Attention-dependent preparatory processing of naturalistic narratives is correlated with speech comprehension

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Abstract

While human speech comprehension is thought to be an active process that involves top-down predictions, it remains unclear how predictive information is used to prepare for the processing of upcoming speech information. We aimed to identify the neural signatures of preparatory processing of upcoming speech. Participants selectively attended to one of two competing naturalistic, narrative speech streams, and a temporal response function method was applied to derive event-related-like neural responses from electroencephalographic data. Regression analysis revealed that neural signatures with latencies as early as -450 ms prior to speech onset were significantly correlated with speech comprehension performance. The preparatory process involved a distributed network. These preparatory signatures were attention dependent; activity prior to the attended speech was negatively correlated with comprehension performance, whereas the opposite was found for unattended speech. Our findings suggest that attention plays an important role in the preparation to process upcoming speech.

Keywords

preparatory processing, attention, speech comprehension, electroencephalogram, temporal response function

Introduction

Humans are a powerful speech recognition system that can comprehend complex and rapidly changing human speech in challenging conditions, e.g., in a cocktail party scenario with multiple competing speech streams and high background noise. To achieve such a capacity, the human brain is equipped with neural architecture that is dedicated to bottom-up processing of perceived speech information, from the low-level acoustics, to the phoneme, syllable, and sentence levels (DeWitt & Rauschecker, 2012; Friederici, 2012; Hickok, 2012a; Pisoni & Luce, 1987; Verhulst, Altoè, & Vasilkov, 2018). In recent years, increasing evidence has also suggested that human speech comprehension is an active process that involves top-down predictions (Arnal, Wyart, & Giraud, 2011; Federmeier, 2007; Fries, 2015; Hickok, Houde, & Rong, 2011; Kutas & Federmeier, 2011; Rao & Ballard, 1999; Tian, Ding, Teng, Bai, & Poeppel, 2018). In the cocktail party scenario, it is believed that a listener should continuously predict what their attended speaker is going to say next to efficiently understand the corresponding speech (Cherry, 1953; O'Sullivan et al., 2015; Zion Golumbic, Cogan, Schroeder, & Poeppel, 2013). These predictions supposedly inform the brain about the 'what' and 'when' of upcoming speech information (Arnal & Giraud, 2012; Auksztulewicz et al., 2018), which allows a listener to prepare for follow-up processing.

Although the idea of top-down prediction in human speech comprehension is gaining popularity, it remains unclear how the brain uses predictive information to prepare for the processing of upcoming speech information. Understanding the preparatory process is essential because it reflects the influence of prediction on subsequent information

processing. Moreover, the available findings on prediction in speech are not sufficient

to determine the neural mechanisms underlying preparation. For instance, the classic

studies of active speech prediction have mainly focused on the neural activity in

response to prediction errors. Event-related potential (ERP) components such as the

N400 and P600 are frequently reported when the perceived word violates semantic and

syntactic congruency of the preceding speech context, respectively (Kutas &

Federmeier, 2011; Lau, Phillips, & Poeppel, 2008; Van Petten & Luka, 2012). These

ERP components normally occur >400 ms after the presentation of the perceived speech,

and so provide only indirect support for the preparatory process. Recent studies have

also reported evidence of the brain's pre-activation before the onset of the upcoming

speech (DeLong, Urbach, & Kutas, 2005; Dikker & Pylkkänen, 2013; Söderström,

Horne, Frid, & Roll, 2016; Söderström, Horne, Mannfolk, van Westen, & Roll, 2018);

these pre-activations have been interpreted as 'predictive' because they have been found

to be correlated with the relative likelihoods of the upcoming speech unit (e.g. words)

in the continuous speech materials (e.g. sentences). However, this is still only indirect

evidence for preparation, as these pre-activations have been represented by event-

related neural responses to the preceding speech unit that are informative about possible

upcoming speech units. Direct neural evidence for the preparatory response should be

derived from neural activity that is directly related to the processing of the upcoming

speech information, and which occurs immediately before speech onset.

While this direct evidence has not been investigated in the speech domain, several

studies on general sensory processing have provided ample support for the existence of

such a preparatory process. For instance, pre-stimulus oscillatory activity has been

reported to have a significant impact on subsequent perceptual consequences (Cao,

Thut, & Gross, 2017; Galindo-Leon et al., 2019; Harris, Dux, & Mattingley, 2018; Kok,

Mostert, & De Lange, 2017; Rassi, Wutz, Müller-Voggel, & Weisz, 2019). Moreover,

synchronization within neural populations responsible for the specific sensory

processing has been proposed to underlie preparation (Engel, Fries, & Singer, 2001;

Galindo-Leon et al., 2019; Lakatos et al., 2009). Following on from this work, the

present study investigated neural activity prior to the onset of upcoming speech

information to identify possible neural signatures of the preparatory process.

One crucial issue that needs to be considered is the possible dependence of the

preparatory process on top-down selective attention. As attention regulates the

processing of the input sensory information, it can be expected to affect prediction and

consequently preparation. Indeed, recent studies have demonstrated the interplay

between attention and prediction (Schröger, Kotz, & SanMiguel, 2015; Schröger,

Marzecová, & Sanmiguel, 2015). Specifically, the magnitude of the prediction error-

related neural response has been shown to be magnified or reversed, depending on the

attentional state (Auksztulewicz & Friston, 2015; Hisagi, Shafer, Strange, & Sussman,

2015; Kok, Jehee, & de Lange, 2012; Marzecová, Widmann, SanMiguel, Kotz, &

Schröger, 2017; Smout, Tang, Garrido, & Mattingley, 2019). Most of these studies have

been conducted within the visual domain, with limited exploration in the auditory

domain, let alone speech processing. Compared to vision, the fast temporal dynamics

of auditory stimuli and speech signals require neuroimaging tools such as EEG that can

track online changes in neural activity with a high temporal resolution.

