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Shared Language: Overlap and Segregation of the Neuronal Infrastructure for Speaking and Listening Revealed by Functional MRI

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Abstract

Whether the brain's speech-production system is also involved in speech comprehension is a topic of much debate. Research has focused on whether motor areas are involved in listening, but overlap between speaking and listening might occur not only at primary sensory and motor levels, but also at linguistic levels (where semantic, lexical, and syntactic processes occur). Using functional MRI adaptation during speech comprehension and production, we found that the brain areas involved in semantic, lexical, and syntactic processing are mostly the same for speaking and for listening. Effects of primary processing load (indicative of sensory and motor processes) overlapped in auditory cortex and left inferior frontal cortex, but not in motor cortex, where processing load affected activity only in speaking. These results indicate that the linguistic parts of the language system are used for both speaking and listening, but that the motor system does not seem to provide a crucial contribution to listening.

Keywords

language comprehension, language production, motor processes, neuroimaging, fMRI adaptation, repetition suppression

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When people speak, their brains convert an intention to communicate a message into a linearized string of sounds. An essential step in this process is the retrieval of relevant concepts and the encoding of the intended meaning, the *semantic structure*. A key aspect of semantics is *thematic role structure*, which refers to the relation between the different concepts and events in a phrase, or "who does what to whom."

To take one example, the thematic role structure ROB(THIEF, LADY(OLD)) can be expressed in different ways, depending on the choice of syntactic structure: *The old lady was robbed by a thief!* or *A thief robbed the old lady!* or even *Did the thief rob an old lady?* The words in this structure then activate their corresponding phonological properties, so the articulatory patterns required to utter the intended sentence can be generated (Levelt, 1989). The listener then segments the incoming sound stream into words, parses the syntactic structure, and deduces that a thief robbed an old lady and not the other way around.

An important question in both psycholinguistic and neuroscientific research is to what extent the processes for speaking and listening overlap (Fig. 1). The aspect of this question that we addressed in the study reported here is how to characterize the neural infrastructure that relates speaking to listening. Listeners and speakers usually understand each other, so it is likely that the linguistic representations generated in speaking and listening are alike (Pickering & Garrod, 2004). However, in psycholinguistic research, language comprehension and production are often investigated and discussed separately. The implicit assumption in such research is often that encoding and decoding of language hardly overlap. For syntax, some researchers have nevertheless argued that encoding and decoding rely on the same processor (Heim, 2008; Kempen, 2000) or the same representations (Branigan, Pickering, & Cleland, 2000). For phonology, however, both neuropsychological evidence (Jacquemot, Dupoux, & Bachoud-Lévi, 2007; Martin, Lesch, & Bartha, 1999) and behavioral evidence (Shallice, McLeod, & Lewis, 1985) have been claimed to support the idea that the representations used in speaking and listening are distinct. Nevertheless, research on aphasic

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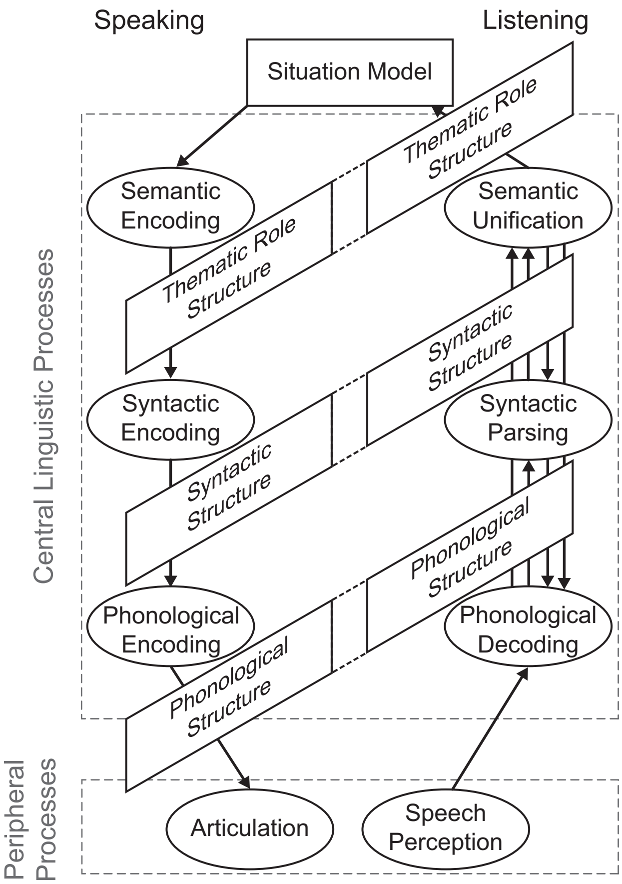

