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Commonalities in alpha and beta neural desynchronizations during prediction in language comprehension and production

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Abstract

The present study investigates whether predictions during language comprehension are generated by engaging the production system. Previous studies investigating either prediction or production highlighted M/EEG desynchronization (power decrease) in the alpha (8-10 Hz) and beta (13-30 Hz) frequency bands preceding the target. However, it is unclear whether this electrophysiological modulation underlies common mechanisms. We recorded EEG from participants performing both a comprehension and a production task in two separate blocks. Participants listened to high and low constraint incomplete sentences and were asked either to name a picture to complete it (production) or to simply listen to the final word (comprehension). We found that in a silent gap before the final stimulus, predictable stimuli elicited alpha and beta desynchronization in both tasks, signaling the pre-activation of linguistic information. Source estimation highlighted the involvement of left-lateralized language areas and temporo-parietal areas in the right hemisphere. Furthermore, correlations between the desynchronizations in comprehension and production showed spatiotemporal commonalities in language-relevant areas of the left hemisphere. As proposed by prediction-by-production models, our results suggest that comprehenders engage the production system while predicting upcoming words.

Keywords: language prediction, language production, alpha–beta oscillations, internal model

1. Introduction

Top-down prediction of upcoming stimuli has been proposed as a prominent feature of human cognition in order to optimize processing (Clark, 2013; de Lange, Heilbron, and Kok, 2018; Friston, 2005). This has been put forward also for language comprehension, whereby sentential and contextual information guide the pre-activation of linguistic representations before the stimuli are actually encountered, thus facilitating subsequent elaboration (Federmeier, 2007; Kuperberg & Jaeger, 2016). Prediction has been investigated by employing different paradigms and techniques (see e.g. reading and evetracking: Staub, 2015 for a review; visual world paradigm: Huettig, Rommers, & Meyer, 2011 for a review; event-related potentials (ERPs): Nicenboim, Vasishth, & Rösler, 2020 for a meta-analysis; Nieuwland et al., 2020 for a large-scale study; Van Petten & Luka, 2012 for a review). Despite the general agreement on the importance of prediction in language comprehension, what are the linguistic representations involved, the underlying mechanisms and their neural underpinnings is still largely unknown (Huettig, 2015). In the present study we investigated the hypothesis that prediction is implemented by engaging the language production system. To do so, we compared how the same person predicted an upcoming target word during comprehension and how they prepared to produce it. In order to tap into such processes, we analyzed the EEG oscillatory activity immediately before the presentation or the production of the target words in contexts in which they were either predictable or not. We anticipate that the results revealed large commonalities between the two modalities.

1.1 Prediction-by-production

Traditionally, language comprehension and production have been independently investigated. However, recent work highlights several commonalities in the representations, processes and the underlying neural circuitry (AbdulSabur et al., 2014; Dell & Chang, 2014; Okada & Hickok, 2006; Gambi & Pickering, 2017; Pickering & Garrod, 2014; Silbert, Honey, Simony, Poeppel, & Hasson, 2014). In particular, it has been proposed that prediction during comprehension is implemented through processes traditionally attributed to language production (Huettig, 2015; Pickering & Gambi, 2018;

Pickering & Garrod, 2013). The proposals in the literature, however, are not entirely in agreement regarding which processes and representations are involved.

Pickering and Garrod (2013) [P&G2013] envisaged language production and comprehension as a form of action and action perception, respectively. In studies of action control, internal forward models are used to predict sensory consequences and future states (Wolpert, 1997; Wolpert & Flanagan, 2001). Similarly, P&G2013 proposed that forward models are used not only to predict the speaker's own speech during production (Hickok, 2012; Hickok, Houde & Rong 2011), but also to predict others' speech during comprehension (prediction-by-simulation). In their view, forward models are "impoverished" representations and are extended to all the linguistic hierarchy (semantics, syntax and phonology), allowing for the rapid generation of predictions without engaging fully-fledged production representations.

According to Huettig (2015), prediction is based on the interaction between multiple mechanisms activated during comprehension (i.e. PACS: production-, association-, combinatorial-, simulation-based prediction). Comprehenders make use of fully-fledged production representations that can be pre-activated through simple associative learning (priming) and through active event simulation. The activation of linguistic representations is further constrained by combinatorial mechanisms sensitive to different linguistic levels. Critically, these mechanisms are shared between comprehension and production.

More recently, Pickering and Gambi (2018) [P&G2018] more explicitly differentiated processes related to prediction-by-association (PA) and to prediction by production (PP). PA is based on the spreading of activation among linguistic levels and it can be equated to semantic/phonological priming. PP is very effective but slow and, since it requires cognitive resources, it is optional. During prediction, comprehenders do not necessarily need to go through all the stages of word production and, according to the specific circumstances, they might predict semantic and syntactic features but not the phonology of upcoming words. On the other hand, PA is automatic and mandatory, but less effective. It leads to the pre-activation of all representations that are semantically and phonologically connected, independently of their relevance to the context, which is taken into consideration only in PP.

Summing up, all three proposals assume an important role of priming and event simulation, although for P&G2013 and P&G2018 simulation is part and parcel of the act of production, while in the PACS model it is a separate mechanism interacting with production; P&G2013 ascribe a prominent role to impoverished representations in the form of forward models, while both the PACS model and P&G2018 propose that prediction is based on the implementation of fully-fledged production representations.

Direct experimental evidence on production-based accounts of prediction is still relatively scarce. In order to determine to what extent prediction involves production representations, some ERP studies focused on the N400 effect during sentence reading by comparing the time-course of effects associated to prediction of meaning and prediction of form (Ito, Corley, Pickering, Martin, & Nieuwland, 2016; Ito, Gambi, Pickering, Fuellenbach, & Husband, 2020). These studies highlighted differences in the latencies of the effects depending on the kind of information predicted. The timing of the effects was suggestive of the steps envisaged by serial models of word production, whereby form is encoded after meaning (Levelt, Roelofs, & Meyer, 1999; Indefrey, 2011), and they have been considered congruent with the hypothesis that production representations are prominently involved in prediction. Similarly, experiments on sign language (Hosemann, Herrmann, Steinbach, Bornkessel-Schlesewsky, & Schlesewsky, 2013) showed that, during sign comprehension, mismatch-related N400 effects are elicited well before the target sign is fully articulated, signaling that predictions included the trajectory leading from one sign to the other in a modality-specific manner. The authors attribute these modality-specific predictions to forward models, thus supporting a version of production-based accounts of predictions. Further evidence is provided by Martin, Branzi, and Bar (2018), who showed that taxing the speech production system in a secondary task while reading the beginning of the sentence (silent syllable production) led to reduced N400 responses at the article preceding the unexpected noun, while other secondary tasks (tongue tapping, listening to syllables) did not. Interesting evidence comes also from developmental studies highlighting the relevance of production competence for the development of predictive abilities. In this respect, by using the visual world paradigm, Mani and Huettig (2012) showed that predictive abilities in 2-year old children were correlated with their production vocabulary size (number of words they

were able to produce according to their parents) but not with the comprehension vocabulary size (number of words that they could only comprehend).