The present study aimed to identify neural signatures that directly reflect the

preparatory processing of human speech. A 60-channel electroencephalogram (EEG)

was recorded from participants while they listened to naturalistic narratives; this

procedure is believed to be of high ecological validity and thus to provide necessary

contextual information for the engagement of top-down prediction and therefore

preparation (Federmeier, 2007; Friston, 2005; Jehee & Ballard, 2009; Rao & Ballard,

1999). A cocktail party paradigm was used, whereby we introduced a complex

perceptual environment that imposed further demands on prediction and preparation

(Broderick, Anderson, Di Liberto, Crosse, & Lalor, 2018). To obtain the neural

responses to continuous, naturalistic speech, we used a temporal response function

(TRF) method, to derive event-related-like neural responses from EEG data, for both

the attended and unattended speech streams in the cocktail party scenario (Crosse, Di

Liberto, Bednar, & Lalor, 2016; Lalor, Pearlmutter, Reilly, McDarby, & Foxe, 2006).

Following studies on the perceptual influence of pre-stimulus neural activities (Iemi et

al., 2019; Rassi et al., 2019; Smith, Johnstone, & Barry, 2006), these TRF-based

responses were analyzed for neural signatures related to speech comprehension

performance, as measured by speech-content-related questionnaires. We considered

that performance-relevant TRF-based responses before speech onset would be direct

neural evidence for the preparatory process, as the comparison between the predicted

and the actual perceived sensorial information cannot be performed during this period.

Furthermore, our experimental design allows the investigation on the attention

dependence of preparatory speech processing. Specifically, regression analyses were

employed with the TRF-based neural responses to attended and unattended speech

streams as the independent variables, and speech comprehension performance as the

dependent variable. Results revealed that neural signatures with latencies as early as -

450 ms prior to speech onset were significantly correlated with speech comprehension

performance. A distributed network was involved in the preparatory process of speech

comprehension. The preparatory activity to the attended speech was found to be

negatively correlated with comprehension performance, whereas the opposite was

found for unattended speech. Our findings suggest that attention plays an important role

in the preparation to process upcoming speech.

Results

Twenty participants took part in 28 'cocktail party' trials. In each trial, two narrative

stories were presented simultaneously to both the left and the right ears and the

participants were instructed to attend to one spatial side. Comprehension performance

was evaluated by questionnaires about the story contents, which were implemented at

the end of each story. There were two four-choice questions for the two simultaneously

heard stories, respectively. The comprehension performance was significantly better for

the 28 attended stories than for the 28 unattended stories (67.0±2.5% (standard error)

vs. 36.0±1.6%; the four-choice chance level: 25%; $t(19) = 10.95$, $p < .001$). The

participants reported a moderate level of attention (8.15±0.34 on a 10-point Likert scale)

and attention difficulties (2.04±0.53 on a 10-point Likert scale). The accuracy for the

attended story was significantly correlated with both the self-reported attention level (*r*

= .476, p = .043) and attention difficulty (r = -.677, p = .001). The self-reported story

familiarity level was low for all the participants (0.86±0.22 on a 10-point Likert scale)

and was not correlated with comprehension performance (r = -.224, p = .342). These

results suggest that participants' selective attention was effectively manipulated, as well

as good reliability of the measured comprehension performance. Most importantly,

there was a large inter-individual difference in the participant-wise average

comprehension performance for the attended stories; the response accuracy varied from

48.2% to 91.1%, which supports the feasibility of using these accuracy values as a

behavioral indicator of comprehension-relevant neural signatures.

The analysis workflow is shown in Figure 1. TRF-derived neural responses to the

attended and unattended speech were calculated separately, at latencies of -500 ms to

500 ms relative to speech onset. Responses within the -500–0 ms latency window are

considered to represent preparatory activity, whereas responses within the 0–500 ms

latency window reflect post-processing of the speech stream. These TRF responses also

underwent time-frequency analysis, and the average single-trial amplitudes and inter-

trial phase-locking (ITPL) values were calculated. We hypothesized that this

decomposition into amplitude and phase responses would yield more detailed insights

into the underlying neural mechanisms of speech processing, as amplitude and phase

have been proposed to play unique roles in networks underlying human cognition

(Engel, Gerloff, Hilgetag, & Nolte, 2013; Fries, 2015; Klimesch, 2012). To achieve this,

we established linear regression models with either amplitude or phase responses from

both the attended and unattended TRFs as the independent variables, and

comprehension accuracy of the attended speech as the dependent variable. The TRF-

based amplitude and phase responses at different channels, latencies, and frequencies

were used in separate regression models. We used regression analysis to take a full

consideration of possible joint contributions from the attended and unattended TRFs,

by deriving different regression coefficients respectively. The regression analyses were

performed by treating each participant's comprehension accuracy averaged over all the

28 attended stories as the dependent variable. This provides a robust estimation of the

comprehension performance, as only two four-choice questions were asked per

attended story. In addition, this design could allow more flexibility in neural data

analysis, e.g. exploring the inter-story variability in phase responses.

Regression models were built separately for the neural responses at each channel-

latency-frequency bin. The regression R-values were obtained to reveal how well the

regression models correlated with individual comprehension performance. Statistical

analyses were performed based on these regression R-values using a nonparametric

cluster-based permutation method (Maris & Oostenveld, 2007). Any significant results

at a latency <0 ms were taken to indicate the neural correlates of preparation for

upcoming speech information. We also calculated the mean of the regression coefficient,

and drew the distribution for every cluster.