Fig. 1. The different processing steps involved in speaking and listening. Both speaking and listening involve central linguistic processes (semantic, lexical, and syntactic) and peripheral sensory and motor processes (speech perception and articulation). In this study, we compared sentences with novel and repeated semantics, words, and syntax in order to investigate whether the representational structures generated by these processes are shared between speaking and listening. Previous studies investigated this question only for peripheral processes.

patients has repeatedly shown that comprehension deficits and production deficits rarely occur independently of each other (Jacquemot et al., 2007; Neuhaus & Penke, 2008).

So far, much of the debate on the neuronal overlap between speaking and listening processes has focused on the role of the motor system in perception of speech sounds. In the experiments reported here, we extended this discussion to look at overlap in linguistic processes. We did so by comparing the neuronal infrastructure underlying linguistic (i.e., semantic, lexical, and syntactic) processing in speaking and listening. In what way do speech comprehension and production overlap in the brain? (See Fig. 1 for an illustration of both peripheral and linguistic processes in speaking and listening, and of the research question.)

Our Study

Language comprehension has been extensively investigated using functional MRI (fMRI), but adequate fMRI sentence-production data to answer the question of whether speech comprehension and production overlap in the brain is lacking. The few neuroimaging studies that have investigated overt sentence-level production either treat speaking as a unitary process (e.g., Awad, Warren, Scott, Turkheimer, & Wise, 2007; Kemeny, Ye, Birn, & Braun, 2005) or isolate only one component of speech production (Indefrey et al., 2001). Two studies have investigated overlap between speaking and listening. In one study using positron emission tomography, participants either told or heard autobiographical stories, and these speaking and listening conditions were contrasted, respectively, with counting and with listening to spectrally rotated speech (which preserves acoustic properties of speech but is incomprehensible). Several brain areas showed overlapping activations between conditions, but motor cortex did not (Awad et al., 2007). In another study that used fMRI, Stephens, Silbert, and Hasson (2010) found extensive correlations in brain activity between a speaker telling a story and listeners hearing that story. These common activations in speaking and listening modalities, though compelling, are hard to interpret because results were based on comparison between complex speaking and listening tasks and very simple baseline tasks. In addition, in the positron emission tomography study, different modalities were investigated with radically different tasks.

In the study reported here, we segregated semantic, lexical, and syntactic processes in order to directly compare their roles across speaking and listening. We disentangled these processes by using an fMRI adaptation paradigm; fMRI adaptation is a phenomenon in which the blood-oxygen-level-dependent response in neuronal populations sensitive to a stimulus attribute is suppressed or enhanced when that attribute is repeated (Grill-Spector, Henson, & Martin, 2006). This paradigm can be used to identify areas sensitive to particular stimulus characteristics by orthogonally manipulating the repetition of those characteristics. Four previous studies on sentence comprehension have used fMRI adaptation, but they either investigated full-sentence repetition (Dehaene-Lambertz et al., 2006), focused on syntactic repetition (Noppeney & Price, 2004; Weber & Indefrey, 2009), or manipulated both semantic and syntactic repetition but confounded word- and sentence-level semantics (Devauchelle, Oppenheim, Rizzi, Dehaene, & Pallier, 2009). We designed our study (Fig. 2) to disentangle sentence-level semantic, lexical, and syntactic processes. By comparing the fMRI adaptation response to semantic, lexical, and syntactic factors across speaking and listening, we were able to test whether the neuronal infrastructure underlying them was the same across modalities.