In conclusion, experimental evidence suggests that even though production and comprehension do not fully overlap, they may interact in more complex ways than previously thought.

1.2 Neural oscillations in language prediction and production

Differently from ERPs that allow to retain information that is both time- and phase-locked to the onset of a stimulus, time-frequency analysis of the electroencephalographic (EEG) signal enables to observe also the modulation unfolding over time of non-phase-locked oscillatory activity at specific frequency bands (Bastiaansen, Mazaheri, & Jensen, 2012). The literature on neural oscillations in language comprehension and production has recently revealed oscillatory correlates (for reviews, see Meyer, 2018, and Prystauka & Lewis, 2019, for comprehension; Piai & Zheng, 2019, for production).

With respect to the prediction processes, the literature is still largely developing. Lewis and Bastiaansen (2015) and Lewis, Wang and Bastiaansen (2015) proposed that oscillations in the beta band (13-30 Hz) could reflect the maintenance/change of the sentence-level representation and the top-down propagation of predictions, whereas oscillations in the gamma band could reflect the matching of predicted and encountered information (low and middle gamma, 30-50 Hz) and the propagation of prediction error (high gamma, 50-100 Hz). This proposal has been put forward on the basis of a large body of literature on sentence processing employing violations, in which oscillatory modulations are observed *after* the presentation of a target stimulus that either disrupts or not the ongoing meaning or grammatical structure processing. In this case, power decreases in the beta range and power increase in the gamma range are reported (see Prystauka & Lewis, 2019, for a review). The pattern has been interpreted in line with the general framework proposed by Engel and Fries (2010) on the role of beta oscillations. Beta power increase (reflecting neural synchronization) would signal the maintenance of the current cognitive set, while power decrease or suppression (reflecting neural desynchronization) would signal that the cognitive set is changing or bound to change. The gamma oscillatory pattern has been interpreted in line with the general framework

proposed by Herrmann, Munk, and Engels (2004). Power increase in this band would reflect the matching of the encountered target stimulus with previously activated memory representations.

Predictive and anticipatory processes have also been investigated using a different approach, in which oscillatory modulations are observed *prior* to the presentation of a target stimulus that is either predictable or not on the basis of the preceding sentence content. Studies implementing this paradigm consistently showed a desynchronization in the beta (but also alpha) range prior to predictable targets (see Table 1). The pattern has been interpreted as reflecting top-down pre-activation of upcoming information. These studies employed the written modality, with words presented one at a time for fixed durations. While most studies employed high and low constraining sentences (Rommers, Dickson, Norton, Wlotko, & Federmeier, 2017; Wang, Hagoort, & Jensen, 2018), Terporten, Schoffelen, Dai, Hagoort, & Kösem (2019) studied the oscillatory activity preand post-target and the evoked response post-target (M/N400) while reading low, medium and high constraining sentences. The results showed alpha and beta desynchronization before target onset. Interestingly, the oscillatory data showed a non-monotonic relation with constraint level (i.e. the strongest desynchronization was elicited by the medium constraint, followed by the high and then the low constraint). The authors argued that pretarget power modulations reflected working memory demands for target pre-selection. These were maximal for the condition of intermediate levels of constraint, in which the pool of activated lexical candidates is larger than in the high constrain condition, in which only one candidate is activated. In other studies, however, maintenance in working memory has been more often associated to alpha-beta synchronization (see Weiss & Mueller, 2012; Meyer, 2018; Piai, Roelofs, Rommers, Dahlslätt, & Maris, 2015). Moreover, as can be seen in Table 1, effects in oscillatory activity have been detected only in partially overlapping cortical areas across studies. Given these inconsistencies in the results, it is still largely unclear what are the processes associated to alpha-beta desynchronization. In fact, it has been shown that the beta band is implicated in a variety of processes, even within the domain of language itself. In their review on the roles of the beta band in language processing, Weiss and Mueller (2012) show that different features of this frequency range (i.e. power, phase) are modulated by multiple aspects (i.e. motor planning, action semantics, working memory, information binding, and - as later elaborated on by Lewis and collaborators – change/maintenance of the current state). Additionally, different sub-bands within the beta range (e.g. beta1: 13-18 Hz; beta2: 19-25 Hz; beta3: 26-30 Hz) may even reflect different processes. Overall, the beta band likely underlies multiple mechanisms, possibly also in overlapping frequencies.

The relevance of the beta band in speech/language production is more straightforward, given its clear and well-documented involvement in motor and action control, as previously mentioned (see Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013, for a review). This holds true also for sensorimotor aspects of speech planning and execution. In particular, it has been shown that sensorimotor alpha and beta power decreases prior to articulation (reaching maximal suppression during articulation), while it increases (beta rebound) after utterance completion. Notably, the desynchronization prior to articulation has been linked to the generation of sensory predictions for speech monitoring (see Saltuklaroglu et al., 2018, for a review). In a series of studies aiming at probing linguistic and motor aspects of word production, Piai and collaborators focused on alpha and beta pre-target modulations by employing context-induced picture naming tasks. In these paradigms, the sentential context preceding the presentation of the target picture either allows or not for predicting the name of the target picture, and therefore plan the appropriate response. Time-frequency analyses of the interval preceding the target revealed alpha-beta desynchronization before predictable pictures (see Table 1). The interpretation of these effects as reflecting activation of linguistic information for word production planning is supported by behavioral results showing faster responses to predictable targets. An open question is what kind of processes and representations are reflected in the alpha-beta desynchronization found in this kind of production task. Piai, Roelofs, Rommers, and Maris (2015) dissociated the memory- and motor-related components by comparing pre-target beta and alpha desynchronization in two different tasks. In one case the task required to name the picture that followed a constraining or non-constraining sentence frame, in the other case participants were asked to judge whether the picture was predictable or not by pressing a key with their left hand. Results showed alpha-beta desynchronization in different areas, depending on the task. The activity in the left temporal areas and in ventral premotor areas observed during picture naming was associated to word retrieval and speech motor programming. The activity in left posterior temporal and inferior parietal areas and in the right motor area observed

during the categorization task were associated to conceptual processing and manual response preparation. In Piai, Klaus and Rossetto (2020), auditory distractors were introduced before picture onset. Alpha–beta desynchronization was delayed when the distractors were semantically related to the target picture with respect to unrelated distractors, suggesting that these power modulations are sensitive to lexico-semantic processing. Along the same lines, Piai, Rommers and Knight (2018) showed that aphasic patients with concomitant left temporal and inferior parietal lesions did not benefit from constraining contexts in terms of response times and did not display the characteristic alpha–beta desynchronization, while patients with left frontal and left temporal (but not inferior parietal) lesions did. According to the authors, this pattern suggests that the desynchronization in the alpha and beta bands elicited in context-induced word production is functionally associated to core semantic memory and lexical retrieval. Whether later stages of word planning (e.g. phonological encoding) are captured and reflected in these modulations in this paradigm remains unanswered.

