Speaking in the Brain: The Interaction between Words and Syntax in Sentence Production

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Abstract

■ This neuroimaging study investigated the neural infrastructure of sentence-level language production. We compared brain activation patterns, as measured with BOLD-fMRI, during production of sentences that differed in verb argument structures (intransitives, transitives, ditransitives) and the lexical status of the verb (known verbs or pseudoverbs). The experiment consisted of 30 mini-blocks of six sentences each. Each mini-block started with an example for the type of sentence to be produced in that block. On each trial in the mini-blocks, participants were first given the (pseudo-)verb followed by three geometric shapes to serve as verb arguments in the sentences. Production of sentences with known verbs yielded greater activation compared to sentences with pseudoverbs in the core language network of the left inferior frontal gyrus, the left posterior middle temporal gyrus, and a more posterior middle temporal region extending into the angular gyrus, analogous to effects observed in language comprehension. Increasing the number of verb arguments led to greater activation in an overlapping left posterior middle temporal gyrus/angular gyrus area, particularly for known verbs, as well as in the bilateral precuneus. Thus, producing sentences with more complex structures using existing verbs leads to increased activation in the language network, suggesting some reliance on memory retrieval of stored lexical–syntactic information during sentence production. This study thus provides evidence from sentence-level language production in line with functional models of the language network that have so far been mainly based on single-word production, comprehension, and language processing in aphasia. ■

INTRODUCTION

Before initiating production, speakers must select relevant words from their mental dictionary and assemble these words together in a suitable syntactic structure to produce an utterance that conveys the desired message in a grammatically correct form. On the basis of behavioral data, psycholinguists have proposed two accounts of lexical–structural processing during production: a lexicalist account where the retrieval of individual words may activate syntactic information tied to those words (Tomasello, 2000; Pickering & Branigan, 1998; Bock, 1982) and an abstract structural account where the selection and generation of a suitable structure is driven by message-level constraints and thus can proceed independently of lexical retrieval (Chang, Dell, & Bock, 2006; Goldberg, 2005; Frazier, 1987; Bock, 1986). Indeed, speakers are able to form grammatically plausible sentences with novel words that do not have entries in the mental lexicon, suggesting that they must have acquired sentence structure templates in the course of language learning that are at least partially abstract (i.e., not bound

to specific words). This debate has motivated behavioral investigations into the time course of structural and lexical processing during sentence production using a range of experimental paradigms (such as object naming, spontaneous event description, structural priming; e.g., Konopka, 2012; Allum & Wheeldon, 2007; Smith & Wheeldon, 1999). Broadly speaking, there is now evidence that utterance production relies on abstract syntactic structures but also that the accessibility of lexical information can influence the process of structural assembly.

Here, we investigate the neural underpinnings of sentence production with different syntactic structures. Neural models of language processing propose different functional roles for the different subcomponents of this language network. In the MUC model, for example, the posterior temporal cortices subserve memory (M), the inferior frontal cortex including Broca's area and adjacent structures supports unification (U), and the dorsal lateral and medial pFCs (including ACC) have been related to control (C) processes (Hagoort, 2005, 2013). This model (Hagoort, 2005, 2013) and a related computational implementation (Vosse & Kempen, 2000) propose that each entry in the mental lexicon is linked to its structural information. For example, verb argument structure is verb

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bound, and the syntactic role of these arguments must be defined for each verb (e.g., an intransitive verb will require only a subject, whereas a ditransitive verb will require a subject, a direct object, and an indirect object). This view is compatible with lexicalist accounts in (psycho) linguistics (e.g., Bresnan, Asudeh, Toivonen, & Wechsler, 2015; Jackendoff, 2002; Pickering & Branigan, 1998) in which lexical items codetermine the temporal dynamics and outcome of syntactic encoding processes. A mental lexicon in the posterior temporal cortex that drives lexical–syntactic processing, however, does not exclude the possibility that more abstract structural information can also be processed or unified by other regions involved in syntactic processing, such as the left inferior frontal gyrus (LIFG). Such an abstract sentence template that is not bound to specific verbs may also reside as a memory representation in the posterior memory areas. Existence of such sentence structure templates will plausibly allow flexibility in sentence construction even when verb-bound lexical–syntactic information is not available.

Existing neural models of language processing are based mainly on data from comprehension studies. fMRI studies on language production studies have been scarce because of the presence of movement artifacts during speaking. There are, however, ways to tackle this problem: use of appropriate MRI sequences (e.g., short acquisition time per volume, securing of the participants' heads in a comfortable manner), extraction of movement-related independent components from the data during data preprocessing, addition of extra nuisance regressors in the model, and so forth. These considerations allow us to study production-related brain activation patterns using fMRI.

Here, we focus on the processing of sentence structure. Earlier meta-analyses of neuroimaging studies on language processing in healthy participants have identified the left frontal and temporal cortices as important structures for syntactic processing (Price, 2012; Indefrey & Levelt, 2004). In a PET study, an increase in LIFG activation was observed when participants produced full sentences compared to when they produced single words (Indefrey et al., 2001). In an fMRI study (Haller, Radue, Erb, Grodd, & Kircher, 2005), an increase in activation was found in the LIFG when participants generated sentences cued by visual scenes or scrambled word orders (e.g., cue: "Throw ball child", response: "The child throws the ball"), compared to when the participants read out the words on the screen in a scrambled order (e.g., "throw ball child") or read the complete sentence presented on the screen (e.g., "The child throws the ball"). This suggests a functional role of the LIFG in syntactic encoding.

More compelling evidence for the organization of the language network comes from priming studies showing that this left-dominant network of the left inferior frontal, middle, and superior temporal cortex involved in sentence production largely overlaps with the comprehension network. Repeating syntactic structures, semantic contents, or lexical items lead to repetition suppression, that is, a decrease in the neuronal activation of the regions involved in processing the repeated features (reviewed in Barron, Garvert, & Behrens, 2016; Segaert, Weber, de Lange, Petersson, & Hagoort, 2013). More specifically, repetition of syntactic structures results in suppression of activation in the left inferior frontal, precentral, and posterior temporal regions; repetition of semantic information in the bilateral posterior temporal cortex and precuneus; and repetition of words in the anterior and posterior temporal cortices and anterior inferior frontal regions and precuneus. These repetition suppression effects are observed not only within modality but also between comprehension and production (Segaert, Menenti, Weber, Petersson, & Hagoort, 2012; Menenti, Gierhan, Segaert, & Hagoort, 2011). However, as neuroimaging studies have mostly considered a very limited set of sentence structures (mostly transitives; Segaert et al., 2012; Menenti et al., 2011; Haller et al., 2005; Indefrey et al., 2001), we know much less about the production of sentences with different levels of structural complexity.

Regarding processing of complex sentence structures, studies on patients with aphasia shed some light on the brain areas involved. A growing number of observations in aphasic studies found the left inferior frontal cortex to be critical in syntactic processing (see a recent review by Tyler et al., 2011), although this view is also contested (Matchin & Hickok, 2019). For verbs, syntactic complexity is strongly related to argument number. Intransitive, transitive, and ditransitive verbs are bound to different numbers of argument slots (intransitive, one slot: "<The girl> sleeps."; transitive, two slots: "<The girls> kicks <the ball>."; ditransitive, three slots: "<The girl> gives <the book> < to the boy>."). This sensitivity is lacking in individuals with Wernicke's aphasia with lesions in the posterior perisylvian regions. A recent study training patients with agrammatic aphasia to produce ditransitive sentences from pictures of simple events (e.g., "The boy is giving the flowers to the woman") showed an improvement in naming of trained three-argument verbs in isolation as well as production of these verbs in full sentences. These patients also showed an increased activity pattern in the angular, supramarginal, and/or superior posterior temporal gyri during an action verb video naming task (Thompson, Riley, den Ouden, Meltzer-Asscher, & Lukic, 2013).