Though our study was designed to complement the discussion on overlap between speech production and comprehension by looking at linguistic processes, the design of our experiments also allowed us to compare basic sensory and motor processes and, hence, test for motor involvement in naturalistic comprehension. Involvement of the motor system in speech perception is well-established (e.g., Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Watkins & Paus, 2006), but opinions differ on whether the motor system is

Fig. 2. Design of the experiments. For each prime trial, six possible target trials were created. These target trials differed in whether the syntax, words, and semantics were novel or repeated from the prime trial. To examine the role of syntax, we compared trials using novel syntax with trials using repeated syntax. In each picture, one actor was colored red, and the other was colored green. On speech-productions trials, syntactic sructure was manipulated by instructing participants to refer to the green person or object before the red person or object. To examine the role of words, we compared target trials using novel words with target trials using repeated words (but novel sentence-level semantics). To examine the role of semantics, we compared target trials using novel semantics (but repeated words) with target trials using repeated semantics. Example words and sentences have been translated from Dutch.

necessary for comprehension (Liberman & Mattingly, 1985; Lotto, Hickok, & Holt, 2009; Pulvermüller & Fadiga, 2010). In some views, the involvement of the motor system depends on how difficult perception is (Pickering & Garrod, 2007); in other views, its involvement is tied to coordinating conversation (Scott, McGettigan, & Eisner, 2009). Part of the confusion also stems from different interpretations of motor involvement: The debate has focused on motor involvement in either comprehending the semantic content of a linguistic utterance or the act of perceiving speech. We focused on the latter. Subjects produced or heard either active sentences ("The boy feeds the girl") or passive sentences ("The girl is fed by the boy"). Passive sentences contain more syllables than do active sentences that use the same set of words, and therefore impose a greater load on articulation in speaking and on perception in listening. By comparing effects of the number of syllables in sentence production and in sentence comprehension, we were able to test whether primary sensory and motor processes overlapped in speaking and listening. We conducted two experiments—one analyzing sentence comprehension and the other analyzing sentence production—with two different groups of subjects to ensure that overlap between modalities was not due to priming between tasks.

Method

Participants

Twenty-four subjects took part in the sentence-comprehension experiment (12 male, 12 female; mean age = 21.1 years, *SD* = 2.13 years). Twenty-four subjects participated in the sentence-production experiment (7 male, 17 female; mean age = 22.6 years, *SD* = 2.03 years), but 4 subjects were excluded because of technical problems with the data. All subjects were right-handed, healthy native Dutch speakers with normal or corrected-to-normal vision and hearing and had attended or were attending a university in The Netherlands. All gave written informed consent prior to the experiment and received a fee or course credit for their participation.

The two experiments

We chose situated paradigms for both the production (speaking) and comprehension (listening) experiments to maximize comparability across experiments, thereby ensuring that the crucial difference in brain activations in response to these processes was indeed linguistic modality.

Speaking experiment. In the speech-production experiment, participants saw transitive verbs (e.g., "strangle") presented via a projection screen and a mirror mounted on the head coil (Fig. 3). Each verb was followed by a picture of two actors performing the action that the verb described. Participants described the picture with a short sentence, using the presented verb. To manipulate whether participants produced active- or passive-voice sentences, we colored one actor red and one actor green. We instructed participants to mention the green person or object before the red person or object (*stoplight paradigm*). The experimenter coded the participants' responses on-line for correctness.

Listening experiment. For the speech-comprehension experiment, we used the sentence-picture matching paradigm (Clark & Chase, 1972), which has been used extensively in the study of language comprehension. The exact cognitive processes involved in the matching aspect of this paradigm, and hence its suitability for research on language comprehension, have been the subject of debate (Tanenhaus, Carroll, & Bever, 1976); however, a recent event-related-potential study supports the idea that this paradigm is appropriate for the study of on-line situated language comprehension (Knoeferle, Urbach, & Kutas, 2011).