Task	Study	Technique	Frequencies	Time- window	Scalp distribution	Cortical sources
COMPREHENSION	Rommers et al. (2017)	EEG	alpha (7-12 Hz) and beta (16-24 Hz)	-500, 0 ms	Alpha: stronger over occipital and central electrodes Beta: stronger over left posterior and anterior electrodes	-
	Wang et al. (2018)	MEG	alpha (8-12 H) and beta (16-20 Hz)	-550, -250 ms	Alpha: left anterior, central and posterior Beta: left centro- posterior	Alpha: left inferior frontal cortex, left posterior temporal cortex (including visual word form area, VWFA), left hippocampus, and right cerebellum Beta: left posterior temporal cortex
	Terporten et al. (2019)	MEG	alpha (8-12 Hz) and beta (16-20 Hz)	-540, 0 ms	Alpha: frontal and posterior, stronger in the right hemisphere Beta: frontal, stronger in the right hemisphere	Alpha: parietal regions with a bias to the right hemisphere Beta: left and right frontal and parietal regions
PRO DUC	Piai et al. (2014)	EEG	alpha–beta (6-30 Hz)	-400, 200 ms	Left frontal, central and posterior	-

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Piai et al. (2015b)	MEG	alpha–beta (4-25 Hz)	Average modulation -800, 0 ms	Left frontal, central and posterior	Left anterior and posterior temporal areas, bilateral ventral premotor areas
Piai et al. (2018)	EEG	alpha–beta (8-25 Hz)	-300, 0 ms	Group average in aphasic patients: bilateral frontal and left posterior (see reference for details).	-
Piai et al. (2020)	EEG	alpha–beta (5-20 Hz)	-350, 0 ms	Posterior sensors	-

Table 1: Summary of the studies on neural oscillations pre-target in prediction during comprehension and in context-induced word production. All these studies report desynchronization in the frequency bands and time-windows specified in the table. (EEG: electroencephalography, MEG: magnetoencephalography)

The oscillatory activity in the beta band reported both in prediction during comprehension and in production has led to the hypothesis of a common mechanism shared by the two processes (Molinaro, Monsalve, & Lizarazu, 2016). Until now, however, no study has directly compared the oscillatory alpha–beta activity in the two domains. Indirect support pointing towards common mechanisms comes from Pérez, Carreiras, and Duñabeitia (2017) who performed an experiment with hyperscanning where the EEG activity was registered while two participants interacted in a conversation. The results showed that alpha and beta oscillations of the speaker and the listener were temporally synchronized, and the authors interpreted this alignment as reflecting coordination between speaker and listener and predictive processing.

1.3 The present study

In order to directly compare how linguistic information is anticipated in comprehension and in production, we implemented a within-subject design in which the same participant engaged in both modalities. More precisely, we used both the cloze probability comprehension task and the context-induced picture naming task in two separated blocks, and focused on the alpha and beta oscillatory activity in an interval immediately preceding the relevant target. Participants listened to sentence frames which could either constrain or not towards a target word (see Table 2). After a silent pause of 800 ms, they either listened to the target word or they completed the sentence by naming the target picture. Time-frequency analyses focused on the silent interval between the sentence frame and the target. The structure of the paradigm allowed to directly compare the effects elicited by the same stimuli in the two tasks. In the constraining condition participants could anticipate the target word before hearing it or seeing the corresponding picture. Importantly, in the production task this means that participants can already plan the response before the picture is displayed. Therefore, measuring oscillatory activity before picture presentation allowed us to tap into processes associated to word production planning. The comparison with word prediction during comprehension in the same time interval would highlight the extent to which the two tasks share common mechanisms.

To our knowledge, this is the first study allowing for such direct comparison. In fact, as previously mentioned, shared mechanisms have been proposed in the literature on the bases of similar oscillatory patterns in separate studies investigating either prediction during comprehension or production. In addition, the present study made use of naturalistic auditory stimuli, contrary to most of the previous studies which employed the written modality in an artificial (word-by-word) fashion.

Following the literature, we expect to replicate the pre-target predictability effects of alpha and beta desynchronization in both comprehension and production. If prediction and production share some common mechanisms, we should observe temporal overlaps of alpha–beta modulations between the two tasks in language-relevant areas of the left hemisphere.

2. Materials and methods

2.1 Participants

Forty participants were recruited on a voluntary basis (11 males; mean age = 23.7, sd = 4.84). Sample size was determined before data collection. Given the 2×2 (task × list) design of the experiment (see below), we aimed at collecting 10 participants for each combination. All participants were right-handed native speakers of Italian (handedness evaluated by means of an Italian translation of the Edinburgh Handedness Questionnaire, Oldfield, 1971; mean laterality index = 86, sd = 15.28). None of them reported a history

of neurological, language-related or psychiatric disorders. All participants signed an informed consent to participate in the experiment. The study was approved by the Ethical Committee for the Psychological Research of the University of Padova (protocol n. 2920).

2.2 Stimuli

One hundred twenty-eight concrete, animate and inanimate nouns were selected and paired with a black-and-white line picture (240 x 240 pixels) representing the word referent. For each picture, a scrambled version was also created, in such a way that the referent was not recognizable. For each target noun, two sentence frames were constructed: one whose semantic content leads to the target word with a high probability (high constraint; HC) and one for which the target word is not particularly likely but is still plausible given the sentential content (low constraint; LC, see Table 2). This resulted in 256 sentences in total (128 HC, 128 LC). Sentence frames associated to the same target were matched for number of syllables, had a similar syntactic structure, and had the same article or preposition as final word. The constraint was modeled as the cloze probability (CP) of the target word given the frame, assessed with an online sentence completion questionnaire involving 71 respondents, none of whom took part in the subsequent experiment, who were asked to complete each sentence frame with the word they considered most appropriate (HC sentences: mean CP = 0.873, sd = 0.092; LC sentences: mean CP = 0.052, sd = 0.078). Subsequently, all sentence frames and target words were recorded from a female native speaker in a quiet room using a microphone connected to a PC using Audacity (sampling rate of 44.1 KHz). Frames and targets were recorded separately. The speaker was instructed to keep the reading pace as steady as possible and to keep a constant distance from the microphone. Recordings were then appropriately trimmed at the beginning and at the end using Audacity. The approximate number of syllables per second for each sentence frame, assuming a constant pace, was estimated as the number of syllables of the sentence divided by the length of each audio file.

Target words and their associated sentence frames were then divided into two lists, A and B, each containing 64 target words and the associated 128 sentence frames (64 HC and 64 LC). The two lists were matched for lexical frequency (log-scaled; obtained from *COLFIS*, Bertinetto et al., 2005), number of phonemes and number of syllables (obtained from *PhonIta 1.10*, Goslin, Galluzzi, & Romani, 2014), number of syllables per second, audio file duration, both across conditions and within conditions. The difference of CP was not significant between lists, and it was significant between conditions, both in the whole set and within each list (see Table 3 for stimuli matching). This ensures that each list elicits comparable levels of high and low constraint.