Lesion studies, for example, the aphasia studies mentioned above, are invaluable in understanding the neural correlates of language production, but the results may be affected by compensatory mechanisms and altered neural responses because of regional deficits. Thus, it is also important to investigate these effects in a healthy population. Neuroimaging studies have found a gradient of activation with an increase in the number of verb arguments in the posterior temporal and inferior parietal parts of the language network. The studies, however, have

mainly focused on verbs comprehended or produced in isolation. That is, the stimuli were verbs with different types of verb argument structure (intransitive/transitive/ditransitive) presented outside a sentence context (e.g., Malyutina & den Ouden, 2017, Exp 2; Thompson et al., 2007). Other studies tested grammaticality or well-formedness judgments for sentences in comprehension paradigms (Malyutina & den Ouden, 2017, Exp 1; Ben-Shachar, Palti, & Grodzinsky, 2004). Nevertheless, all these studies found activation differences in the posterior perisylvian area. These findings suggest that verbs may be stored in the mental lexicon together with their syntactic information and are therefore consistent with lexicalist accounts of structural processing (Jackendoff, 2002; Pickering & Branigan, 1998).

However, as these studies did not examine sentence-level production, they cannot speak to the way these verbs are retrieved and used in more complex contexts, such as during the generation of full sentences. Moreover, a problem in the previous single-verb production studies is that the images or videos used to cue the production of verbs with different argument structures often contained different numbers of depicted objects (e.g., 1 vs. 2; den Ouden, Fix, Parrish, & Thompson, 2009). Thus, the differences in neuronal patterns of activation found across conditions in those studies might be because of differences in the visual complexity of the displays used to cue the production of the verb rather than in differences in verb classes and argument structures.

In summary, the brain structures involved in sentence production as well as the factors that affect neural computation during spontaneous sentence production are still understudied. In the current experiment, we address these questions by measuring behavioral and brain responses during sentence production.

Participants produced sentences with different structures (intransitives, transitives, and ditransitives), allowing us to assess the role of verb argument number and thus structural complexity on neural responses during sentence production. To circumvent the problem of using different displays across conditions observed in earlier studies, participants saw identical visual displays with three objects across conditions, thus keeping the total number of nouns to be used in each sentence constant. On each trial, participants first saw a screen with the verb to be used in the upcoming trial (e.g., "*wash*" in the case of the transitive condition), followed by three geometrical objects (a triangle, a circle, and a square), and they were instructed to produce an intransitive, transitive, or ditransitive sentence (e.g., "*The triangle, the circle and the square [verb]*"; "*The triangle and the circle [verb] the square*"; "*The triangle [verb] the circle to the square*"). Participants were cued to use either existing verbs (i.e., known verbs) or verbs that do not exist in the Dutch lexicon (i.e., pseudoverbs) in these sentences.

This design allows us to focus on two experimental questions regarding the neurobiology of sentence generation. The first experimental question concerns the role of different verb argument structures in modulating production-specific neural responses. We expected to see a graded activation pattern within the language network reflecting the complexity of the sentence structures (in this case, the number of verb arguments): We expected structural complexity to modulate the unification load in the inferior frontal gyrus.

The second experimental question concerns the contribution of lexical representations to structural processing during sentence production. We tested whether the neural computation for sentences differs when the lexical entry of the target verb provides syntactic feature information compared to when the verb has no lexical representation (known verbs vs. pseudoverbs). If argument structure information is verb bound, as proposed by the lexicalist account, there should be more activation during the production of sentences using known verbs than pseudoverbs in regions related to the processing and representation of words within the language network. In contrast, if representations for sentence structures are abstract, as proposed by the abstract structural account, there should be no difference between the verb argument structure effect for known verbs and pseudoverbs beyond activation related to having a memory entry for the known verbs but not the pseudoverbs. Thus, the activation modulation across the verb argument structures should be similar in the known-verb and pseudoverb conditions.

As we were particularly interested in the brain responses to processing of sentence structure and potential lexical–syntactic components of sentence processing, the analyses focused on two ROIs linked to syntactic processing: the LIFG and the left posterior middle temporal gyrus (LpMTG). If the activation of entries in the mental lexicon also entails the activation of syntactic information, a graded activation pattern might also be found in the posterior temporal cortex.

To summarize, in this study, we asked whether (1) the brain activation pattern during sentence-level production is similar to what prior studies have shown using comprehension tasks, single-word production tasks, or production tasks that involve only one type of sentence structure; (2) the production of sentences with different levels of verb argument structure shows a differential brain activation pattern; and (3) the existence of lexical representations has an impact on sentence-level production. We expected to see (1) similar patterns of activation in the LIFG and posterior temporo-parietal areas for sentence-level production to what has been reported in earlier studies in comprehension and word production tasks, (2) modulation of activation in the LIFG with increasing complexity of verb argument structure, and (3) modulation of activation in the posterior perisylvian areas with the presence of representation(s) to be retrieved from memory (i.e., lexically specified verbs).

METHODS

Participants

Thirty right-handed native Dutch students (23 women, $M = 21.8$ years, range: 18–28 years) participated in the experiment for course credit or monetary compensation after giving written informed consent. The study was approved by the CMO Committee on Research Involving Human Participants (Region Arnhem-Nijmegen). Participants had no history of neurological or language-related disorders and reported having normal or corrected-to-normal vision and hearing. Two participants were excluded from the analyses: One participant made too many mistakes during the sentence production task (only 69% correct sentence productions), and another participant was excluded because of technical failure during image acquisition, leaving 28 participants for the final analyses.

Materials

Stimuli

Eighteen verbs (six to be used in each construction: intransitive, transitive, and ditransitive) were selected, and another 18 pseudoverbs were constructed conforming to Dutch phonotactic rules (also divided into three sets of six pseudoverbs each). In addition, three new verbs and three new pseudoverbs were used as examples for each of the conditions.

Three simple shapes (a square, a circle, and a triangle; see Figure 1) were used as stimuli. On all trials, the shapes were presented as white figures on a black background (with a 10° visual angle separation), and participants were instructed to produce sentences naming the shapes in a left-to-right order. This presentation eliminated differences in visual input across conditions (and thus eliminated confounds observed in prior studies). The order of the shapes displayed was randomized across trials (see Table 1).

Experimental Procedure

Sentence Production Task

Participants were instructed to produce sentences following the example presented on the screen during the instruction phase (Figure 1). Before the fMRI session, participants underwent a short practice session outside the scanner to be acquainted with the task using both
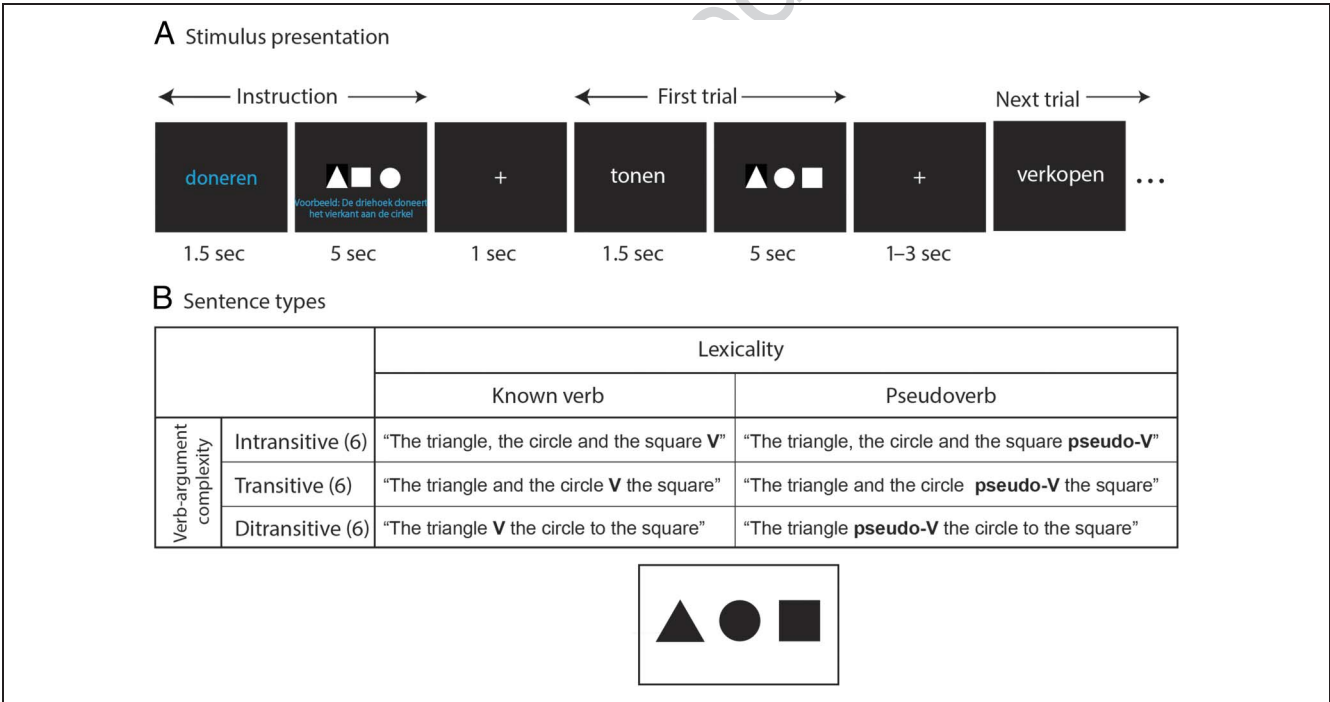

