalt') by matching long-term memory representations ('adaptive resonance'; Grossberg 2009) is likely to be accompanied by comparably focal bursts of enhanced gamma-band synchrony (for review, see e.g., Fries 2009). This synchrony is argued to surface as power enhancements (compared to selected baseline periods) in the gamma-band range of the EEG.

The main results of Obleser and Kotz (2011) can be summarised as follows: First, auditory evoked responses to a degraded sentence's onset (N100) correlated with participants' comprehension scores (at generally highly comprehensibly 16-band speech, subjects comprehending less showed larger N100 responses). Second, the N400 in response to low-cloze sentence-final words, reflecting the integration effort of words into context, depended on speech intelligibility. This finding was recently replicated and extended by Strauß and colleagues (Strauss et al. 2013), and I will return to this extension below.

Third, a transient enhancement in gamma-band power (~40–70 Hz) during the more predictable high-cloze sentence-final words was taken to reflect top-down-facilitated integration of sentence meaning. This gamma-band effect and its left-central scalp topography matched well earlier reports of gamma-band enhancements in top-down-aided speech perception (Eulitz and Hannemann 2010; Hannemann et al. 2007). Here, however, the effect additionally covaried parametrically with signal degradation.

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Lastly, a negative correlation of N100 amplitude at sentence onset and the later gamma-band response was found in moderately degraded speech. If an enhanced N100 component is taken to reflect increased perceptual effort and the later enhanced gamma-band activity to reflect ease of semantic integration, this negative correlation would indicate that listeners can rely on partly distinct neural strategies when dealing with moderately degraded speech and that these strategies 'trade off' against each other: A more 'bottom-up', resource-allocating, and effortful versus a more 'top-down', associative, and facilitatory listening strategy (Obleser et al. 2011b).

3. *Other Forms of Context in Challenging Listening Situations*

While the focus of this short primer on context in speech comprehension has necessarily remained narrow and has mainly looked at semantic context, arguably more low-level sources of context should be mentioned briefly (see also Table 1): signal familiarity and signal predictability. For example, knowing the voice you are listening to (or, intricately, the voice you are trying to ignore in a given situation) can be beneficial for your speech comprehension (Johnsrude et al. 2013).

Also, comparably low-level regularities that are not limited to but also present in speech, like the temporal regularity with which sounds occur, have been now shown various times to benefit listening performance (e.g., Bendixen et al. 2009; Rimmele et al. 2012). Most of these studies have not used or tested speech directly. However, a very recent study by Bendixen and colleagues has shown, by analogy, that the processing of omitted (speech) sounds elicits comparable EEG components with overlapping contributions from – again – left angular gyrus, both in a single-word lexical context as well as in a simple sentence context (Bendixen et al. 2014).

As outlined above, sources of context might be grouped by their 'remoteness' from the speech signal itself (see also Table 1 for a more comprehensive survey of contextual factors). By following this 'remoteness' order, one could think of familiarity and regularity as 'secondary' or derived, but nevertheless acoustic, features. These context sources such as voice familiarity (i.e., patterns of known spectro-temporal configurations or covariations) or temporal regularity can be inferred from the acoustic input itself and play out their beneficial potential in speech comprehension accordingly. They are arguably less dependent on the 'bottleneck' of speech intelligibility, which sets them apart from semantic benefits. Semantic cues can only play out after acoustic and linguistic abstraction stages have been passed (Obleser and Eisner 2009; i.e,, the contextual information itself needs to be decoded from the signal and recognised as semantically coherent).

4. *Neural Top-down Modulation and Neural Facilitation through Context*

It is tempting to think of 'context' as of an extraneous bit of information that is provided outside of, previous to, or after the actual signal. This might be the case when the context is provided by written language (e.g., Sohoglu et al. 2012), facial expressions (e.g., McGettigan et al. 2012), or bodily movements (e.g., Jessen and Kotz 2013; Jessen et al. 2012); all of which often become available in advance and hence can shape the neural processing of auditory speech information in a truly 'top-down' fashion. Also, different tasks and goals of the listener are of course conceivable and are known to top-down modulate auditory cortical activity (e.g., Fritz et al. 2010; Lakatos et al. 2013; Mesgarani and Chang 2012).