Task	Condition	Sentence frame	Target	Trials
COMPREHENSION	HC	Il contadino munge una 'The farmer milks a'	тисса	64
»(::	LC	<i>Il bambino disegna una</i> 'The child draws a'	- 'cow'	64
PRODUCTION	НС	<i>Il calciatore colpiva la</i> 'The soccer player kicked the'		64
	LC	Il bambino voleva la 'The child wanted the'	B	64

Table 2: Examples of stimuli used in the experiments.

	LISTS						
	Mean (sd) List A	Mean (sd) List B	<i>t</i> -value	df	<i>p</i> -value		
Lexical frequency (log-scaled)	3.776 (1.252)	3.849 (1.305)	-0.46	235.56	0.6476		
No. phonemes (word)	6.063 (1.701)	6.281 (1.631)	-1.05	253.55	0.2947		
No. syllables (word)	2.578 (0.728)	2.672 (0.641)	-1.09	250.06	0.2751		
No. syllables (sentence frame)	10.680 (2.012)	10.672 (2.248)	0.03	251.07	0.9766		
Audio length (sec) (sentence	2.388 (0.397)	2.381 (0.414) 0.15		253.54	0.8851		
frame)							
No. syllables/sec (sentence	4.482 (0.485)	4.480 (0.523)	0.05	252.52	0.9643		
frame)							
Cloze probability overall	0.456 (0.421)	0.468 (0.421)	-0.23	245	0.8215		
Cloze probability HC	0.868 (0.094)	0.878 (0.09)	-0.62	125.84	0.5351		
Cloze probability LC	0.045 (0.068)	0.058 (0.086)	-1	119.69	0.3193		
		CONDI	FIONS				
	Mean (sd) HC	Mean (sd) LC	<i>t</i> -value	df	<i>p</i> -value		
No. syllables (sentence frame)	10.750 (2.074)	10.602 (2.182)	0.56	253.34	0.5774		
Audio length (sec) (sentence	2.413 (0.407)	2.356 (0.402)	1.12	253.97	0.2629		
frame)							
No. syllables/sec	4.459 (0.441)	4.504 (0.56)	-0.71	240.87	0.4758		
Cloze probability overall	0.873 (0.092)	0.052 (0.077)	77.47	246.66	< 0.001		
Cloze probability List A	0.868 (0.094)	0.045 (0.068)	56.96	114.71	< 0.001		
Cloze probability List B	0.878 (0.09)	0.058 (0.086)	52.69	125.62	<0.001		

Table 3: Variables controlled across lists and conditions (Welch's *t*-tests). Means and standard deviations (in parenthesis) are reported. HC: high constraint, LC: low constraint.

2.3 Procedure

Participants were seated in a comfortable chair in a soundproof room with a computer connected to a CRT monitor, built-in speakers, a keyboard and a microphone to record responses. Stimuli were presented with E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). Each participant performed the comprehension task and the production task in a blocked design. The structure of the trials in the two tasks is shown in Figure 1. After a silent interval of 800 ms, a sentence frame was played through the computer speakers, and it was followed by a second silent gap of 800 ms. Throughout this phase the fixation cross remained on the screen. Afterwards, the target was presented. In the comprehension task, the auditory target word was presented together with a visual stimulus, which was constructed by scrambling the picture corresponding to the target in such a way that the referent was not recognizable. In the production task, the visual stimulus was the picture of the target word. Pictures were presented for 2 seconds. In the comprehension task, participants were instructed to listen carefully to the sentence. Following preceding literature (e.g. Terporten et al., 2019; Wang et al., 2018), to ensure that participants paid attention to the sentence, 26 trials (20%) included a statement about the preceding sentence appearing as written text after the target for 2 seconds. Participants were asked to judge whether it was true or false by providing a vocal response. In the production task, participants were instructed to name the picture as fast and as accurately as possible.



Figure 1: Trial structure in the comprehension (top) and the production (bottom) tasks.

For each participant, list A or B was associated to one of the tasks (e.g. list A for comprehension and list B for production). Task order and the lists associated to the tasks were counterbalanced across participants, resulting in a 2×2 design (2 lists \times 2 tasks). Trial order presentation was pseudo-randomized for each participant by using Mix (van Casteren & Davis, 2006) in such a way that the minimum number of trials between the first and the second presentation of the same target word was seven, and no more than three consecutive trials belonged to the same condition. The inter-trial interval varied from trial to trial (1, 1.2 and 1.5 seconds). After every 32 trials participants could take a short break. Responses were recorded through the microphone, positioned at a fixed distance from the participant (~50 cm). During the experimental session participants were instructed to minimize eye movements, blinks and facial muscle activity during the presentation of the stimuli. Before each task, a training session of 8 trials (not included in the experimental session) was used to familiarize the participant. Each task lasted approximately 20 minutes.

2.4 **Response coding and production RT analyses**

For the comprehension task, true/false responses were coded as correct or incorrect. Trials with incorrect responses were excluded from the EEG analyses. If error rate for a given participant was above 25%, the participant was excluded from further analysis of the EEG signal in both tasks.

In the production task, audio recording started at the onset of the picture and lasted for 2 sec. Responses were manually coded as incorrect when participants: 1) failed to provide an answer, 2) produced hesitation sounds, 3) started producing a word but then produced another word, 4) produced the correct target word before recording onset. Trials with incorrect responses were excluded from the EEG analyses. Response onset was measured from each audio recording using Chronset (Roux, Armstrong, & Carreiras, 2017). In case Chronset returned some *NA* values, the correspondent audio waveforms were inspected manually with Audacity in order to determine the response onset. The set of correct responses was then analyzed using R (R Core Team, 2014). RTs were analyzed by means of linear mixed-effects models (Baayen, Davidson, & Bates, 2008) using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015), with random intercept for participant and target word. The *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017) was used to estimate the *p*-values for model parameters. First, a null model including random effects only was computed, and in each subsequent model a predictor or an interaction between predictors was added. An ANOVA between models was then performed, and the best-fit model was selected considering AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion) as indices of fit and the *p*-value of the test between models.

2.5 EEG data acquisition and pre-processing

Electroencephalogram was recorded with a system of 64 active Ag/AgCl electrodes (Brain Products), placed according to the 10–20 convention (ActiCap). Sixty of them were used as active electrodes (Fp1, Fp2, AF3, AF4, AF7, AF8, F1, F2, F3, F4, F5, F6, F7, F8, Fz, FT7, FT8, F1, F2, F3, F4, F5, F6, Fz, FC1, FC2, FC3, FC4, FC5, FC6, T7, T8, C1, C2, C3, C4, C5, C6, Cz, TP7, TP8, CP, CP2, CP3, CP4, CP5, CP6, CPz, P1, P2, P3, P4, P5, P6, P7, P8, PO3, PO4, PO7, PO8, PO9, PO10 POz, O1, O2, Oz). Reference was placed at the left earlobe. Three electrodes were used to record blinks and saccades (external canthi and below the left eye). Electrode impedance was kept below 10 k Ω throughout the experiment. The signal was amplified and digitized at a sampling rate of 1000 Hz. Before the tasks, a resting state of 5 minutes was recorded, which is not analyzed further here. Each task was recorded separately. As a result, 3 recordings were obtained for each participant (resting state, production, comprehension).