Figure 1. The production task. (A) Stimulus presentation: Each block started with an instruction trial (see "Instruction" example) where the verb was shown in the middle of the screen in blue font for 1.5 sec, followed by three shapes and the required corresponding sentence for 5 sec. Participants were instructed to read the example sentence silently. After a 1-sec interval, the experimental trials started. Each block consisted of six trials, and participants were asked to use the same sentence structure as in the example throughout the block. At the beginning of each trial, the (pseudo)verb to be used in that trial was shown in the center of the screen in white font for 1.5 sec, followed by the three shapes shown for 5 sec. Participants were instructed to overtly produce the sentence while the shapes were on the screen mentioning the three geometrical objects from left to right and using the verb shown before picture presentation. The next trial began after a 1- to 3-sec intertrial interval. Instruction: "*doneren*" = "donate" and "*Voorbeeld: De driehoek doneert het vierkant aan de cirkel*" = "Example: The triangle donates the square to the circle." Trials: "*tonen*" = show and "*verkopen*" = sell. (B) Sentence types: The condition consisted of two levels of Lexicality (known verbs/pseudoverbs) and three levels of Verb argument structure complexity (intransitive/transitive/ditransitve). Please refer to Table 1 for the actual (pseudo)verbs used.

Table 1. Dutch Verbs and Pseudoverbs (with English Translations) Used in the Production Task

	Known Verbs (English)	*Pseudoverbs*
Intransitive	*zitten (sit)*	*verdorgen*
	stralen (shine)	nieflen
	bewegen (move)	aalzen
	rollen (role)	speven
	keren (turn)	glappen
	groeien (grow)	flimmen
	staan (stand)	voensten
Transitive	*pesten (pester)*	*stoeffelen*
	kleuren (color)	spaffen
	passeren (pass)	greppen
	wassen (wash)	kemtelen
	vangen (catch)	slorgen
	krijgen (get)	nelden
	slaan (hit)	prengelen
Ditransitive	*doneren (donate)*	*hiemsteren*
	schenken (give)	malfen
	tonen (show)	trassen
	verkopen (sell)	oessen
	melden (report)	strijselen
	bevestigen (confirm)	grummelen
	geven (give)	wargelen

Words in *italic* were used as example verbs in each of the conditions.

existing verbs and pseudoverbs for each of the three verb argument structure conditions. The (pseudo)verbs used in the practice session were not used in the main task.

For the task in the scanner, participants completed 30 blocks of six trials each (for a total of 180 trials during the whole experimental session). Crossing the variables Verb argument structure (three levels) and Lexicality (two levels) resulted in six experimental conditions. Conditions were grouped into blocks, so that all sentences within each block belonged to the same condition. As there were 30 blocks, each condition was shown five times. In each block, all six verbs were used only once but were presented in a different order across blocks.

Each block started with an instruction screen. First, the example verb appeared on screen (visual angle: 2.5°–3.5°) for 1.5 sec, followed by a screen with three shapes (visual angle: 10°) and the required sentence structure printed under the shapes for 5 sec. Participants were instructed to read the example silently. They were then given six experimental trials of the same condition (i.e., six trials requiring use of the same sentence structure). In each of these six trials, the (pseudo)verb appeared on screen for 1.5 sec first, followed by three shapes presented for 5 sec. Participants were instructed to produce a sentence with the same sentence structure as in the instruction at the beginning of the block, mentioning the shapes from left to right and using the (pseudo)verb shown just before the presentation of the shapes.

The three sentence structures were (a) intransitives (e.g., "*De driehoek, de cirkel en het vierkant stralen*"; The triangle, the circle, and the square shine), (b) transitives (e.g., "*De cirkel en het vierkant wassen de driehoek*"; The circle and the square wash the triangle), and (c) ditransitives (e.g., "*Het vierkant geeft de driehoek aan de cirkel*"; The square gives the triangle to the circle). Verbs needed to be inflected as third-person singular or plural. Participants were instructed to speak as soon as the three shapes appeared on the screen. The screen was replaced with a central fixation cross after 5 sec, and after a varying intertrial interval (1, 2, 2.5, or 3 sec), the next trial started. The experiment lasted approximately 30 min.

Participants' verbal responses were recorded using a noise cancellation system suppressing scanner noise and analyzed offline for accuracy and two production variables: Production onset and Production duration. Production onset was calculated as the time between picture onset and start of the utterance, and Production offset was calculated as the time between picture onset and sentence completion. In case the sentence was not completed within the 5-sec trial window, the Production offset time was coded as unfinished and the trial was rejected. Next, Production duration was calculated as the time between Production onset and Production offset. For the behavioral analyses, we rejected sentences that were unfinished (e.g., "*Het vierkant, de driehoek en de cirkel ….*") and used an incorrect structure (e.g., a transitive sentence in a ditransitive block) or an incorrect verb (e.g., "*De driehoek geeft de cirkel aan het vierkant*", when cued with the verb <*melden*>). In Dutch, noun gender is marked with the definite article, with the square (singular form) taking the neuter article "het" (*het vierkant*) and the other two figures with the nonneuter gender article "de" (*de cirkel*, *de driehoek*). However, because we were interested in brain activation areas in the production of sentences with correct structures, we included trials where article selection was not always correct (e.g., *de vierkant*, instead of *het vierkant*). All other responses were categorized as incorrect.

Overt/Covert Task

To control for brain response related to overt production, participants completed another run with 10 blocks after the main sentence production task. Here, they were

instructed to produce sentences overtly in five blocks and covertly in the remaining five blocks. Each block consisted of three sentences and only elicited intransitive sentences. The procedure was similar to that of the main task. The two condition blocks alternated. The verb to be used was shown on screen for 1.5 sec, followed by the three figures shown on screen for 5 sec. Participants were instructed to construct a sentence in the same format as the example sentence at the beginning of the block. We then compared BOLD responses to overt and covert sentence production.

Data Acquisition

fMRI Data

MRI data were recorded in a 3-T magnetic resonance scanner (PrismaFit, Siemens Healthcare) using a 32-channel head coil. Whole-brain functional images were collected using a multiband (accelerator factor of 8) T2*-weighted sequence: repetition time = 735 msec, echo time = 39 msec, field of view = 210 × 210 mm, 64 slices, voxel size = 2.4 × 2.4 × 2.4 mm. To correct for distortions, fieldmap images were also recorded. Participants' heads were secured comfortably with a Tempur pillow to reduce motion as much as possible. Furthermore, we attached a tape across the participants' foreheads such that, if they moved, they would feel it as a feedback (Krause et al., 2019). These procedures indeed led to very small head movements during the experiment (average of the maximum transition movement across all participants: 0.95 [range: 0–5.75] mm, rotation: 0.02° [range: 0°–0.19°]).

In addition, T1-weighted anatomical scans at 1-mm isotropic resolution were acquired with a repetition time of 2300 msec, an echo time of 3.03 msec, a flip angle of 8°, and a field of view of 256 × 256 × 192 mm.