In our experiment, subjects were presented with pictures in gray scale via a projection screen, and they listened to sentences describing each picture via headphones (Fig. 3). We instructed subjects to press a button if they detected mismatches between picture and sentence (e.g., if a picture showed a woman strangling a man but the sentence said "The man strangles the woman"). The response hand was counterbalanced. To perform well, subjects had to pay attention to semantic, lexical, and syntactic content of the sentences. Mismatches occurred on 10% of trials and did not enter into the analyses (see Supplementary Methods in the Supplemental Material available online).

Design. The design (Fig. 2) was identical in the two experiments. For a given target sentence, three factors (syntactic structure, semantic structure, words) could each be either repeated or novel compared with the prime sentence that preceded it. If meaning was repeated, then the thematic role structure (e.g., STRANGLE(MAN,WOMAN)) was the same for the prime and target. If meaning was novel, then the semantic structure was reversed between the prime and target (e.g., prime: STRANGLE(MAN,WOMAN); target: STRANGLE(WOMAN, MAN)). If the words were repeated, then the verb, the agent, and the patient were the same in the prime and target (e.g., prime: STRANGLE(MAN,WOMAN); target: STRANGLE (WOMAN,MAN)). If the words were novel, the verb, agent, and patient were all different in the prime and target (e.g., prime: STRANGLE(MAN,WOMAN); target: FEED(BOY,GIRL)). In both cases, the thematic role structure was therefore different in the prime and target. This design allowed us to investigate repetition of sentence meaning without confounding it with repetition of words, and vice versa. Finally, if syntactic structure was repeated, then both the prime and the target were in either the active voice or the passive voice. If the syntactic structure was novel, then one sentence was in the active and one was in the passive voice. Repetition of syntactic structure was orthogonal to repetition of words and meaning. The number of syllables in a sentence (active or passive sentence structure) was orthogonal to all other factors.

Procedure. The experiments were conducted in Dutch. Subjects performed the experiments while lying in a magnetic-resonance scanner. There were two runs in each experiment, each of which consisted of alternating miniblocks of fillers and targets, with each combination of picture and sentence (either produced or heard) constituting one trial. Each run started with three to six filler trials (see Supplementary Methods in the Supplemental Material). These filler trials were followed by three to six experimental trials. The first of these trials was a prime, followed by two to five target trials, each of which also served as a prime for the next target trial. Filler and target miniblocks alternated in this fashion for a total of 64 blocks, split over two sessions in the scanner (see Supplementary Methods in the Supplemental Material for additional details). Between a prime sentence and its target sentence, the semantic, lexical, or syntactic content could be repeated or novel, leading to six different prime-target combinations (see Fig. 2).

Data acquisition and analysis

Data acquisition took place in a 3-T Siemens Magnetom Tim-Trio magnetic resonance imaging scanner using a 12-channel surface coil. To acquire functional data, we used parallel-acquired inhomogeneity-desensitized fMRI (Poser, Versluis, Hoogduin, & Norris, 2006). In this multiecho-planar imaging sequence, images are acquired at multiple echo times following a single excitation. Accelerated parallel imaging reduces motion and susceptibility artifacts and thus is a good method to acquire data when participants are speaking in the scanner. The number of slices did not allow acquisition of a full brain