Pre-processing and analyses were performed using the MATLAB toolbox Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011; Tadel et al. 2019), which is documented and freely available for download online under the GNU general public license. A high-pass filter at 0.5 Hz with 60 dB attenuation was applied to the raw data. Noisy or flat channels were marked as 'bad' and excluded (max 2 channels marked as 'bad' per participant). No interpolation of bad channels was performed. Segments with extreme muscle artifacts were marked as 'bad'. Subsequently, Independent Component Analyses (ICA) with 60 components was computed to detect and remove artifact components with known time-series and topographies (blinks, saccades, and power-line noise at 50 Hz).¹ Markers for incorrect responses were manually added to the continuous EEG recording according to the off-line evaluation of the audio files. Finally, 3-second epochs (from -1.5 to 1.5 s) were imported around two event markers: (1) the onset of the trial (fixation cross), and (2) the onset of the 800 ms gap pre-target. The epochs in (1) were not divided into conditions and constitute the condition-average baseline for the event-related synchronization / desynchronization (baseline_{comp} and baseline_{prod}). This ensures a higher signal-to-noise ratio given the higher number of trials included as baseline, and therefore a better estimate of the relative power change (Cohen, 2014). The epochs in (2) were divided into HC and LC conditions (HC_{comp}, LC_{comp}, HC_{prod} and LC_{prod}). All epochs were visually inspected, and those with artifacts (uncorrected blinks/saccades, muscle activity, channel drifts, transient electrode displacements) were rejected. All trials in (2) which included a marker of incorrect response were rejected.

2.6 Time-frequency decomposition and statistical analyses (sensor-level)

In the time-frequency (TF) decomposition, power was computed by using Morlet wavelets. According to Morlet wavelet implementation in Brainstorm software, wavelets were built starting from a mother wavelet with central frequency = 1 and FWHM = 3 (7-cycle wavelets), and then generating new wavelets spanning from 5 Hz to 30 Hz with step 1 Hz.² TF maps were obtained for each trial for all conditions (baseline_{comp}, HC_{comp}, LC_{comp}, baseline_{prod}, HC_{prod}). Due to the large windows for epoching (3 seconds), edge effects at the selected frequencies did not involve the windows of interest. Subsequently, TF maps were averaged within each condition for each participant.

Event-related synchronization/desynchronization (ERS/ERD) was used as normalization method.³ For each participant, the average TF map of the two conditions

$$^{3} ERS/ERD_{t} = (Power_{t} - \overline{Power_{baseline}}) / \overline{Power_{baseline}} \times 100$$

¹ If any channels were marked as 'bad', the number of components for the ICA was reduced to the number of good channels.

 $^{^{2}}$ The delta band (0.1-4 Hz) was excluded because the wavelets at these frequencies were too large and temporal smearing introduced noise in the production task (HC condition) due to muscle activity after the gap of interest.

were normalized against the mean computed over the interval [-550 -250] ms of the average baseline TF map (baseline_{comp} for HC_{comp} and LC_{comp}; baseline_{prod} for HC_{prod} and LC_{prod}). This yielded the %-change of power over time relative to the baseline for each frequency.

After having obtained the normalized TF map for each participant, non-parametric cluster-based permutation tests were performed for each task on the 800 ms pre-target gap (Maris & Oostenveld, 2007). The critical α level was set to 0.05, the minimum number of neighboring channels set to 2, and the number of Monte Carlo simulations for the permutations to 1000. Based on previous research, we formulated a specific directional hypothesis for the contrast between HC and LC conditions. Specifically, our alternative hypothesis was that HC conditions elicited reduced power compared to LC conditions. To ensure consistency between research hypotheses and statistical hypotheses (Cho & Abe, 2013; Harrington, 2020) we employed cluster-corrected one-tailed paired *t*-tests when contrasting the conditions within each task. In absence of any directional hypothesis, to examine the interaction between constraint and task (production *vs.* comprehension), a cluster-corrected two-tailed paired *t*-test was performed between the differentials (HC–LC) of the two tasks. From now on we refer to the difference between HC and LC in each task as Δ_{comp} and Δ_{prod} , and to the statistical contrast between them as interaction.

2.7 Time-frequency decomposition and statistical analyses (source-level)

To estimate EEG activity at source level we implemented the following steps. First, a noise covariance matrix for each task was computed from the baseline epochs in the timewindow [-550 -250] ms. OpenMEEG BEM (Boundary Element Method) with 8002 vertices was used as forward solution⁴ (Gramfort, Papadopoulo, Olivi, & Clerc, 2010) with ICBM152 as template anatomy. This method models three realistic layers (scalp, inner and outer skull) in addition to the cortical surface; for this reason, it is recommended for EEG data, given the differential electrical propagation through the types of tissue. Minimum Norm Imaging (NMI) normalization with sLORETA (Standardized Low

⁴ For the other layers (scalp, inner and outer skull) Brainstorm defaults settings were kept.

Resolution Brain Electromagnetic Tomography; Pascual-Marqui, Michel, & Lehmann, 1994) was used as inverse solution. The dipole orientation was unconstrained, to obtain a better estimation in lack of individual anatomy scans.⁵ Time-frequency decomposition was performed on each epoch, averaged and normalized against the baseline as for the TF at sensor level. Following practices adopted in previous studies (e.g. Piai et al., 2015b; Wang et al., 2018), TF maps were then averaged across frequencies based on sensor-level results. Specifically, we identified four frequency ranges: alpha (8-12 Hz), beta1 (13-19 Hz), beta2 (20-25 Hz) and beta3 (26-30 Hz). This subdivision allowed to reduce the computational burden while preserving the widespread modulations that contributed to the effects in the two tasks. Incidentally, these ranges nicely overlap with a possible subdivision suggested by Weiss and Mueller (2012). Subsequently, ERS/ERD maps were downsampled at 150 Hz, to further reduce the computational burden. Cluster-based permutation tests for effects of condition in each task (one-tailed paired *t*-tests) and their interaction (two-tailed paired *t*-tests) on source-space TF data were performed as described for sensor-level testing.