Data Analysis

Behavioral Data

Analyses compared accuracy and two production measures (Production onset and Production duration) across conditions. Table 2 lists the types and numbers of incorrect responses (incorrect structures, incorrect verb uses, incorrect determiner uses, incomplete utterances, and combinations of these categories). We compared the number of correctly produced sentences across conditions using mixed-effects logit models and Production onsets and Production durations using a mixed-effects model (Barr, Levy, Scheepers, & Tily, 2013; Jaeger, 2008; Pinheiro & Bates, 2000) in R (R Core Team, 2012). All three models contained the factors Verb argument structure (three levels: intransitive, transitive, and ditransitive) and Lexicality (known verb, pseudoverb). Deviation coding was used for the factor Lexicality, and we looked at the linear contrast (first polynomial) for the factor Verb argument structure. The models included random effects for participants and items. Following Barr et al. (2013), we report models with the maximal random effects structure, leading to convergence. When a model with a complex random structure did not converge, we iteratively removed random slopes for factors with the lowest variance one at a time. Consequently, the accuracy model included random slopes for Lexicality for items, whereas the Production onset model included random slopes for Lexicality for participants, and the Production duration model included random slopes for Lexicality for both participants and items and Verb argument structure for participants.

MRI Data

First, DICOM images were converted to nifti images. Then, functional volumes were realigned using the field-map correction using preprocessing tools in SPM12 (www.fil.ion.ucl.ac.uk), coregistered to the individual structural image, and further normalized to a standard Montreal Neurological Institute (MNI) space (resampled at a voxel size of 2 × 2 × 2 mm). Finally, the images were spatially smoothed with a kernel of 5-mm FWHM. Noise-affected volumes were detected using the ArtRepair program (www.cibsr.stanford.edu/tools/human-brain-project/artrepair-software/), and regressors modeling these affected volumes were added to the model to account for these time points.

For the sentence production task, for the first-level single-participant analysis, we computed a general linear model with nine experimental conditions (correct trials for each of the six conditions, all incorrect trials, instruction phase at the beginning of each mini-block, and a baseline phase at the offset of the production for all trials), together with six motion parameters and a regressor for each of the affected volumes detected as nuisance regressors. For the six experimental condition regressors and the instruction phase regressor, the onset of each trial was defined as the picture onset time, and for the baseline phase, we modeled time just after the production was completed using the Production offset as the onset of this regressor, convolved with the canonical hemodynamic response function. For each of the experimental conditions, a contrast image of condition minus the baseline phase was computed and compared across participants on the group level.

First, we sought the activity difference between conditions in areas that are known to be involved in syntactic processing. For this, we defined functional ROIs using Neurosynth (www.neurosynth.org/, checked on January 21, 2015). This program allows one to select voxels that are reported to be active in multiple studies relating to a key search word. We selected ROIs using "syntactic" as the key search word, with a threshold of $z = 6$. This revealed two clusters (Figure 2): one in the LIFG and the other in the LpMTG. For these two ROIs, we extracted

Table 2. Types and Counts of Errors across All Participants and Conditions

Lexical Status	Verb Argument Structure	No. of Trials	Incorrect Trials (Incorrect Verb, Construction or Object, Incomplete Utterance)	Incorrect Construction	Incorrect Verb	Incorrect Determiner (Trials Included in the Analysis)
Known verb	Intransitive	840	118	2	69	28
	Transitive	840	73	7	37	28
	Ditransitive	840	40	10	21	28
Pseudoverb	Intransitive	840	234	6	173	24
	Transitive	840	246	35	171	27
	Ditransitive	840	92	18	61	28

mean beta values for each of the conditions relative to the baseline phase using MarsBar (www.marsbar.source-forge.net/) and compared these values using a mixed-effects model in R (R Core Team, 2012). The model contained the factors Verb argument structure (three levels: intransitive, transitive, ditransitive), Lexicality (known verb vs. pseudoverb), and Region (LIFG vs. LpMTG). Deviation coding was used for the factors Lexicality and Region, and we looked at the linear contrast (first polynomial) for the factor Verb argument structure. The model included random effects for participants. To allow convergence, we used the same simplification approach as in the analysis of Production onsets and Production durations; thus, the final model included only by-participant random slopes for Region.

In the next step, we performed a whole-brain analysis using flexible factorial analysis embedded in SPM12, with Lexicality (known verb, pseudoverb) and Verb argument
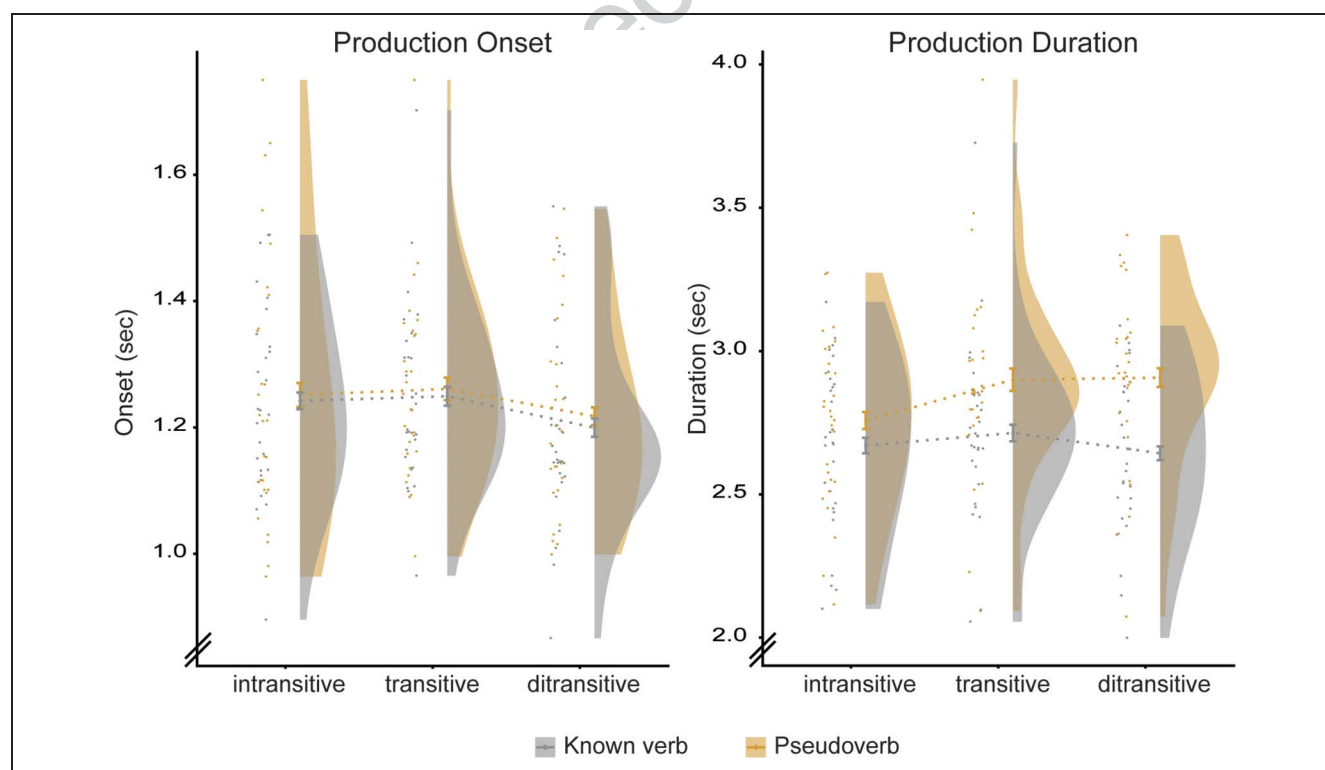

Figure 2. ROI activation pattern. (Top) ROIs in the LIFG (left) and left middle temporal gyrus (right) defined using the term "syntactic" on neurosynth.org. (Bottom) Mean beta weights extracted from the predefined ROI in the LIFG (left) and the LpMTG. Dots represent individual participants' data with the mean, *SEM*, and density represented on their right-hand side.

structure (intransitive, transitive, ditransitive) as factors of interest. On the group level comparison, we first thresholded the brain responses on the voxel level at $p = .001$ (uncorrected) and took the cluster-size statistic as the test statistic with FWE-corrected $p_{FWE} < .05$ as the cluster threshold (Hayasaka & Nichols, 2003).