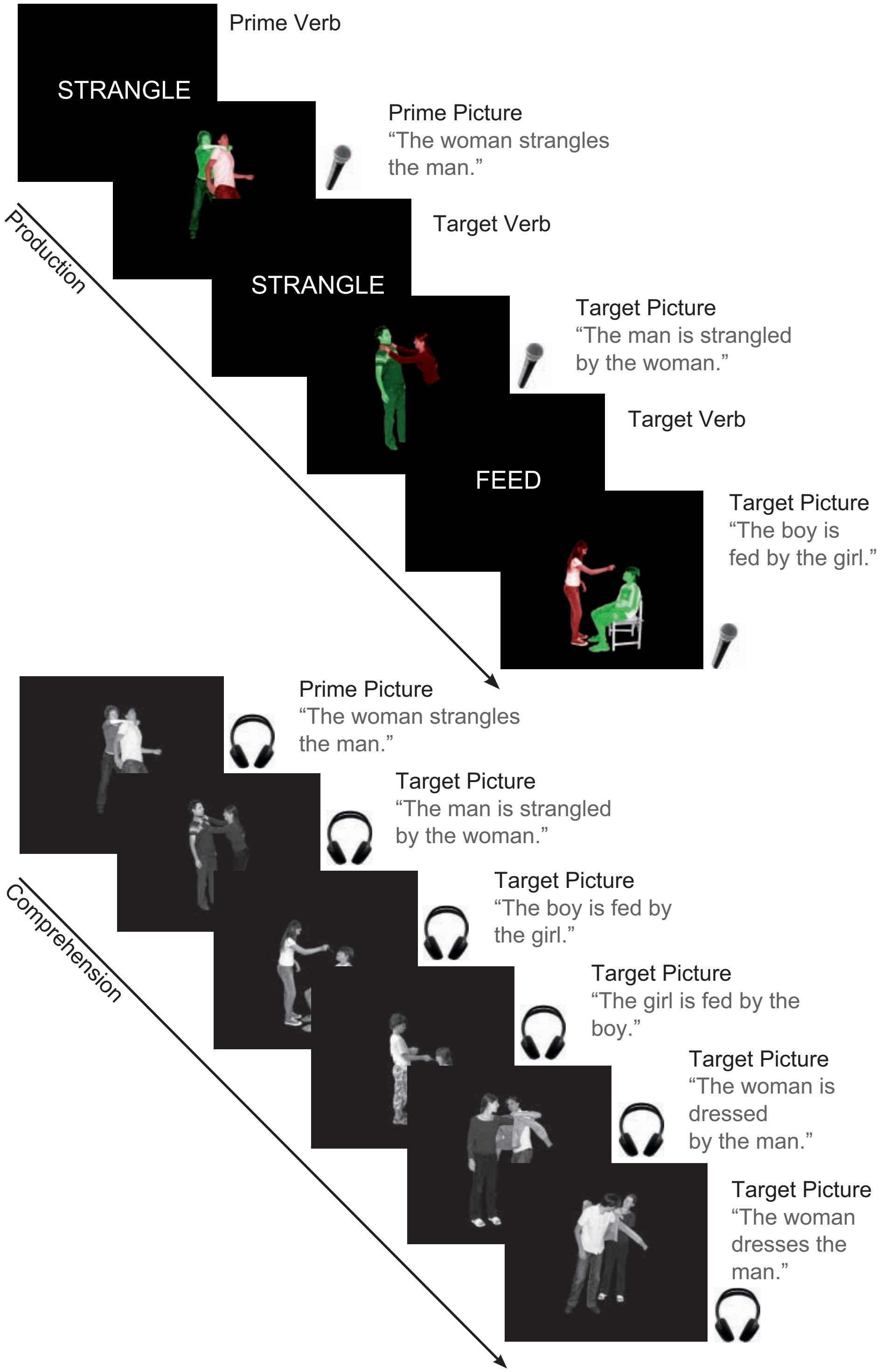

Fig. 3. Sample sequences of speech-production and speech-comprehension trials. In each speech-production trial (top), an action verb was presented on a coil-mounted mirror and followed by a picture of two actors (one colored red and the other colored green) performing that action. Subjects were required to produce a sentence describing the picture using the verb they had been shown; sentences had to start with the actor colored green, which forced subjects to produce either an active- or a passive-voice sentence. Each miniblock consisted of a prime trial followed by two to five target trials, each of which served as a prime for the following target trial. In each speech-comprehension trial (bottom), subjects saw a picture of an action being performed and heard a sentence describing the picture in either the active or the passive voice. Subjects pressed a button when they detected a mismatch between the spoken description and the picture. As in the speech-production experiment, each miniblock consisted of a prime trial followed by two to five target trials, each of which also served as a prime for the following target trial. Example words and sentences have been translated from Dutch.

volume in most participants. We made sure that the entire temporal and frontal lobes, where the fMRI adaptation effects of interest were expected, were scanned. This meant that superior posterior frontal lobe and superior anterior parietal lobe (thus, the top of the head), as well as the extreme ventral parts of the brain, were not scanned in several participants and thus were not included in the group data.