Figure 1. The analysis workflow

(A) The experimental paradigm. Participants attended to one of two simultaneously presented naturalistic, narrative speech streams while 60-channel EEG was recorded. (B) EEG data analysis. Neural responses were characterized using a TRF-based modeling method. The TRF-based neural responses were then further subjected to a time-frequency analysis at the single-trial level and decomposed into single-trial amplitude and phase (by inter-trial phase locking, ITPL) responses based on the time-frequency representations (denoted by 'Amp' and 'ITPL'). This procedure was conducted for attended (Att-) and unattended (Unatt-) speech streams separately. (C) Comprehension performance. The participants completed a comprehension task after each speech comprehension trial. The average response accuracy over all trials per participant was taken as comprehension performance. (D) Regression analysis for comprehension performance-related neural responses. We established linear regression models with either amplitude or phase responses from both the attended and unattended TRFs as the independent variables, and comprehension accuracy of the attended speech as the dependent variable, for each channel-latency-frequency bin. The neural responses with significant regression model fitting are reported. We defined neural activity before 0 ms as preparatory processing and activity after 0 ms as post processing.

Preparatory neural activities were correlated with speech comprehension performance

The nonparametric cluster-based permutation analysis revealed a significant correlation between the multi-channel time-frequency representation of the TRFs and individual speech comprehension performance of the attended speech. This corresponded to six

clusters in the observed data (all, $p < .05$), as shown in Figure 2.

There were four clusters with latencies prior to 0 ms, which suggested that the brain

actively prepares for upcoming speech information. The earliest cluster (*Prep-A*)

extended from around -450 ms to -300 ms, and spread from the theta to low beta range

(6–18 Hz) over the right parietal region (permutation $p = .005$). The average prediction

model within the cluster revealed a significant correlation between the predicted and

the actual comprehension performance ($r = .678$, $p = .001$). The following cluster (*Prep-*

B) extended from around -400 ms to -350 ms, and spread from the alpha to beta range

(12–25 Hz) over the left frontal region (permutation $p = .030$; model prediction $r = .625$,

$p = .003$). There were two clusters with latencies around 0 ms. While *Prep-C* was based

on amplitude responses, much like *Prep-A* and *Prep-B*, *Prep-D* was based on the ITPL.

The amplitude cluster (*Prep-C*) extended from -50 ms to 0 ms, and spread from the

alpha to low beta range (9–19 Hz) over the central-parietal region (permutation $p = .015$;

model prediction $r = .725$, $p < .001$). The ITPL cluster (*Prep-D*) extended from -30 ms

to 20 ms, and spread from the alpha to low beta range (10–17 Hz) over the right central

region (permutation $p = .002$; model prediction $r = .746$, $p < .001$).

There were also two clusters with latencies >0 ms. The first cluster (*Post-E*) occurred

at 80–200 ms, and spread within the alpha range (7–9 Hz) over the right temporal region

(permutation $p = .035$; model prediction $r = .774$, $p < .001$). The other cluster (*Post-F*)

occurred at 180–300 ms, and spread from the theta to alpha range (4–11 Hz) over the

central parietal region (permutation $p = .008$; model prediction $r = .673$, $p = .001$).

These clusters were speech-following responses that likely reflect post processing of

the speech information for comprehension.

Figure 2. Neural responses that were correlated with speech comprehension performance

There are six clusters showing significant correlations with the comprehension performance of the attended speech, shown as six sub-plots. Each sub-plot is divided into five panels (A~E, labeled only in the upper left sub-plot titled 'Prep-A'), as explained below.

(A) Grand average topography of the regression *R*-values in the time windows of the significant clusters (depicted by the gray shadowed area in (D) and (E)). Black dots indicate the channels of interest included in these clusters.

(B) Time-frequency profile of the *R*-values averaged over the channels of interest. The dashed red rectangles indicate the time and frequency of interest included in the clusters.

(C) Scatter plots of the comprehension performance (y-axis) and the predicted values by the regression model averaged over all the channel-latency-frequency bins within the corresponding clusters (x-axis). Each dot represents an individual participant.

(D) and (E) Response time courses of attended-TRF(D) and unattended-TRF(E). The three red (D) and green (E) lines of different darkness represent the averaged responses over the participants with comprehension performance of the attended speech ranking in the top, middle, and bottom tertiles (7, 6, and 7 participants, respectively). The

histograms illustrate the distribution of coefficients of the selected channel-latency-frequency bins. The number displayed beside the histogram is the mean regression coefficient within the selected channel-latency-frequency bins.

Preparatory activities were attention dependent

The regression models for both attended and unattended responses revealed a joint contribution of the preparatory activities related to the attended and the unattended speech streams for the speech comprehension performance. For all six clusters, the mean regression coefficients within the selected channel-latency-frequency bins were significantly different from zero. For example, the mean of the coefficients for the attended and unattended activities of *Prep-A* were -0.018 and 0.032, respectively (the 99% bootstrap confidence intervals for the attended activity: [-0.019, -0.016]; for unattended activity: [+0.030, +0.033]; for all means and distributions, see Fig. 2D and 2E). Thus, both the attended and unattended activities significantly contributed to individual comprehension performance. By plotting the average TRF responses within the channel-latency-frequency of interest in these clusters for the participants with comprehension performance ranking in the top, middle, and bottom tertiles, we observed primarily reversed trends for the attended and unattended responses. Interestingly, reduced preparatory activities to the attended speech were seen for the top-performance tertile (corresponding to the negative mean coefficients), whereas the opposite effect was seen for the unattended speech (except for *Prep-B*, in which both mean coefficients were positive). The post-processing activities showed the reverse pattern, whereby participants with a better performance exhibited enhanced responses to the attended speech (as reflected by positive mean coefficients) and reduced

responses to the unattended speech (as reflected by negative mean coefficients). The

99% bootstrap confidence intervals for the means of all the coefficients are provided in

Table S1.