However, contextual benefits in speech comprehension might well arise without such online 'top-down' modulation of auditory processing (Davis et al. 2011). As for the angular gyrus activity highlighted in Figure 1 (Golestani et al. 2013; Obleser and Kotz 2010; Obleser et al. 2007), it is for example somewhat unlikely that its activation would be fast and/or specific enough to effectively alter online patterns of neural activation in auditory cortex in a strictly feed-back fashion (but see indirect evidence by Gow et al. 2008 arguing in this direction). Also

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speaking against such a mechanism, the studies reviewed here in-depth did not observe directly context-driven differences in auditory cortex proper (Heschl's gyrus, planum temporale).

Also, the attentive reader might take issue with the terminology suggested ('facilitation') for the mechanism behind this impact of contextual cues onto comprehension of degraded speech: In fact, not all facilitation effects reviewed here are commensurable with the expected *reduction* in neural magnitude for a facilitatory effect. Also, the conceptual relation to (semantic) priming would lead us to expect generally reduced neural activity in cases where contextual cues facilitate comprehension (for review see e.g., Henson 2003; Race et al. 2009). Recall that the reductions of STG/STS activation (Obleser and Kotz 2010) and N400 magnitude (Obleser and Kotz 2011; Strauss et al. 2013) are well in line with such a 'facilitation equals a reduction in neural magnitude' concept – at first glance, however, the observed increases in BOLD activity (most prominently in angular gyrus) and in gamma-band power are not.

This can be reconciled, however, if we consider that the angular gyrus typically shows *most* BOLD signal change in a seemingly idle or *default* state and is hence often considered part of the default or resting-state network (Binder and Desai 2011). In fact, the present studies also found the signal change in angular gyrus to be on average across conditions *suppressed* compared to a task-free baseline (silent trials). A first reconciling argument might thus be that the contextual-cue-dependent upregulation of angular gyrus reflects a return to default-like levels of processing ease. Note that this would also hold for other areas activated in the same contrast, see e.g., the strikingly midline/default-network-proximate activations in medial prefrontal and posterior cingulate/restrosplenial cortex in Obleser et al. 2007. However, this interpretation of course remains subject to dedicated experiments including individual, true resting-state data.

A second argument would assume that the comprehension-related increases in BOLD and/or gamma power reflect (semantic, conceptual) stages of neural processing that can only be triggered once the access to the necessary (semantic, conceptual) information is facilitated. Thus, what we observe in the respective neural magnitude increase would reflect the *outcome* of a critical, facilitated processing stage, rather than this critical stage itself (for a more in-depth coverage of this logic see *Box 2* in Obleser and Eisner 2009).

In short, the gamma power increases in fronto-temporal cortex, and the angular gyrus activity increases might reflect the context-facilitated, and thus successful formation of a word-like or conceptual 'Gestalt' in degraded or fragmented speech (e.g., Bendixen et al. 2014; Eulitz and Hannemann 2010; Shahin et al. 2009a; for a framework see Grossberg 2009). Whether these effects are epiphenomenal, that is, neural outcomes or byproducts of successful comprehension, or whether they are true prerequisites of comprehension remains an open empirical question.

5. When Context Goes Awry: (Mal-)adaptive Reliance on Context?

Here is a running gag in Hergé's world famous cartoon series *Tintin* (e.g., Cyr et al. 2004): Professor Calculus is hard of hearing, which drives Captain Haddock mad. The professor has very obviously serious problems in speech comprehension. Surprisingly, however, this does not seem to bother him at all. He not only is notoriously hearing-impaired but also associates wildly and bases his interpretations only loosely on the phonetics of what has been said. Professor Calculus' communication behaviour is a fine, if fictional, example for a mechanism you might have experienced yourself (in milder forms) in adverse listening situations, maybe at a noisy party: We inevitably try to make sense of what we hear. And, as shown above, the sense we conceive might be very much shaped by the semantic or other context provided to us. There is also evidence that ageing listeners and listeners with hearing loss do in fact draw not less but the same or even more comprehension gain from context than

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younger listeners would – at least as long as potential differences in sensory acuity are adequately controlled for (e.g., presentation of materials at a more favourable signal-to-noise ratio; Pichora-Fuller et al. 1995).