For the overt/covert task, a similar general linear model was run with the conditions overt and covert as the main regressors of interest together with instruction and baseline phases as two extra regressors. Because we cannot derive the Production offset for the covert condition, we calculated the mean Production offset time for the intransitive condition in the sentence production task for each participant and used this time as a proxy of Production offset for this run. Furthermore, six motion regressors and affected volume regressors as detected by the ARTrepair program were included as nuisance regressors to the design matrix. Contrast image of overt versus covert was computed for each participant, and this contrast image was tested using a one-sample t test on the group level. We applied the cluster-level statistic ($p_{FWE} < .05$) to this comparison as well.

RESULTS

Behavioral Results

Accuracy

Participants produced more correct sentences in the ditransitive than the transitive and intransitive conditions (mean proportion correct: ditransitive = 0.92, transitive = 0.81, intransitive = 0.79; $\beta = 0.89$, $z = 8.95$, $p < .001$) and more correct sentences in the known-verb condition (proportion correct: $M = 0.91$) than the pseudoverb condition ($M = 0.77$; $\beta = -1.24$, $z = -10.6$, $p < .001$). The two effects did not interact ($|z| < 1$). In other words, accuracy was highest in the condition where the verb had to be kept in working memory for the shortest amount of time (ditransitive) and lowest when it had to be kept in working memory the longest (intransitive). The largest number of incorrect responses in this data set was because of participants using incorrect verbs (532 responses out of 5040 in total) rather than incorrect structures (78 responses out of 5040 responses in total), and most of these rejections were because of incorrect use of pseudoverbs (see Table 1 for the distribution of errors across conditions).

RTs

Production onsets and Production durations are shown in Figure 3. Production onsets show how much time speakers needed to prepare the sentence-initial shape name but typically also vary with structural complexity: Sentences beginning with a simple noun phrase are initiated more quickly than sentences beginning with a complex noun phrase (e.g., Smith & Wheeldon, 1999). We

performed a mixed-effects analysis with Lexicality and Verb argument structure as fixed effects, as well as random by-participant and by-item slopes for Lexicality. This analysis showed a main effect of Verb argument structure ($\beta = -0.027$, $t = -3.02$, $p = .003$). Follow-up comparisons revealed that ditransitives had shorter onsets than transitives ($\beta = 0.048$, $t = 3.84$, $p < .001$), whereas transitives were not different from intransitives ($\beta = -0.01$, $|t| < 1$). Neither a main effect of Lexicality nor an interaction between Lexicality and Verb argument structure was observed (both ts < 1). This result is consistent with earlier findings showing that speech onsets depend on the phrasal "distance" between the first shape and the second shape to be produced in the sentence and thus indicate that the timing of sentence production is at least partially subject to structural constraints (e.g., Smith & Wheeldon, 1999).

Production duration was measured as the time between Production onset and Production offset. We performed an analysis with Lexicality and Verb argument structure as fixed effects, as well as random by-participant slopes for both factors. The results revealed a main effect of Lexicality ($\beta = 0.17$, $t = 6.34$, $p < .001$), as Production durations were shorter in the known-verb condition than the pseudoverb condition. There was no effect of Verb
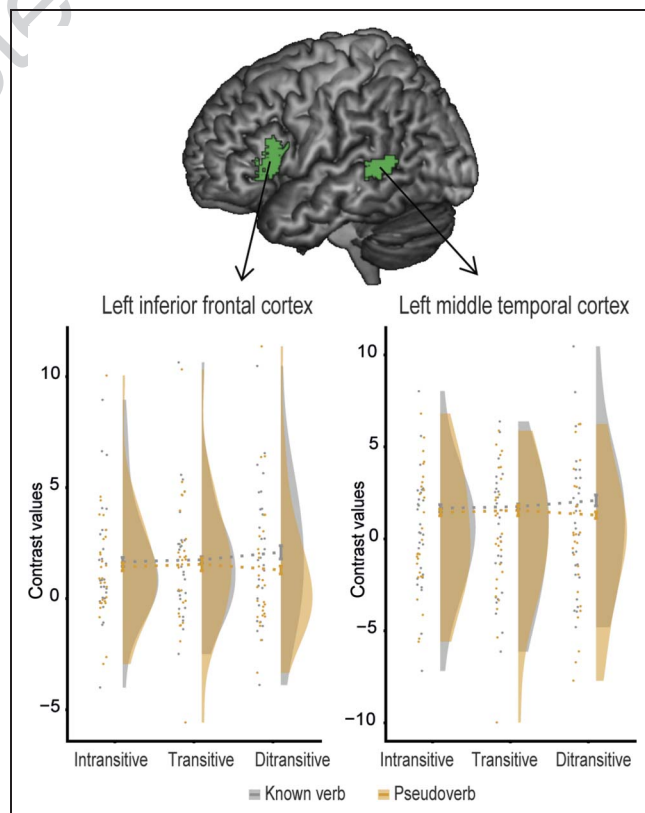

Figure 3. Behavioral results. (Left) Production onsets (after picture onset). (Right) Production durations (time between production onset and offset). Dots represent individual participants' data with the mean, *SEM*, and density represented on their right-hand side.

Table 3. fMRI Whole-Brain Results (Local Maxima More Than 20 mm Apart Are Reported)

Anatomical Location	Brodmann's Area	p(FWE-Corr)	Size	Z Score	x	y	z	Post Hoc t Test
Verb argument structure effect (F test)								
Left middle temporal/angular	37/39	<.001[a]	330	5.54	−40	−64	20	Ditransitive > intransitive Transitive > intransitive
Left precuneus	7	<.001[a]	179	4.68	−4	−60	34	Ditransitive > intransitive Transitive > intransitive
Right superior temporal pole/parahippocampus	36/35	<.001	267	5.70	32	4	−28	Intransitive > transitive
Right (para)hippocampus	35			4.87	22	−14	−20	Intransitive > ditransitive Intransitive > transitive
Right hippocampus	20			3.35	40	−18	−6	Intransitive > ditransitive
Right calcarine	17	<.001	715	5.56	14	−88	0	Intransitive > ditransitive Transitive > ditransitive
Right inferior occipital	19	<.001		3.59	38	−74	−6	Intransitive > ditransitive
Right middle frontal	46	<.001	509	5.55	32	48	26	Intransitive > ditransitive Intransitive > transitive
Right middle frontal	46			3.83	40	30	38	Intransitive > ditransitive
Right thalamus		<.001	165	5.34	2	−24	−2	Intransitive > transitive
Left parahippocampus	36	.001	139	5.32	−26	−12	−28	Intransitive > ditransitive Intransitive > transitive
Right middle/superior temporal	21	<.001	363	5.26	46	−26	−6	Intransitive > ditransitive Intransitive > transitive
Right superior temporal	22			4.36	66	−32	10	Intransitive > ditransitive Intransitive > transitive
Right pallidum		<.001	214	5.21	20	2	4	Intransitive > ditransitive Intransitive > transitive
Right thalamus				4.42	4	−4	18	Intransitive > ditransitive Intransitive > transitive
Right SMA	6	<.001	947	5.07	6	10	56	Intransitive > ditransitive Transitive > ditransitive
Right middle cingulum	32			4.67	8	26	34	Intransitive > ditransitive

Table 3. (*continued*)

Anatomical Location	Brodmann's Area	p(FWE-Corr)	Size	Z Score	x	y	z	Post Hoc t Test
Left superior frontal	32			3.66	−10	20	42	Intransitive > ditransitive
Left anterior cingulum	24			3.58	−6	28	16	
Left calcarine	17	<.001	555	5.02	−4	−80	2	Intransitive > ditransitive Transitive > ditransitive
Left cuneus	18			4.45	−10	−92	20	Intransitive > ditransitive
Left middle cingulum	23	<.001	449	4.72	−6	−24	38	Intransitive > ditransitive transitive > ditransitive
Left precuneus	5/7			3.68	2	−38	52	Intransitive > ditransitive
Right insula/inferior frontal		<.001	211	4.7	44	16	4	Intransitive > ditransitive
Left middle frontal	9/46	<.001	391	4.58	−32	44	36	Intransitive > ditransitive
Left middle frontal	46			4.58	−30	52	16	Intransitive > ditransitive
Left inferior parietal	40	.008	96	4.54	−56	−50	46	Intransitive > ditransitive Intransitive > transitive
Left superior temporal	20/21	.002	119	4.53	−42	−24	−4	Intransitive > ditransitive
Right inferior parietal/supramarginal	40	<.001	210	4.11	56	−38	38	Intransitive > ditransitive Intransitive > transitive
Lexicality effect (F test)								
Left posterior middle temporal/angular	37/39	<.001[a]	480	5.39	−40	−62	20	Verb > pseudoverb
Left posterior middle temporal/occipital	37/39			4.45	−50	−74	18	Verb > pseudoverb
Left posterior middle temporal	21	.016[a]	96	5.03	−62	−54	4	Verb > pseudoverb
Left inferior frontal (pars triangularis)	45	.013[a]	100	4.22	−54	22	24	Verb > pseudoverb
Left inferior frontal (pars triangularis)	45			3.98	−54	24	14	Verb > pseudoverb
Right cerebellum		.004	125	4.67	22	−64	−46	Pseudoverb > verb