We further computed partial correlations between these preparatory neural activities

and the comprehension performance, while controlling for the post-processing neural

activities (i.e., *Post-E* and *Post-F*). *Prep-B* and *Prep-C* had significant partial

correlations with the comprehension performance ($r = .610$ and $.560$, $p = .007$ and $.016$,

respectively), which is suggestive of a unique functional contribution to comprehension

performance of the two preparatory neural responses. The partial correlations of *Prep-*

A and *Prep-D* with the comprehension performance failed to reach significance ($r = .32$

and $.44$, $p = .189$ and $.068$, respectively). Nevertheless, as these preparatory activities

occurred substantially earlier than the post-processing activities, the non-significant

results do not necessarily undermine the importance of these responses, but rather

indicate there to be shared neural mechanisms for preparation and post-processing.

Indeed, both the spectral and spatial signatures of *Prep-A* and *Post-F* largely overlapped,

and *Prep-D* and *Post-E* shared similar spatial patterns. In support of these observations,

significant correlations were found between *Prep-A* and *Post-F* ($r = .648$, $p = .002$) and

between *Prep-D* and *Post-E* ($r = .672$, $p = .001$). The pairwise correlations between all

six clusters are shown in Table S2, and the partial correlation results are shown in Table

S3.

Attention modulation was reflected by post-onset processing: replication of previous TRF-based studies

Several previous studies have employed a similar paradigm to investigate the attentional modulation of speech processing (Broderick et al., 2018; Mirkovic, Debener, Jaeger, & Vos, 2015; O'Sullivan et al., 2015). In these studies, the attentional modulation effect was operationalized as the difference between TRF responses to attended and unattended speech, whereas the present study focused on neural signatures that were associated with speech comprehension performance. To replicate their findings, we computed the attention-related neural activities according to these previous studies.

To this end, a cluster-based permutation analysis was performed to search for differences between the TRF-based neural responses to the attended and unattended speech, based on the multichannel time-frequency responses of either amplitude or phase responses. Selective attention resulted in significant differences the neural activities related to the attended and unattended speech streams, as represented by an amplitude-based cluster and a phase-based cluster. Both clusters had latencies well after 0 ms. Compared to the unattended speech, the attended speech was associated with a larger amplitude response at 50–180 ms at 5–13 Hz over the parietal region ($p = .018$) and a stronger ITPL at 100–260 ms at 4–8 Hz over the left-central parietal region ($p = .028$). None of the clusters, however, were significantly correlated with speech comprehension performance ($r = -.110$ and $-.187$, $p = .646$ and $.431$).

Figure 3. Attention-related neural responses were not correlated with speech comprehension performance

There are two clusters showing significant difference between attended and unattended speech streams. Each sub-plot is divided into four panels (A~D, labeled only in the upper sub-plot), as explained below.

(A) Grand average topography of *t*-values on the difference between the attended and unattended responses in the time windows of the significant clusters (depicted by the gray shadowed area in (C)). Black dots represent the channels of interest.

(B) Time-frequency profile of the *t*-values averaged over the channels of interest. The dashed red rectangles indicate the time and frequency of interest included in the clusters.

(C) Grand average time courses of the attended (red) and unattended (green) TRF responses averaged over the channels and frequencies of interest. Gray shaded areas indicate the time windows of interest.

(D) Scatter plots of the comprehension performance (y-axis) and the response differences averaged over all channel-latency-frequency bins within the corresponding clusters (x-axis). Each dot represents one participant.

Discussion

The present study aimed to identify neural signatures that directly reflect preparatory

processing of upcoming speech. We used naturalistic narrative speech materials in a

selective attention paradigm using a TRF-based approach for modeling the neural

activity, and observed preparatory neural activities before the onset of speech power

envelope fluctuations. These preparatory activities were correlated with the

comprehension performance of individual participants, with latencies as early as -450

ms. The preparatory process involved spatially distributed brain areas, taking the form

of an amplitude response rather than phase synchronization, with the most relevant

frequencies within the alpha and beta ranges. There was also an interplay between

attention and preparation, whereby preparatory activities to the attended and the

unattended speech contributed to comprehension performance, but with opposite

mechanisms. Our results provide direct neural evidence for how the brain prepares for

the processing of upcoming speech.

Before detailed discussions, it is necessary to state that our assumption for a preparatory

process is based on the observation that the TRF-based neural activities prior to speech

onset were significantly correlated with comprehension performance. Recent TRF-

based studies using naturalistic stimuli have reported reasonable latencies that

resembled their ERP counterparts for describing selective auditory attention (~200 ms)

(Mirkovic et al., 2015; O'Sullivan et al., 2015), semantic violation processing (~400

ms) (Broderick et al., 2018), and visual working memory (200–400 ms) (Huang, Jia,

Han, & Luo, 2018). Although our findings have mainly focused the window of < 0 ms,

these studies support the rationale of using the TRF-based responses to reflect the time

course of information processing in general. Therefore, the pre-onset latencies observed

in the present study can be considered to represent a preparatory state that precedes

speech processing.

Preparatory activities involve a distributed neural network

To prepare for the processing of upcoming speech information, multiple neural

signatures with different time, space, and frequency characteristics were identified,

which is indicative of the engagement of multi-center neural networks for active speech

perception. We did not base our analysis on preselected regions of interest, and so our

results provide a complete overview of all activities for preparation. Notably, one

preparatory cluster was found to be located over the left frontal region (*Prep-B*), which

supports the popular notion of a left-lateralized frontal network for top-down speech

prediction (Federmeier, 2007; Hickok, 2012b). Previous studies that have reported

involvement of the left frontal region in prediction have focused on post-processing of

either violations of linguistic congruency (e.g. the MMN and N400 responses; (Kutas

& Hillyard, 1984; Lau et al., 2008; Szewczyk & Schriefers, 2018) or contextual speech

cues (Dikker & Pylkkänen, 2013; Söderström et al., 2016). However, our results

indicate that this region plays an active role in preparation of speech processing, with

latencies of ~400 ms before speech onset.