But what if listeners, not unlike Professor Calculus, rely too much on what they have identified as the current 'context'? And how to strike a balance between the (degraded, ambiguous) sensory evidence provided by the afferent signal on the one hand and the (mal-)adaptive ability to synthesise or fuse previous contextual information with the present, degraded sensory evidence on the other? At least two lines of empirical evidence deserve consideration here.

One line of research is currently revisiting the idea that the neural processing of context might change under more or less severe forms of degradation (Strauss et al. 2013; see also Mattys et al. 2009 for theoretical implications). These data imply that listeners might limit their reliance on context, if the sensory evidence becomes scarce. As outlined below, the N400 deflection elicited by a sentence-final keyword reflects the extent to which the word requires neural resources to become integrated into the previously set context; if the word matched the expectancies formed, the N400 effect is weak or absent. Following this logic, one might argue that listeners do simply not form specific expectancies under severe forms of degradation, as Strauss et al. (2013) and Obleser and Kotz (2011) did not observe N400 effects in their most severely degraded conditions at all. In clear speech, an N400 effect was observed only for low-expectancy contexts (e.g., 'he gets…') and hence all possible sentence-final words required neural integration into context.

At an intermediate degradation level of 8-band vocoding, however, the neural process of predictively forming a semantic context (and hence yielding a reduced or absent N400 for word-to-context integration) in Strauss et al.'s participants seemed less 'liberal': Only the most highly expected sentence endings (e.g., 'he peels' – 'potatoes') yielded the expected N400 reduction, while the semantically as fitting but acoustic-phonetically distinct endings (e.g., 'he peels' – 'bananas') yielded a pronounced N400 effect. We interpreted this as an adaptive narrowing of expectancies under acoustic degradation. Put rather in psychological terminology, we might see here effects of perceptual load that affect, and potentially limit, further cognitive processes (e.g., Lavie 2005; Lavie and Tsal 1994) – such as prediction formation from context.

A second, almost opposite line of evidence so far builds on behavioural studies in ageing listeners but should spur more neuroscientific interest: 'False hearing'. Rogers et al. define it as 'a high-confidence, subjective experience of having actually heard a misperceived word' (e.g., 'lark' – 'shark'; Rogers et al. 2012). It is observable in particular in ageing listeners, which appear to outweigh 'global' or contextual evidence against 'local', sensory evidence such as phonemic category. While the authors link this to a deterioration of cognitive control, it is an open empirical question at which neural stage of sensory and cognitive processing such a maladaptive reliance on context would emerge.

6. *Conclusions*

In this short essay on the role of context in speech comprehension, I have focussed on the neural and in particular neurocortical foundations of the benefit listeners draw from contextual information when comprehending speech. In conclusion, it is worthwhile to emphasise that

(1) *We rarely encounter speech without being provided some form of context.* As for an attempt of classifying the various sources of context from which we as listeners can draw, the reader is referred to Table 1.

(2) *The neural basis of contextual benefit is likely to be found in brain areas and brain networks that may include but are clearly not limited to auditory cortex proper.* If at all, the absence of clear-cut activation differences in the brain responses from auditory cortex is what is striking about the

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studies reviewed in detail here. In line with a predictive coding framework (e.g., Friston 2010; for applications to speech see e.g., Sohoglu et al. 2012), context seems, if at all, to have a *decreasing influence* on parameters of neural magnitude in auditory cortex and wider superior temporal brain areas.

(3) *The role of the angular gyrus in mediating the benefits from context deserves further study.* Its appearance in a critical amount of semantic contextual facilitation experiments (using diverse brain imaging techniques such as functional MRI, EEG, and TMS) in combination with its node-like properties (as part of the default or resting-state network) might push open the door for a more integrated view on language and semantic processes in the context of current systemic thinking about human brain networks (e.g., Binder and Desai 2011; Raichle 2011; Sporns 2013; Weisz and Obleser 2014).

Short Biography

Jonas Obleser studies processes of auditory cognition and neuroscience at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. After training and obtaining a PhD in Psychology at the University of Konstanz, he worked at the Institute of Cognitive Neuroscience, University College London, as well as at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig before setting up the Research group 'Auditory Cognition' (http://auditorycognition.com). His current research interests include neural oscillations in sensation, perception and cognition as well as executive functions like attention and memory, with a keen eye on how these processes neurally interface with human listening and comprehension.

Note

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