Table 3. (*continued*)

Anatomical Location	Cluster Brodmann's Area	p(FWE-Corr)	Size	Peak Voxel Z Score	MNI Peak Coordinates x	y	z	Post Hoc t Test
Right cerebellum		.033	82	4.65	26	−68	−24	Pseudoverb > verb
				4.50	30	−62	−18	Pseudoverb > verb
				3.15	18	−66	−20	Pseudoverb > verb
Right superior frontal	6	.013	99	4.12	18	18	66	Pseudoverb > verb
	8			4.04	16	16	58	Pseudoverb > verb
	6			4.02	22	8	66	Pseudoverb > verb

Interaction

- No significant clusters observed

[a]Increase with levels of complexity.

argument structure ($t = 1.68$), but there was an interaction between the two factors as the Lexicality effect increased with Verb argument structure complexity ($\beta = 0.123$, $t = 3.78$, $p < .001$). Follow-up tests showed that this effect was driven by an increase in Production duration over the levels of Verb argument structure for the pseudoverbs ($\beta = 0.1$, $t = 3.04$, $p = .005$), but not the known verbs ($\beta = −0.02$, $|t| < 1$). Although we cannot attribute the source of these differences to a specific production process (e.g., word articulation times or the insertion of pauses), the results suggest that producing sentences with pseudoverbs was cognitively more demanding than producing sentences with known verbs, especially when producing these verbs in a more complex sentence structure.

Imaging Results

Sentence Production Task

ROI analyses. First, we considered how the brain areas related to syntactic processing would respond to changes in Verb argument structure complexity and Lexicality. Our assumption was that there would be a difference in brain responses (1) across sentences with differing numbers of verb arguments (i.e., the Verb argument structure effect: intransitive vs. transitive vs. ditransitive) and (2) in sentences using known words versus pseudoverbs (i.e., the Lexicality effect). For the first point, we expected to find a linear activation increase with an increasing number of verb argument slots to be filled (intransitive < transitive < ditransitive). For the second point, we expected to find differences in brain activation

reflecting the presence (known verb) versus absence (pseudoverb) of a lexical memory representation. Moreover, if argument structure information is verb bound, we should find an interaction with more activation during the production of sentences using known verbs than pseudoverbs.

The mixed-effects model on the mean beta values extracted from the two ROIs (LIFG and LpMTG) included the factors ROI (LIFG, LpMTG), Verb argument structure (intransitive, transitive, ditransitive), and Lexicality (known verb, pseudoverb). The model revealed a main effect of ROI ($\beta = 0.62$, $t = 2.46$, $p = .02$), a main effect of Lexicality ($\beta = −0.19$, $t = −2.78$, $p = .006$), and a significant interaction between Lexicality and Verb argument structure ($\beta = −0.3$, $t = −2.53$, $p = .01$). No main effect of Verb argument structure (linear contrast: $t < 1$) nor any additional interaction with ROI (all ts $< |1|$) was found. To interpret the interaction of Lexicality and Verb argument structure complexity, we ran separate models per level of the factor Lexicality. These analyses revealed a linear increase with Verb argument structure complexity for the known verbs ($\beta = 0.39$, $t = 2.34$, $p = .02$), but not for the pseudoverbs ($\beta = −0.2$, $t = −1.25$, $p = .2$).

Flexible factorial: Verb argument complexity (intransitive/transitive/ditransitive) vs. lexicality (known verb/pseudoverb). Next, we performed an analysis looking at the whole brain using the flexible factorial analysis with Verb argument structure complexity (intransitive, transitive, ditransitive), Lexicality (known verb, pseudoverb), and Subjects as factors included in the model.
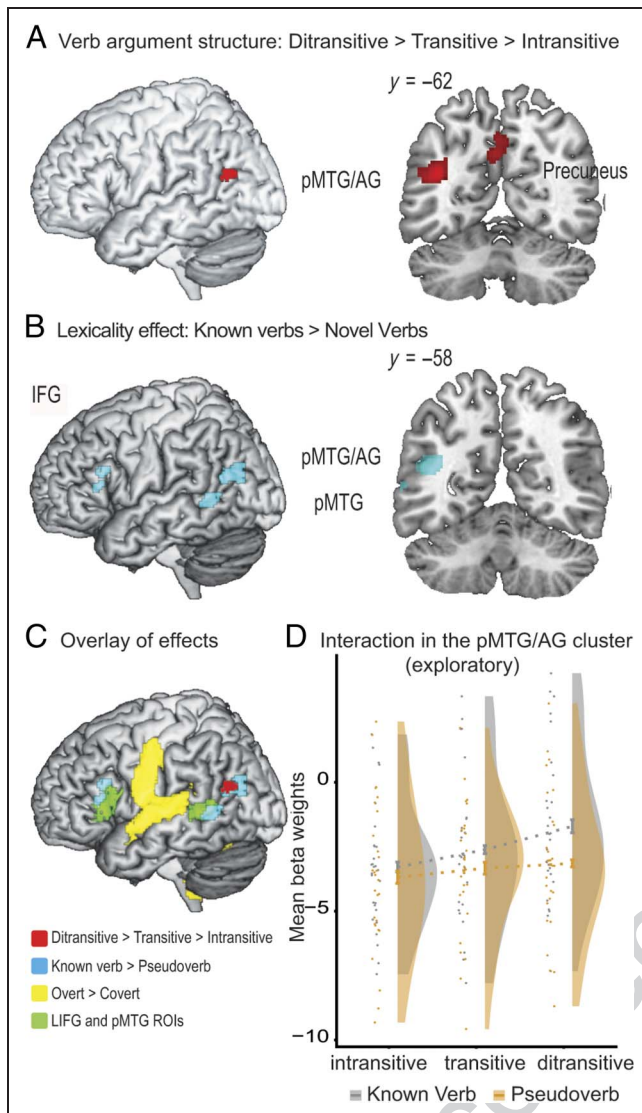
Figure 4. Imaging results. (A) Significant clusters for increasing Verb argument structure complexity were found in the LpMTG/AG and a cluster in the bilateral precuneus. (B) Significant clusters for the Lexicality effect (known verb > pseudoverb) are superimposed on the surface rendering and coronal slice at $y = -58$. (C) Overlap between increase over verb argument structure complexity (red), known verbs > pseudoverbs (blue), and ROIs (green) as well as the distinct overt > covert production effect (yellow). (D) An exploratory analysis of the interaction of mean beta weights per condition extracted from the LpMTG/AG cluster shown here. Dots represent individual participant's data with the mean, *SEM*, and density represented on their right side.

Verb Argument Structure Effect

The *F* contrast for Verb argument structure conditions revealed a large set of areas (see Table 3) with significantly different activation levels among conditions. Of these significant clusters, an increase over Verb argument structure complexity levels was found in the LpMTG/angular gyrus (AG) and the precuneus (see Figure 4A). The rest of the clusters were more active for simpler verb argument structures (intransitive > transitive > ditransitive).

The latter activation pattern likely reflects the processing demand for the more complex sentence-initial noun phrases, as the intransitive condition had the longest sentence-initial noun phrases.

Additional models were tested comparing the above factors of interest, by adding Production onsets or Production offsets into the model (using parametric modulation) to account for possible RT differences that might affect the activation patterns. Both models did not change the activation pattern in the areas reported above. Thus, it is less likely that the activation patterns are affected by different RTs across conditions. It is also less likely that this contrast reflects brain responses related to mind wandering, which involves the so-called default mode network that includes areas such as the precuneus and the AG (Raichle & Snyder, 2007).