Furthermore, the preparatory process was broadly distributed beyond the left frontal

region, including the parietal (*Prep-A*), central-parietal (*Prep-C*), and right central

(*Prep-D*) regions. The central-parietal responses could be related to the predictive

processing of speech meaning, and could recruit a mechanism that is similar to that

underlying the classical central-parietal N400 response (Federmeier, 2007; Lau et al.,

2008; Szewczyk & Schriefers, 2018). The right-lateralized finding (i.e., *Prep-D*),

however, may indicate a possible functional contribution of the right hemisphere to

prediction. Some studies have suggested that the right hemisphere is engaged in

language processing, primarily during complex narratives (Brownell HH, Michel D,

Powelson J, & Gardner H, 1983; George, Kutas, Martinez, & Sereno, 1999; Robertson

et al., 2000). As naturalistic speech materials used in the present study were likely to

engage speech processing at all levels, our results demonstrate the involvement of a

distributed neural network for the preparation of naturalistic speech processing.

Higher frequency neural activity for preparation and lower frequency activity for

post-processing

The neural mechanisms of the preparatory process were investigated using a time-

frequency analysis of the TRF-based neural activity. Similarly to recent TRF-based

studies, we observed attention-related neural responses (Mirkovic, Bleichner, De Vos,

& Debener, 2016; Mirkovic et al., 2015; O'Sullivan et al., 2015), with the peak attention

effect represented by theta and alpha oscillatory activities at 100–200 ms post-stimulus

onset over the frontal regions. Similarly, the comprehension-related post-onset

processing was mainly reflected in lower frequency bands from theta to low alpha

bands, as has been frequently reported in previous speech literatures (Ding & Simon,

2014; Giraud & Poeppel, 2012; Luo & Poeppel, 2007). In contrast, the comprehension-

related pre-onset neural signatures were in a higher frequency range, mainly within the

alpha and beta bands. This observation is in accordance with recent studies on pre-

stimulus ERPs in sensory perception, in which pre-stimulus alpha-band activity was

found to be significantly correlated with post-stimulus perception, especially in the

visual modalities (Bauer, Stenner, Friston, & Dolan, 2014; Milton & Pleydell-Pearce,

2016; Rohenkohl & Nobre, 2011; van Ede, Jensen, & Maris, 2010). These results have

been interpreted for a functional role of alpha band for a top-down inhibitory

mechanism to achieve the preparatory process. Meanwhile, several studies have

suggested that beta-band power reflects updating the content of a prediction (Bauer et

al., 2014; Sedley et al., 2016), as well as maintenance of ongoing cognitive context

(Engel & Fries, 2010). Accordingly, the pre-onset alpha and beta activity in our study

may reflect inhibitory of unattended speech and maintain the expectation in speech

preparatory processing (Kayser, Ince, Gross, & Kayser, 2015; Keitel, Gross, & Kayser,

2018). Taken together, these results suggest possibly of distinct functional roles of

neural activity at different frequency bands for speech processing, with alpha- or

higher-band activity reflecting top-down speech preparation, and the lower-frequency

activity reflecting post-stimulus processing.

In addition, three out of the four preparatory activities took the form of an amplitude

response rather than ITPL, including the earliest activities (*Prep-A* and *Prep-B*). At a

first glance, our observation may seem to be inconsistent with the popular view on the

functional roles of amplitude and phase responses, as phase synchronization is

frequently suggested to reflect the coordination of long-distance neuron communication

and therefore more likely to reflect top-down regulation of sensory information

processing (Engel et al., 2001, 2013; Galindo-Leon et al., 2019; Klimesch, 2012;

Lakatos et al., 2009; Salinas & Sejnowski, 2001; Sauseng et al., 2007; Schyns, Thut, &

Gross, 2011; Zhang, Hong, Gao, & Röder, 2017). Nevertheless, as the preparation

process reflects the usage of top-down predictive information for facilitated speech

processing rather than prediction *per se*, it is likely that these preparatory activities

mainly exhibited the actual implementation of prediction in speech-processing-specific

brain regions. In support of such a hypothesis, the distributed neural network indeed

covered the typical speech processing regions. Therefore, the amplitude-based

preparatory activities could be the result of localized speech-related information

processing as proposed in previous studies on general sensory processing (Engel et al.,

2001; Klimesch, Sauseng, & Hanslmayr, 2007; Mathewson et al., 2011; Zhang et al.,

2017). These activities could be related to the processing of the contextual information

relevant for the upcoming speech and thus provide the basis for the enhanced

comprehension performance. As limited previous studies have addressed the

dissociation between amplitude and phase responses, further work is necessary to

elucidate this issue.

Attention dependence of the preparatory neural signatures

The neural mechanisms of the preparatory process were further explored by inspecting

their relationship with attention. We further decomposed neural activity into amplitude

and phase responses. Specifically, our findings of the earliest preparation-related

amplitude modulation (*Prep-A*) in the alpha and beta bands support the recent reports

of beta power reduction during temporal prediction (Arnal & Giraud, 2012; Nobre &

Van Ede, 2018); in high-performing participants, comprehension performance was

associated with reduced amplitudes in response to attended speech and enhanced

amplitudes in response to unattended speech (i.e., the positive and negative regression

coefficients as displayed in Fig. 2D and 2E). Similar patterns were also seen for *Prep-*

C and *Prep-D* (ITPL in this case). The reduced amplitude responses and ITPL could

reflect a well-prepared state for processing upcoming attended speech (Bauer et al.,

2014; Chao, Takaura, Wang, Fujii, & Dehaene, 2018; Jensen & Mazaheri, 2010). The

neural activities related to the unattended speech were also correlated with speech

performance, but with opposite effects. Thus, the different modulation effects could

contribute towards an enlarged activity difference between the neural activities to the

attended and the unattended speech, for an efficient processing and thus comprehension

of the attended speech information.