2.8 Between-task source-level correlations

Pearson correlations between Δ_{comp} and Δ_{prod} at the source level were performed. This provides an estimate of putative shared cortical generators of the desynchronizations in prediction during comprehension and in word planning in production. Correlations were computed separately for the alpha band (8-12 Hz) and the three beta sub-bands (13-19, 20-25 and 26-30 Hz) on Δ %-power change averaged in intervals of 200 ms (0-200, 200-400, 400-600 and 600-800 ms), resulting in 16 correlation maps. For each vertex of the cortex model, two vectors of values were correlated. Each vector contained 36 values, one for each participant, representing the average Δ %-power change at a given frequency band and time-window in the two tasks. We decided to average in time because it is likely that cortical modulations underlying possible shared processes are not temporally aligned across the two tasks due to different demands influencing participants' performance. In this way we can capture desynchronizations at the same vertex that are slightly shifted in

⁵ The other settings were kept at Brainstorm default settings (Noise covariance regularization: 0.1; Signal-to-noise ratio: 3).

time. For each frequency band, correlations were thresholded for p < 0.05 and minimum size = 50 (number of connected vertices), in order to exclude not only statistically non-significant correlations, but also statistically significant but spatially isolated and likely meaningless correlations. In other words, only significant correlations that are spatially connected on a relatively extended area of the cortex model have been displayed and considered. Given the exploratory nature of these analyses and the fact that many factors can hinder the possibility to detect commonalities between the tasks (e.g. variability in the timing of the processes under study, inter- and intra-subject variability, spatial inaccuracy of the technique), we opted for this spatial criterion for identifying significant correlations without adopting a multiple comparisons correction approach. Then, correlations were inspected, and the intervals with the strongest and more spatially extended correlations were identified. To provide a clearer summary of the results, we performed additional correlations on the averages of the identified time-windows. For this additional analysis we only focused on the positive correlations.

3. Results

3.1 Word production response times

Response accuracy was very high (98.5%). Only 84 responses were coded as incorrect, 59 in the LC condition and 25 in the HC condition. Error rates were not analyzed. Figure 2 shows response times of correct trials divided by condition.



Figure 2: Violin plot of the response times of correct trials in the production task for the HC and the LC conditions. HC: mean = 507 ms, sd = 184.786; LC: mean = 698 ms, sd = 172.22.

Latencies of correct responses were fitted to mixed-effects models; Table 4 shows the results of the ANOVA between models. The model which best explained the data is M4, which included Repetition, Condition, Lexical frequency and the interaction Condition \times Lexical Frequency as fixed effects.

Model	Effects	Df	AIC	BIC	X^2	<i>p</i> -value
M0	Random effects (R.E.)		66966	66992		
M1	R.E. + Repetition	5	66705	66737	263.22	< 0.001
M2	R.E. + Repetition + Condition	6	64857	64897	1849.1	< 0.001
M3	R.E. + Repetition + Condition + Lexical	7	64858	64904	1.134	0.287
	Frequency					
M4	R.E. + Repetition + Condition + Lexical	8	64851	64903	9.195	0.002
	$Frequency + Condition \times Lexical$					
	Frequency					
M5	R.E. + Repetition + Condition + Lexical	9	64852	64911	1.231	0.267
	$Frequency + Condition \times Lexical$					
	$Frequency + Condition \times Repetition$					

 Table 4: Statistics of model selection.

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The model showed a main effect of Repetition (estimate = -85.023, t = -20.74, p < 0.001, 95% CI: -93.06 – -76.987) – with estimated faster responses at the second presentation of the same target picture – and of Condition (estimate = 232.085, t = 17.871, p < 0.001, 95% CI: 206.626 – 257.543) – with estimated faster responses in the HC relative to LC condition. There was no main effect of Lexical Frequency (p = 0.962), but there was an interaction between Frequency and Condition (estimate = -9.78, t = -3.034, p < 0.01, 95% CI: -16.1 – -3.46): the effect of Lexical Frequency was present in the LC condition, with decreasing RTs when lexical frequency increases. Table 5 shows all the parameter estimates of the model.

Parameter	Estimate	SE	df	<i>t</i> -value	<i>p</i> -value	95% CIs
Intercept	548.022	22.158	188.58	24.733	< 0.001	[504.375 – 591.676]
Repetition	-85.023	4.1	4870.027	-20.740	< 0.001	[-93.0676.987]
Condition	232.085	12.987	4870.745	17.871	< 0.001	[206.626 – 257.543]
Lexical Frequency	0.222	4.604	162.17	0.048	0.962	[-8.854 – 9.302]
Condition × Lexical Frequency	-9.78	3.224	4870.594	-3.034	0.002	[-16.13.46]

 Table 5: Parameter estimates of model M4.

3.2 Sensor-level time-frequency analysis

The data of two participants were excluded from all subsequent EEG analyses due to an excess of trials coded as incorrect in the comprehension task (34.6% and 53.9%). Another two participants were excluded due to excessively noisy EEG recordings. The mean percentage of epochs retained are the following: baseline_{comp}: 88.8%, HC_{comp}: 89.7%, LC_{comp}: 87.5%, baseline_{prod}: 87.7%, HC_{prod}: 89.3%, LC_{prod}: 89.7%.

The cluster-based permutation tests contrasting HC vs LC conditions in the two tasks were significant. In the comprehension task, the effect was associated to a negative cluster (p = 0.003, t-sum = -324052, size = 134070; Figure 3a). In the production task, the effect was associated to a negative cluster (p = 0.001, t-sum = -946882, size = 361719; Figure 3b). This suggests that high target predictability elicited desynchronization before

its presentation, be it an auditory word or a picture to name overtly. The effects were widespread across all sensors and appeared to span the entire alpha and beta ranges, with variability of modulations across the gap. The analysis testing for the interaction did not yield significant results (all clusters p > 0.05; see Supplementary Material).



Figure 3: Time-frequency maps averaged across groups of sensors for the comprehension (a) and the production (b) tasks. The averaging is only for visualization purposes; statistical testing was performed on all electrodes. Each column represents a group of sensors, specified on the scalp model above. The rows represent the average TF maps of the HC condition, the LC condition, the HC-LC differential ($\Delta_{comp/prod}$), and the *t*-values of the statistical contrast (*t*-maps are masked for values associated to the significant cluster).

3.3 Source-level time-frequency analysis

Source-level contrasts identified two significant negative clusters in the comprehension task (cluster 1, left hemisphere: p = 0.02597, *t*-sum = -742975, size = 326126; cluster 2, right hemisphere: p = 0.04995, *t*-sum = -645503, size = 280809) and two negative clusters in the production task (cluster 1, left hemisphere: p = 0.001, *t*-sum = -1820707, size = 719067; cluster 2, right hemisphere: p = 0.002, *t*-sum = -1405540, size = 562307). The interaction analysis did not yield significant results (all clusters p > 0.05; see Supplementary Material). Results are shown in Figure 4a and Figure 4b.

In comprehension, alpha desynchronization was stronger towards the end of the gap and involved the bilateral frontal and temporal cortex; early in the gap it involved the left posterior temporal cortex. Beta desynchronization was found in the temporal (beta1) and inferior frontal (beta1, beta2, beta3) cortices of the left hemisphere, and in temporoparietal-occipital areas (beta1, beta2, beta3) of the right hemisphere. In production, alpha desynchronization involved the bilateral prefrontal, temporal and inferior parietal cortices, with a bias in the right hemisphere. Beta desynchronization involved various cortical areas, including the temporal, parietal and frontal cortex in the left hemisphere, and the parietal cortex in the right hemisphere.