Lexicality Effect

An *F* contrast for the Lexicality effect (see Table 3) revealed multiple significant clusters. Post hoc *t* tests revealed that higher activation was observed for known verbs than pseudoverbs in three clusters: the LpMTG, the LpMTG extending to the AG (LpMTG/AG), and the LIFG (Figure 4B). The opposite contrast (pseudoverb > known verb) revealed clusters in the right superior frontal and cerebellar regions.

Interaction Lexicality and Verb Argument

At the whole brain level, we did not find any areas showing an interaction between Verb argument structure complexity and Lexicality. However, the increase in activation in the posterior middle temporal gyrus (pMTG)/AG cluster overlapped to a great extent with the cluster found for the Lexicality effect (see Figure 4C). To test for interactions between Lexicality and Verb argument structure complexity, we carried out a further exploratory analysis within this cluster (mean beta values extracted from the significant cluster of the main effect of Verb argument structure; see Figure 4D). This revealed a significant interaction between Lexicality and Verb argument structure complexity (linear contrast: $\beta = 0.37$, $t = 2.52$, $p = .01$). Follow-up tests by level of Lexicality showed an activation increase for known verbs ($\beta = 1.12$, $t = 5.6$, $p < .001$). However, no such effect but only a trend in the same direction was observed for pseudoverbs ($\beta = 0.38$, $t = 1.86$, $p = .068$)

Overt vs. covert production. To verify whether the regions stated above reflected movement-related or motor-related brain activation that may be different across conditions, we contrasted the brain activation pattern observed during overt production to that observed during covert production of intransitive sentences in a similar manner to the main task reported above.

Table 4. Overt Versus Covert Production: fMRI Whole-Brain Results (Local Maxima More Than 20 mm Apart Are Reported)

Cluster				Peak Voxel			
Anatomical Location					MNI peak coordinates		
Overt > Covert	Brodmann's Area	p(FWE-Corr)	Size	Z Score	x	y	z
Left precentral	3/6	<.001	9436	>10	−40	−16	36
Left cerebellum				7.73	−16	−60	−20
Right cerebellum				7.39	18	−60	−20
Right postcentral	4	<.001	4053	7.68	48	−10	34
Right Heschl's				6.95	40	−26	12
Right superior temporal	22			6.67	60	−18	4
Right putamen		<.001	200	7.24	28	−6	−8
Right thalamus		<.001	277	6.21	14	−20	0
Left thalamus				5.19	0	−6	0
Left thalamus				4.07	0	−22	6
Left postcentral	4/6	.002	152	5.6	−18	−28	62
Right caudate		<.001	315	5.38	20	16	18
Right anterior cingulate	47			4.85	24	38	0
Right middle frontal	46			4.7	24	30	20
Right precentral	4/6	.002	158	5.13	20	−26	60
Left caudate		<.001	314	5.11	−18	20	20
Left middle frontal	47			4.89	−20	34	18
Left insula				4.24	−24	30	12
Left superior frontal		.005	136	5.08	−18	6	42
Left precentral				4.25	−22	−2	40
Left superior frontal				4.1	−12	16	44
Right precuenus		.03	94	4.93	20	−46	30
Right precuneus				3.43	22	−52	38
Right precuneus				3.29	26	−48	24
Left calcarine	19	<.001	1502	4.78	−28	−64	8
Left calcarine	17			4.77	−14	−72	10
Right calcarine	19			4.57	18	−78	16

The contrast overt > covert was tested using a one-sample t test on the difference contrast images. This contrast showed activation in bilateral motor areas and superior temporal areas known to process motor output and speech perception, respectively (see yellow areas in Figure 4C; Table 4). The differences between conditions found during the main task (sentence production task) did not overlap with this contrast apart from the cerebellum, suggesting that the cortical areas reported for the main task are not because of any differences in motor-related processes or because of movement artifacts.

DISCUSSION

In this study, participants produced sentences using three different syntactic structures with known verbs and pseudoverbs. At the behavioral level, the results are consistent with production data reported for sentences with a range of different structures and lexical items: Participants were more accurate and faster to produce sentences beginning with simple noun phrases rather than complex noun phrases and sentences using known verbs than pseudoverbs (e.g., Konopka, 2012; Martin, Crowther, Knight, Tamborello, & Yang, 2010; Smith & Wheeldon, 1999). Thus, despite the use of a simple and repetitive task, we find effects of structural complexity and verb lexicality that reflect differences in processing load normally shown in spontaneous production. More importantly, at the neural level, the Verb argument structure effect revealed greater activation with increasing verb argument structure complexity (intransitive < transitive < ditransitive) in the LpMTG/AG. A Lexicality effect (known verb > pseudoverb) was found in the LIFG as well as the LpMTG and the AG. The Verb argument structure effect in the LIFG and LpMTG regions was stronger for the known-verb condition compared to the pseudoverb condition, whereas the LpMTG/AG cluster showed both Verb argument structure and Lexicality effects. We discuss each of these findings in turn.

Before doing so, we want to highlight that this is one of the small number of studies focusing on language production instead of language comprehension. In classical models of language processing, it has been argued that language production is subserved by areas in the left frontal cortex, whereas language comprehension is subserved by left temporal cortex areas (Tremblay & Dick, 2016). Our results show that this distribution of labor is not supported by the data. Although the ROIs were defined by a substantial number of comprehension studies on "syntax" (in Neurosynth), these very same areas were found to be activated in our language production task. This is in agreement with earlier studies on language production (Hagoort & Indefrey, 2014; Segaert, Kempen, Petersson, & Hagoort, 2013), indicating that, in line with computational models of language comprehension and production (Vosse & Kempen, 2000), the neural

architecture for comprehension and production is shared. Our data, therefore, are another piece of evidence that the classical model of the neural basis for language should be given up, despite its ongoing popularity.

Verb Argument Structure Effect

Our displays prompted the production of sentences with three structures: intransitive, transitive, and ditransitive. The difference in structural complexity across these sentences was operationalized as a difference in the number of verb arguments per structure, and this is the main focus of the neuroimaging analyses. However, it is important to note that these structures also differed in verb placement. The verb is sentence-final in intransitive sentences and sentence-medial in transitive and ditransitive sentences but occurs earlier in ditransitive than transitive sentences. This clearly affected the behavioral results. Participants were more accurate at producing sentences with ditransitive structures than with transitive and intransitive structures, suggesting that early verb placement reduced working memory load as the (pseudo)verb was not present on the screen at the time of production. Production onsets in ditransitive sentences were also slightly faster than in the other two sentence types. This is consistent with the observation that planning scope (and thus the onset of articulation) is sensitive to the complexity of the sentence-initial noun phrase (e.g., Konopka, 2012; Allum & Wheeldon, 2007; Smith & Wheeldon, 1999): Sentences beginning with a simple noun phrase (e.g., "The circle gives…") are normally initiated faster than sentences beginning with a complex noun phrase (e.g., "The circle and the square wash…"). The presence of this onset difference in the data suggests that production in this task approximated production in tasks with a less repetitive trial structure and in "natural" production: Participants did not wait to begin speaking until they planned an entire sentence but rather began their sentences as quickly as they could (Levelt, 1989) and encoded the shapes shown on the screen in the order of mention.

By contrast, effects of the number of verb arguments on production are better captured by Production duration and neuroimaging data. Production durations were longer for the ditransitive condition especially when pseudoverbs were used. Looking at the whole-brain imaging results of the correct responses, both the LpMTG/AG region and the precuneus showed greater activation with increasing complexity levels of Verb argument structure. In the LpMTG/AG cluster, the Verb argument structure effect was clearly present for verbs with a lexical status (known verbs), but only trendwise for the pseudoverb condition. The finding that the effect was stronger in the known-verb condition might reflect the retrieval of the lexical–syntactic information that is verb bound instead of a less specified abstract template (whole construction; Goldberg, 2005).