Interestingly, although the neural activities related to both the attended and the

unattended speech also jointly contributed to comprehension performance at the post-

processing stage (*Post-E* and *Post-F*), a reversed pattern was observed as compared to

the preparatory stage. In participants with better performances, performance was

associated with enhanced responses to the attended speech and reduced responses to

the unattended speech. This reversed pattern is in accordance with the classical view

on attention modulation, and reflects enhanced processing to attended information and

suppressed processing to unattended information (Carrasco, 2011; Luck, Woodman, &

Vogel, 2000). The sharp contrast between the preparatory and the post-processing

processing stages supports the idea that there is an interplay between preparation and

attention. While our results are in line with previous research that has reported there to

be an interaction between attention and prediction (Friston, 2009; Kok, Rahnev, Jehee,

Lau, & de Lange, 2012; Smout et al., 2019), we provide further evidence on how such

interactions could affect behavior (i.e., comprehension). Namely, given that the

preparatory process supposedly reflects how prediction is implemented to facilitate

information processing, our results imply that attended speech may be favored by the

predictive or preparatory mechanism. Indeed, the neural activity associated with the

attended speech was inhibited during the preparatory stage, but enhanced during the

post processing stage, both mechanisms have been linked to more efficient processing

by previous studies (Rohenkohl & Nobre, 2011; Rommers, Dickson, Norton, Wlotko,

& Federmeier, 2017; Smith et al., 2006).

This study has some limitations that should be noted. The present study used the speech

power envelope as the reference signal from which the TRF models were derived,

which could reflect the speech information at all linguistic levels due to the highly

redundant information shared across levels (Daube, Ince, & Gross, 2019; Di Liberto,

O'Sullivan, & Lalor, 2015). While such an operation has the advantage of providing a

general overview about preparatory processing, further investigations are necessary to

differentiate possible contributions at different linguistic levels (Broderick et al., 2018;

Di Liberto et al., 2015). Meanwhile, caution must be taken when interpreting the timing

of the preparatory activities. While the preparatory activity as early as 450 ms before

speech onset could be the result of an optimized utilization of the rich contextual

information provided by the naturalistic speech materials, such timings may be

dependent upon the materials per se. Further studies are necessary to investigate the

possible material dependence of these timings, for instance, by employed an extended

amount of speech materials. In addition, an inter-individual level regression analysis

method was chosen, as the average comprehension questionnaire accuracies across all

stories within each participant was believed to provide a more reliable estimation the

speech comprehension performance than the single-trial accuracies. Thus, our results

do not necessarily imply that the observed neural signatures reflect the participants'

trait-like, stable speech processing style. Alternatively, it could be more plausible to

consider these neural signatures to reflect a more or less efficient speech processing

state. More theoretical and empirical research is needed to clarify the underlying

mechanisms.

Summary

We found that individual participants' comprehension performance was significantly

correlated with neural responses as early as -450 ms relative to speech onset. A widely

distributed brain network was involved in the preparatory process. Higher-frequency

activity in the alpha and beta bands were more closely related to top-down processing,

while lower-frequency activity was more closely associated with post processing.

Neural activities related to both the attended and the unattended speech contributed to

the comprehension performance, but with distinct mechanisms. Attended speech was

more efficiently processed when neural activity was inhibited in the preparatory stage

and enhanced during post processing, whereas the opposite effects were observed for

unattended speech. Our study provides a mechanistic description of how the brain

prepares to process upcoming speech information.

Materials and Methods

Ethics statement

The study was conducted in accordance with the Declaration of Helsinki and was

approved by the local Ethics Committee of Tsinghua University. Written informed

consent was obtained from all participants.

Experimental model and participant details

Twenty college students (10 female; mean age: 24.7 years; range: 20–43 years) from

Tsinghua University participated in the study as paid volunteers. All participants were

native Chinese speakers, reported having normal hearing, and had normal or corrected-

to-normal vision.

Data acquisition and pre-processing

EEG was recorded from 60 electrodes (FP1/2, FPZ, AF3/4, F7/8, F5/6, F3/4, F1/2, FZ,

FT7/8, FC5/6, FC3/4, FC1/2, FCZ, T7/8, C5/6, C3/4, C1/2, CZ, TP7/8, CP5/6, CP3/4,

CP1/2, CPZ, P7/8, P5/6, P3/4, P1/2, PZ, PO7/8, PO5/6, PO3/4, POZ, Oz, and O1/2),

which were referenced to a common average, with a forehead ground at Fz. A

NeuroScan amplifier (SynAmp II, NeuroScan, Compumedics, USA) was used to record

EEG at a sampling rate of 1000 Hz. Electrode impedances were kept below 10 kOhm

for all electrodes.

The recorded EEG data were first notch filtered to remove the 50 Hz powerline noise,

bandpass filtered to 0.5–40 Hz and then subjected to an artifact rejection procedure

using independent component analysis. Independent components (ICs) with large

weights over the frontal or temporal areas, together with a corresponding temporal

course showing eye movement or muscle movement activities, were removed. The

remaining ICs were then back-projected onto the scalp EEG channels, reconstructing

the artifact-free EEG signals. Around 4–9 ICs were rejected per participant.

Next, the EEG data were segmented into 28 trials according to the markers representing

speech onsets. The analysis window for each trial extended from 5 to 55 s (duration: 50

s) to avoid the onset and the offset of the stories.