Figure 4: Summary of the statistical contrasts between HC and LC conditions in the comprehension (a) and production (b) tasks. Selected cortical maps of *t*-values are shown for each of the frequency bands (α : 8-12 Hz; β 1: 13-19 Hz; β 2: 20-25 Hz; β 3: 26-30 Hz) in averaged time-windows determined from inspecting the time-course of the results. For each map, the time-window used for averaging is indicated by the red line below each plot (comprehension: α : 0-100, 500-800 ms; β 1: 300-400, 400-800 ms; β 2: 400-600 ms; β 3: 400-700 ms; production: α : 0-600 ms; β 1: 0-200, 200-600 ms; β 2: 250-350; 500-800

ms; β 3: 500-800 ms). Averaging is for visualization purposes only; analyses were performed on all timepoints after downsampling. Only *t*-values ranging from -1 to -4 and part of a significant cluster are shown. Complete results are provided in the Supplementary Material.

3.4 Source-level correlations

Figure 5 shows positive correlations between Δ_{comp} and Δ_{prod} as defined in the Method section (complete correlation maps are reported in the Supplementary Material). The areas highlighted include the left temporal cortex, the inferior frontal cortex, motor and supplementary motor cortices, the left insula, and the left inferior parietal cortex.



Figure 5: Positive correlations between Δ_{comp} and Δ_{prod} at the source level at each frequency band. The timeline at the bottom represents the 800 ms silent interval between sentence frame and target; the red lines below each cortical map represent the time-window of the correlation displayed above it (α : 400-800 ms; β 1: 200-600 ms; β 2: 200-400 ms; β 3: 0-400 ms).

4. Discussion

We employed a within-subject design in order to directly compare alpha and beta oscillatory modulations elicited by predictive processes in comprehension and production by manipulating cloze probability. We found alpha and beta desynchronization in HC relative to LC conditions preceding the target stimulus. The cortical sources appeared to be left frontal, temporal and inferior parietal, involving areas traditionally associated to language processing, but also right parietal and temporo-parietal areas. Positive correlations between Δ_{comp} and Δ_{prod} were found in the left temporal, frontal, and inferior parietal cortices.

In the following paragraphs we will discuss: 1) the desynchronizations in the left hemisphere in relation to language-specific and domain-general processing; 2) the desynchronizations in the right hemisphere; 3) how these results are compatible with production-based accounts of prediction; 4) limitations of the present study and future developments and directions.

4.1 Alpha–beta desynchronization in the left-lateralized language areas as index of predictive information retrieval and encoding

In both tasks, HC contexts induce desynchronization of the alpha and beta bands relative to LC contexts. We interpret the desynchronization as marker of pre-activation of linguistic information, both in predicting during comprehension and in planning for word production.

In the comprehension task, language-relevant areas are engaged in actively updating the sentence-level representation in a top-down fashion. In the HC condition the preceding context allows for the generation of strong predictions about the upcoming word. The information retrieved from long-term memory in this case is rich and specific. This predictive process is reflected in the desynchronization of oscillatory activity in the alpha and beta band observed in language-relevant areas (left temporal and left inferior frontal areas).

In the production task, the HC condition leads to faster naming latencies with respect to the LC condition. Moreover, the effect of lexical frequency was found in the LC but not in the HC context (replicating previous studies, Griffin & Bock, 1998; Piai et al., 2014, 2018). The pattern clearly signals that lexical retrieval in the HC condition

occurs before picture onset, and the alpha–beta desynchronization effect observed before picture presentation reflects the retrieval of specific lexical information, and possibly other stages of word planning. Consistent with this hypothesis, Youssofzadeh et al. (2020) showed MEG beta (17-25 Hz) desynchronization in language-related areas of the left hemisphere in picture naming and auditory description naming, more specifically in a 600 ms time-window ending 100 ms before response onset. The authors interpreted these modulations as reflecting later stages of word production, such as phonological planning and motor speech preparation.

These conclusions are compatible with the 'information by desynchronization' hypothesis put forward by Hanslmayr, Staudigl, and Fellner (2012). According to this study, information encoding and retrieval is associated with desynchronized firing of neural populations in the alpha and beta frequencies. By applying mathematical modeling, the authors showed that the power of local field potentials at these frequencies (and consequently of the scalp-level EEG fluctuations) is negatively related to the richness of information represented in the brain. The stronger the desynchronization of neural populations, the stronger the decrease in alpha–beta power, and the richer the information encoded or retrieved. In agreement with this conclusion, previous research reported a power decrease in the alpha–beta range associated to the processing of open *vs.* closed class words (Bastiaansen, Van Der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005) and to deep *vs.* shallow semantic encoding of words (Hanslmayr, Spitzer, & Bäum, 2009). These effects seem to suggest that the desynchronization of oscillatory activity in these bands might be related to the semantic richness of the representation retrieved from memory.

From this perspective, therefore, our results are in line with studies showing that alpha–beta desynchronization is related to prediction in spatial attention (Bauer, Stenner, Friston, & Dolan, 2014) and pitch change (Chang, Bosnyak, & Trainor, 2018), in successful word memory formation (Griffiths, Mazaheri, Debener, & Hanslmayr, 2016) and word encoding (Meeuwissen, Takashima, Fernández, & Jensen, 2011), and fidelity of stimulus-specific information tracking in the visual and auditory domains (Griffiths et al., 2019).

Beta desynchronization has been proposed to reflect a change in the cognitive set in response to unexpected targets (Lewis & Bastiaansen, 2015; Lewis, Wang & Bastiaansen, 2015). However, consistently with literature analyzing oscillations before

target onset, we found alpha-beta desynchronization associated with more predictable conditions. These results can be reconciled by assuming that desynchronization of the alpha and beta band reflects that a change is undergoing or bound to happen, but such change would be qualitatively different according to whether it is detected *pre*- or *post*target. When encountering unexpected or new information, desynchronization is associated to a change in the current representation due to bottom-up processing; when anticipating new information, desynchronization is associated to a change induced by topdown pre-activation of upcoming information. This interpretation is in line with other studies focusing on pre-target modulations. For instance, Magyari, Bastiaansen, de Ruiter, and Levinson (2014), in a turn-taking experiment, asked participants to listen to conversations and to press a button precisely when the current turn was going to end, encouraging the prediction of the sentence content. The authors found alpha-beta desynchronization well before the end of the turn in predictable relative to unpredictable contexts, suggesting that lexico-semantic and syntactic information was guiding the anticipation of upcoming content, and consequently turn ending. Similarly, Gisladottir, Bögels, and Levinson (2018) employed conversations that constrained towards specific speech acts. The results highlighted alpha-beta desynchronization before predictable relative to less predictable targets, signaling that pragmatic cues enable the prediction of future speech acts for faster recognition.

In conclusion, our findings are in line with previous studies showing alpha–beta desynchronization in left-lateralized language areas before target onset, compatible with the role of alpha–beta desynchronization in signaling active change in the cognitive set.