Greater activation levels for the (pseudo)verb intransitive and transitive conditions compared to the ditransitive condition in other regions listed in Table 3, including areas such as the superior temporal and inferior parietal areas, may be driven by the difference in sentence-initial noun phrase complexity. The larger number of incorrect verb responses in the intransitive condition may also arise from failure to maintain the verb in working memory successfully. We acknowledge that this may pose a constraint on the generalizability of findings regarding the Verb argument structure effect. If the same area was also affected by sentence-initial noun phrase complexity, the BOLD activation levels between the conditions could have canceled each other out. This is because the two factors (Verb argument structure and Verb position) may make opposite demands on processing; that is, the ditransitive condition had the highest level of Verb argument structure complexity but the lowest level of sentence-initial noun phrase complexity. This may explain why we did not see as clear an effect in the LIFG as we had predicted. That being said, in the ROI analysis, we still found a linear Verb argument structure effect in line with our prediction (intransitive < transitive < ditransitive) in both the LIFG and LpMTG for the known-verb condition.

Another region that showed the Verb argument structure effect (smallest activation for intransitive) was the bilateral precuneus. The precuneus is a higher-order association structure that is known to be involved in multiple processes (Cavanna & Trimble, 2006), including memory retrieval (reviewed in Gilmore, Nelson, & McDermott, 2015) and language processing (reviewed in Rodd, Vitello, Woollams, & Adank, 2015). Repetition suppression studies have also found this area to be involved in semantic processing (Menenti et al., 2011) and syntactic repetition (Schoot, Menenti, Hagoort, & Segaert, 2014). As this area was not among those in which we expected to show a Verb argument structure effect, future studies will have to delineate its functional role.

Lexicality Effect

Overall, participants were able to construct sentences using both known verbs and pseudoverbs within the appointed time. This finding is consistent with the expectation that speakers have acquired at least partially abstract sentence structure templates (construction) in the course of language learning that are not bound to specific verbs (Konopka & Bock, 2009; Goldberg, 2005; Fisher, 2002a, 2002b; Bock & Loebell, 1990; Frazier, 1987) and that they are able to apply default rules of verb inflection (Ullman, 2001). Having such template sentence structures (or "abstract" structures not bound to specific verbs) enables speakers to deduce the word categories of pseudowords or unknown words encountered during comprehension (as in the case of the famous poem "Jabberwocky" in Lewis Carroll's "Through the Looking Glass") and to use the same sentence template (including the correct verb

conjugation) in production, as observed in our study. At the same time, speakers made fewer errors, began production earlier, and completed their sentences more quickly when using known verbs than pseudoverbs, suggesting parallel use of abstract structural information and lexical–syntactic information, which is only available in the case of known verbs, when producing sentences.

Considering the imaging results, production of sentences using verbs with an existing lexical representation activated areas that are known for syntactic processing in the LIFG and the LpMTG. In addition, a more posterior pMTG extending to the AG (LpMTG/AG) also showed greater activation for the known verbs relative to pseudoverbs. This suggests that the production of sentences using known verbs activated the core language network more than when the sentences used pseudoverbs without existing lexical–syntactic information. These areas very much overlap with those reported in single word comprehension studies (reviewed in Price, 2010), especially for the posterior middle temporal regions that are proposed to store lexical information. Thus, whether we are comprehending or producing sentences using words we know, processing seems to involve overlapping networks (Hagoort & Indefrey, 2014; Segaert, Kempen, et al., 2013). The increase in activation in the LIFG that we found for known verbs relative to pseudoverbs might reflect a process of assembling the information retrieved from the mental lexicon into a coherent sentence-level representation (Hagoort, 2013). One of the advantages of activating syntactic information in the lexicon is that it may lead to efficient sentence production. We observed this as more accurate and faster responses to known verb trials compared to pseudoverb trials in the current task.

Interaction Verb Argument Structure and Lexicality

As mentioned before, the pMTG/AG showed a Verb argument structure effect that was present for both known and pseudoverbs but stronger for known verbs, showing an interaction between Verb argument structure and Lexicality. The Verb argument structure effect for known verbs found in the LpMTG/AG cluster is in line with findings from aphasia (Thompson, Bonakdarpour, & Fix, 2010), comprehension (Thompson et al., 2007), and single-word production (den Ouden et al., 2009) studies. Lesion in this area causes patients to have difficulty in producing sentences with multiple verb argument structures. Poststroke treatment targeting the use of sentences with complex argument structure shows changes in this region, accompanied by improvement in behavior (Thompson et al., 2013).

Moreover, the ROIs of the syntax network, LIFG and LpMTG, which is more anterior than the LpMTG/AG effect mentioned above, also showed an increase over the levels of Verb argument structure for the known verb that was not present for the pseudoverb. These regions constitute the core syntactic processing network (Price,

2012; Indefrey & Levelt, 2004). Although our findings did not differentiate between the LIFG and the LpMTG, they are nonetheless not incompatible with models that attributed a mental lexicon function to posterior temporal regions and unification to LIFG (Hagoort, 2013), as both retrieval of more complex lexical–syntactic representations and their unification might lead to the observed pattern. It remains to be seen whether the more posterior temporal activation extending into the AG (LpMTG/AG) is more related to this lexical–syntactic function or whether its pattern could also be accounted for in terms of event information differences related to verb argument structure that has been ascribed to the AG (Matchin, Liao, Gaston, & Lau, 2019; Binder, 2016).

Our imaging result suggests that the brain relies on both abstract structural representations and lexical–syntactic representations during production. Speakers are able to produce constructions with pseudoverbs in a grammatically well-formed way. The increase in activation with increasing numbers of verb argument complexity found in the LpMTG/AG for both known verbs and pseudoverbs suggests that these areas might support constructions independent of lexical-verb information. However, when a lexical representation including syntactic information is present, speakers may benefit from retrieving this information from their memory for the purposes of sentence assembly, leading to faster RTs and more accurate responses in the known-verb condition compared to the pseudoverb condition. The efficiency in the use of this lexical–syntactic information may also lead to the reduction in sentence duration differences between conditions. Neural response modulation to different levels of verb argument structure found only for the known-verb condition in the LIFG and LpMTG may reflect the processing of this lexical–syntactic information in these areas.

Limitations

Like most studies on language production, this study has some limitations. As mentioned earlier, one limitation regards the complexity of the sentence-initial noun phrase that might have worked against finding all the brain activation patterns reflecting the Verb argument structure effect. Other limitations relate to the fact that the same verbs were repeated across blocks and the same sentence structure was repeated within each block (although no verbs were repeated within a block). These repetitions might have led to adaptation effects that reduced the magnitude of both the lexicality and verb argument structure effects on production. Specifically, speakers could afford to plan their sentences by encoding shapes one by one and from left to right across all conditions. This is similar to earlier studies requiring sequential object naming (Meyer, Wheeldon, & Konopka, 2012; Smith & Wheeldon, 1999; Meyer, Sleiderink, & Levelt, 1998). This type of radically incremental (object-by-object planning) is advantageous in so far as it minimizes processing load and reduces production costs (e.g., Ferreira & Swets, 2002) and may have been further exaggerated by the repetitive nature of the task (Meyer et al., 2012; Griffin, 2001). Furthermore, repeated use of the same structure within each block might have enabled fast reuse of the sentence structure template retrieved in the preceding trial on subsequent trials. Nevertheless, the fact that differences in brain activation were observed across conditions demonstrates the strength of the structural effect. In addition, the number of repetitions per word and the number of sentence structures per block were the same across all conditions, and the order of words within a block as well as condition blocks during the task was randomized across participants; thus, the effects reported here are present over and above the repetition effects. Finally, the frequencies of the bigrams and trigrams appearing in the known-verb and pseudoverb conditions were not completely matched. This might have affected the motoric responses to be less fluent for infrequent combinations. Although we assume the usage of infrequent bigrams and trigrams affecting sentence production preparation to be minimal, future studies should take this factor into account.

Conclusions

Speakers successfully produced sentences with different verb argument structures using both known verbs and pseudoverbs, although production with known verbs was faster and more accurate compared to when using the pseudoverbs. Imaging results revealed that the production process engages the core language network in the LIFG and LpMTG as well as the AG. These areas increased in activation with increasing verb argument complexity, but this was more obvious when sentences were constructed using a known verb compared to when using a pseudoverb. We speculate that retrieval and unification of such lexical–syntactic information that is verb bound may support more efficient production of sentences, especially when the sentence structure is associated with complex verb arguments.

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