Stimuli

The speech stimuli were recorded from two male speakers using the microphone of an

iPad2 mini (Apple Inc., Cupertino, CA) at a sampling rate of 44,100 Hz. The speakers

were college students from Tsinghua University, who had more than four years of

professional training in broadcasting. Both speakers were required to tell 28 1-min

narrative stories in Mandarin Chinese; the stories were either those about daily-life

topics recommended by the experimenter and told by the speaker improvising on their

own (14 stories), or those selected from the National Mandarin Proficiency Test (14

stories). The speakers were presented with the recommended topic or story materials

on the computer screen. They were allowed to prepare for as long as required before

telling the story (usually ~3 min). When they were ready, the speakers pressed the

SPACE key on the computer keyboard and the recording began with the presentation

of three consecutive pure-tone beep sounds at 1000 Hz (duration: 1000 ms; inter-beep

interval: 1500 ms). The beep sounds served as the event marker to synchronize the

speech audios in the main experiment, in which two speech streams were presented

simultaneously. The speakers were asked to start speaking as soon as the third beep had

ended (within around 3 sec). The speakers were allowed to start the recording again if

the audio did not meet the requirements of either the experimenter or the speakers

themselves (which mainly concerned speech coherence). The actual speaking time per

story ranged from 51 to 76 sec.

Two four-choice questions per story were then prepared by the experimenter and two

college students who were familiar with comprehension performance assessment.

These questions and the corresponding choices concerned story details that required

significant attentional efforts. For instance, one question following a story about one's

hometown was, "What is the most dissatisfying thing about the speaker's hometown?

(推测讲述人对于家乡最不满意的地方在于?)", and the four choices were A) There is no

heating in winter; B) There are no hot springs in summer; C) There is no fruit in autumn;

D) There are no flowers in spring (A. 冬天没暖气；B. 夏天没温泉；C. 秋天没水果；D.

春天没鲜花). Both the speech audio and corresponding questions are available for

downloads.

Experimental procedure

The main experiment consisted of 4 blocks of 7 trials. During each trial, two speech

streams were played simultaneously to the left and right ears. The two speech streams

within each trial were from the two different speakers to facilitate selective attention.

Considering the possible duration difference between the two audio streams, the trial

ended after the longer speech audio had ended. Each trial began when participants

pressed the SPACE key on the computer keyboard. Participants were instructed which

side to attend to by plain text ("Please pay attention to the [LEFT/RIGHT]") displayed

on the computer screen. A white fixation cross was also displayed throughout the trial.

The speech stimuli were played immediately after the keypress, and were preceded by

the three beep sounds to allow participants to prepare. At the end of each trial, four

questions (two for each story) were presented sequentially in a random order on the

computer screen, and the participants made their choices using the computer keyboard.

After completing these questions, participants scored their attention level of the

attended stream, the experienced difficulty of performing the attention task, and the

familiarity with the attended material using three 10-point Likert scales. Throughout

the trial, participants were required to maintain visual fixation on the fixation cross

while listening to the speech and to minimize eye blinks and all other motor activity.

We recommended that participants take a short break (of around 1 min) after every trial

within one block, and a long break (no longer than 10 min) between blocks.

The to-be-attended side was fixed within each block (two blocks for attending to the

left side and two for attending to the right side). Within each block, the speaker identity

remained unchanged for the left and right sides. In this way, the to-be-attended spatial

side and the corresponding speaker identity were balanced within the participant, with

seven trials per side for both speakers. The assignment of the stories to the four blocks

was randomized across the participants.

The experiment was carried out in a sound-attenuated, dimly lit, and electrically

shielded room. The participants were seated in a comfortable chair in front of a 19.7-

inch Lenovo LT2013s Wide LCD monitor. The viewing distance was approximately 60

cm. The experimental procedure was programmed in MATLAB using the

Psychophysics Toolbox 3.0 extensions (Brainard & Brainard, 1997). The speech stimuli

were delivered binaurally via an air-tube earphone (Etymotic ER2, Etymotic Research,

Elk Grove Village, IL, USA) to avoid possible electromagnetic interferences from

auditory devices. The volume of the audio stimuli was adjusted to be at a comfortable

level that was well above the auditory threshold. Furthermore, the speech stimuli

driving the earphone were used as an analog input to the EEG amplifier through one of

its bipolar inputs together with the EEG recordings. In this way, the audio and the EEG

recordings were precisely synchronized, with a maximal delay of 1ms (at a sampling

rate of 1000 Hz).

Temporal response function modeling

The neural responses to the speech stimuli were characterized using a temporal

response function (TRF)-based modeling method. The TRF response describes the

impulse response to fluctuations of an input signal, and is based on system identification

theories (Crosse et al., 2016; Lalor et al., 2006). We used the power envelope of the

speech signal as the input signal required by TRF, which has been demonstrated to be

a valid index by which to extract speech-related neural responses (Bednar & Lalor,

2018; Broderick et al., 2018; Ding & Simon, 2012; Huang et al., 2018; Mirkovic et al.,

2015; O'Sullivan et al., 2015).

Prior to the modeling, the preprocessed EEG signals were re-referenced to the average

of all scalp channels and then downsampled to 128 Hz. Likewise, the power envelopes

of the speech signals were obtained using a Hilbert transform and then downsampled

to the same sampling rate of 128 Hz. When denoting the downsampled EEG signals

from channel i, trial k as $R(i,t)$ and the input speech power envelope as $S(t)$, the

corresponding neural response $TRF_{i,k}$ can be formulated as follows:

$$R(i, t) = TRF_{i,k} * S(t) \qquad\qquad (1)$$

Where * represents the convolution operator. The latency in the neural response models

($TRF_{i,k}$) was set to vary from -1000 ms to 1000 ms post-stimulus to provide sufficient

data for the planned latency of -500 ms to 500 ms in the following time-frequency

analysis.