4.2 Alpha–beta desynchronization in the right hemisphere

The alpha and beta desynchronization effects we reported involved also the right hemisphere. Source analyses showed that the effect extended mainly in the prefrontal and anterior temporal corteces (alpha range) and in the occipito-temporo-parietal cortex (beta range) in comprehension, and in the temporal, parietal and prefrontal corteces (both alpha and beta ranges) in production. Among the studies considered in Table 1, only one found effects also in the right hemisphere. Terporten et al. (2019), in a comprehension task contrasting three different levels of sentential constraint, report bilateral desynchronizations in fronto-parietal areas with a bias towards the right hemisphere. The authors interpreted this modulation as reflecting attentional and/or working memory demands. In our study, while the alpha desynchronization is more ventrally widespread, the beta desynchronization is primarily found in posterior temporo-parietal regions for both tasks. Right posterior regions are involved in a variety of functions, such as attention (specifically, attentional reorienting following unexpected stimuli; e.g. Corbetta, Patel, & Shulman, 2008), memory (e.g. Anticevic, Repovs, Shulman, & Barch, 2010), social cognition (e.g. Theory of Mind, Van Overwalle, 2009), and aspects of language processing (e.g. narrative comprehension, Paunov, Black, & Fedorenko, 2019) and the intention to speak (Carota et al., 2010). Our experimental conditions might have induced differences in terms of attention and working memory. For instance, we might hypothesize that constraining sentences aid attentional orienting towards predictable targets to facilitate elaboration. Similarly, the memory load required for sentence processing might be modulated by semantic constraint.

However, the involvement of posterior regions in such a variety of domains led researchers to propose unifying accounts identifying commonalities across the different domains (Geng & Vossel, 2013; Carter & Huettel, 2013). In particular, Geng and Vossel (2013) proposed that the temporo-parietal junction (which includes portions of the inferior parietal and the posterior superior and middle temporal cortices), represents a hub for the contextual updating of internal models in order to adjust top-down expectations about upcoming events and guide planning of future actions. This account directly relates attentional and memory-related effects to the contextual generation of predictions. We speculate that our results may be compatible with such view. Further research is needed in order to replicate the results and, in case of replication, clarify their interpretation.

4.3 Compatibility with prediction-by-production models

We observed that in both comprehension and production, alpha–beta power decreased before encountering a predictable stimulus. To what extent do these effects reflect common processes involving shared representations? The positive correlations between desynchronizations in the two tasks reveal commonalities in areas of the left hemisphere, and more specifically the anterior temporal, inferior parietal, temporo-parietal, and inferior frontal cortices. It is relevant to note that all these areas are generally associated not only with lexical-semantic retrieval but also with word production. The consensus on the neural bases of word production is that lexical-semantic retrieval involves the anterior and middle temporal cortex, phonological retrieval involves the posterior temporal– inferior parietal cortex and syllabic planning involves the inferior frontal cortex and premotor cortex, which activates the associated articulatory sequences in the motor cortex (for reviews see Indefrey, 2011; Roelofs & Ferreira, 2019; Strijkers & Costa, 2016). Correlation analyses highlighted the involvement of all these areas, suggesting that when predicting a word, comprehenders engage, at least to some extent, areas associated to word production, as proposed by prediction-by-production accounts (Huettig, 2015; Pickering & Gambi, 2018; Pickering & Garrod, 2013).

As presented in section 1.1, production-based accounts of prediction suggest the involvement of other processes essential for communication, i.e. internal modeling, inference of intention. We speculate that the desynchronization in the right posterior parietal area, which we tentatively discussed in the previous section, may be compatible with such views. The lack of temporal overlap between task desynchronizations in this region may be due to the fact that the actual intention to produce a word may be responsible for the anticipation of the recruitment of posterior parietal regions in the production task. Indeed, the effect emerged in beta2 around 300 ms in production and later, around 500 ms, in comprehension. Consistently, Strijkers and Costa (2016) suggest that top-down modulations (including the intention to speak) originating in the prefrontal and parietal cortices can influence the timing of subsequent computations of word production. Further research will clarify the involvement of right posterior areas, and better characterize their function.

4.4 Limitations and future directions

Our study allows us to bring brain oscillatory evidence for the engagement of the production system in prediction during spoken language comprehension. However, our results do not allow us to make strong claims on the exact representations involved, specifically whether phonology is activated or not. Techniques with higher spatial resolution (such as MEG), experimental manipulations that better elicit phonological

planning, and the study of special populations with speech–language disorders would contribute to characterize the cortical locations of the effects and help in understanding what representational levels are implicated. A potentially useful approach would be to include cloze probability as a continuous variable with stimuli not clustered around extreme values and observe how the oscillatory pattern modulates accordingly.

With respect to the commonalities between comprehension and production, it could be argued that, by including a production task, the experimental design might induce participants not only to anticipate the target word in the comprehension task, but also to covertly produce it, yielding the commonalities identified with the production task. This possibility was minimized by a series of procedural precautions: the two tasks were part of separate blocks, task order was counterbalanced across participants, and taskspecific instructions were given to the participants only before each block. Therefore, we deem unlikely that the presence of the production task is causing covert production in comprehension. However, for ultimately ruling out this possibility, further research employing both comprehension and production tasks in the same experiment is needed

As a remark on the interpretability, it must be underlined that EEG oscillatory activity is merely correlated with the observed experimental conditions. Because of this, we cannot make strong claims about whether the activity in a given brain area is necessary to a given process. However, the results of this study set the basis for further investigations with neurostimulation techniques (such as TMS) that could tease apart and clarify the role of these areas in language comprehension and production. Finally, we point out that intra-, inter-subject, and task-related differences may heavily hinder the ability to detect shared cognitive elaboration and neural activation, since we are assuming that if there are shared processes, they are unfolding at the same time in the two tasks and across all subjects; this may well not be the case. Despite these limitations, we argue that we bring sufficient evidence to stimulate further research along these lines, in an emerging effort to reconcile the study of language comprehension and production (McQueen & Meyer, 2019).

5. Conclusion

In this study we tested whether prediction-by-production accounts are supported by patterns of alpha and beta neural oscillations. Participants performed both a comprehension and a production task with predictable and non-predictable (but always plausible) target stimuli following constraining and non-constraining incomplete sentences. To our knowledge, this is the first attempt at studying both processes in the same set of participants, thereby investigating how the same mind-brain tackles the two tasks and directly comparing their neural responses. In addition, we employed naturalistic auditory stimuli differently from previous studies, replicating the modulations in a less artificial setting. We found alpha and beta power decrease (desynchronization) before predictable targets in both tasks, signaling that participants were retrieving and encoding rich linguistic information, compatible with the 'information via desynchronization' hypothesis. Source estimation and correlations suggest that participants engage the leftlateralized word production areas when predicting during comprehension. Right posterior temporo-parietal areas resulted involved during prediction in both tasks and we tentatively hypothesized that this might reflect processes related to internal modeling and contextual updating of expectations. These results stress the strict relationship between production and comprehension processes, lending support to prediction-by-production models.

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Declaration of Interest

The authors declare no competing interests.

Supplementary material

Supplementary material for this manuscript can be found on the Open Science Framework at the following URL: <u>https://osf.io/tcbsh/</u> Available under a CC-BY-NC-ND International license.

Pre-registration

No part of the study procedures or analyses was pre-registered prior to this research being undertaken.

Sample size and exclusion criteria

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

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