The TRF modeling analysis was performed on each EEG channel for each trial per

participant. TRF models were calculated for attended and unattended speech processing

separately using the corresponding speech streams as the input signal. It should be noted

that we did not consider the input lateralization for the TRF models, as the observed

behaviorally related findings were insensitive to the physical origin of the speech audios,

but rather likely to reflect the lateralization of the human speech network. Figure S3

provides the topographical information of our main results; it is similar to Figure 2, but

all results were calculated separately for speech stimuli from the left and right sides.

The topographies were comparable, even for the highly lateralized responses (e.g.,

Prep-B and Post-E).

The TRF-based neural responses were then further subjected to a time-frequency

analysis at the single-trial level. The TRF temporal profile was transformed using the

Hanning taper (2-cycle time window; for example, FWHM = 2 sec for 1 Hz wavelet)

at each time sample from -500 ms to 500 ms, with frequencies ranging from 1 to 30 Hz

at 1-Hz increments. Both single-trial amplitude and phase were recorded and denoted

as $\text{TRF}_{i,k}^{A}(\tau, f)$ and $\text{TRF}_{i,k}^{P}(\tau, f)$, where τ represents TRF latency relative to the onset

of speech power envelope fluctuations, and f represents the TRF frequency.

Given the number of trials denoted by N, the TRF-based single-trial amplitude and

phase responses were calculated as follows:

$$A_i(\tau, f) = \sum_{k=1}^{N} TRF_{i,k}^{A}(\tau, f) \qquad (2)$$

$$\text{ITPL}_i(\tau, f) = |\sum_{k=1}^{N} \exp(j \cdot TRF_{i,k}^{P}(\tau, f)|/N \qquad (3)$$

A large-amplitude value indicates a neural response of high magnitude across all trials,

and the phase-related ITPL value varies between 0 and 1; 0 refers to a situation in which

the phase responses of different trials are uniformly distributed between 0 and 2π, and

1 means the phase responses from all trials are entirely locked to a fixed phase angle.

These phase and amplitude responses were further transformed into z-scores within the

-500 ms to 500 ms time window for each channel separately per participant. These z-

scores were then used for the cross-participant statistical analyses.

The TRF analysis was conducted in MATLAB using the Multivariate Temporal

Response Function (mTRF) toolbox (Crosse et al., 2016). All the other EEG processing

procedures, as well as the statistical analyses, were conducted using the FieldTrip

toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011).

Quantification and statistical analysis

The extracted TRF-based amplitude and phase responses were used as independent

variables into a regression model to predict the speech comprehension performance of

the attended speech at the participant level (denoted by *CompreScore*). Given that we

aimed to explore the neural correlates of speech comprehension, we built different

regression models for amplitude and phase responses, for each EEG channel (*i*) at

individual latency (τ) and frequency (*f*) separately. Nevertheless, the responses to the

attended and unattended speech streams were incorporated into the same regression

model, as follows:

$$CompreScore = \alpha_1 \cdot A_i^{Attended}(\tau, f) + \alpha_2 \cdot A_i^{Unattended}(\tau, f) \qquad (4)$$

$$CompreScore = \alpha_1 \cdot ITPL_i^{Attended}(\tau, f) + \alpha_2 \cdot ITPL_i^{Unattended}(\tau, f) \qquad (5)$$

Statistical analysis was performed to examine the significance of these regression

model predictions over all channel-latency-frequency bins by computing the regression

R-values. Nonparametric cluster-based permutation analysis was applied to control for

multiple comparisons. In this procedure, neighboring channel-latency-frequency bins

with an uncorrected *p*-value below 0.01 were combined into clusters, for which the sum

of correlational *t*-statistics corresponding to the regression *R*-values were obtained. A

null-distribution was created through permutations of data across participants ($n = 1000$

permutations), which defines the maximum cluster-level test statistics and corrected *p*-

values for each cluster.

We also examined the coefficients of the regression. We calculated the distribution and

the mean of every selected channel-latency-frequency bin. We also calculated 99%

regression coefficient confidence intervals using the bootstrap method for every cluster.

To investigate the attention modulation effect, we performed paired t-tests on the TRF-

based neural activities related to the attended speech versus the unattended speech. Both

amplitude and ITPL were included in the analysis. A similar cluster-based permutation

was used to control for the multiple comparison problem (*p* < .01 as the threshold, *n* =

1000 permutations).

Supporting information

690   Fig S1. Topographies of the six responses as shown in Figure 2 (A) and calculated

691   separately for the speech stimuli delivered to the left side (B) and the right side (C) only.

Table S1: CIs of all Clusters

	Att	Unatt
Prep-A	[-0.019, -0.016]	[+0.030, +0.033]
Prep-B	[+0.002,+0.007]	[+0.036, +0.040]
Prep-C	[-0.016, -0.009]	[+0.035, +0.040]
Prep-D	[-0.010, -0.006]	[+0.040, +0.045]
Post-E	[+0.044, +0.049]	[-0.041, -0.035]
Post-F	[+0.009, +0.013]	[-0.033, -0.029]

Table S2: Pairwise Correlation between all clusters

	Prep-A	Prep-B	Prep-C	Prep-D	Post-E
Prep-B	.589**				
Prep-C	.421	.439			
Prep-D	.480*	.408	.486*		
Post-E	.596**	.361	.474*	.672**	
Post-F	.648**	.378	.483*	.562**	.646**

** p<.01

 * p<.05

Table S3: Partial correlation

	Partial-r	p
Prep-A	.323	.189
Prep-B	.560	.016*
Prep-C	.610	.007*
Prep-D	.439	.068

* p<.05

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Author contributions

J.L. conducted the experiments and data analysis; D.Z. designed the experiments and wrote the paper; B.H., G.D., and A.K.E. edited the manuscript.

Declaration of interests

The authors declare no competing interests.

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