For preprocessing and first-level statistics, see Supplementary Methods in the Supplemental Material. The second-level model consisted of a 6 (condition: novel vs. repeated syntax, words, or semantics) × 2 (sentence length: long vs. short) × 2 (modality: speech production vs. speech comprehension) factorial design. We performed two types of analyses: To investigate the intersection of effects in speaking and listening modalities, we computed conjunction analyses, which yield a significant result only if a relevant contrast is significant in both modalities (Friston, Penny, & Glaser, 2005). To investigate differences between modalities, we computed interactions between the linguistic factors (syntax, words, and semantics) and modality. We also computed simple effects for each modality, masked exclusively for the other modality at a very low threshold ($p < .50$, uncorrected voxel-wise). Clusters showing both an interaction of effect and modality and an exclusive effect only for one modality were likely to be specific to either comprehension or production. The cluster size at voxel-wise threshold ($p < .001$, uncorrected) was the test statistic. Only clusters significant ($p < .05$, corrected) for multiple nonindependent comparisons are reported in this article. The anatomical labels we use are derived from the Automatic Anatomical Labeling Atlas (Tzourio-Mazoyer et al., 2002) and Brodmann's map.

Results

In the speech-production task, subjects responded correctly on 91.6% of the trials. In the speech-comprehension task, the average d' was 0.92. These results show that the subjects performed well on both tasks.

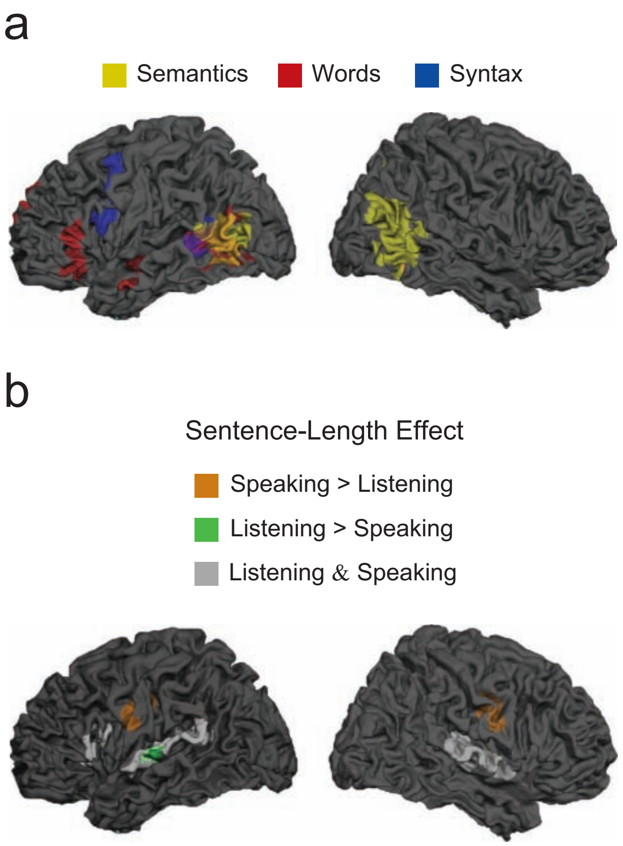

Fig. 4. Results for (a) linguistic processes and (b) peripheral processes. The images in (a) show brain areas in which repetition of semantics, words, and syntax resulted in suppression of activation in both speech production and speech comprehension. For every factor (semantics, words, syntax), the figure shows results from the contrast of repeated versus novel trials ($p < .05$ cluster-level, family-wise-error corrected; voxel-wise threshold of $p < .001$, uncorrected). See Table S1 in the Supplemental Material for coordinates and statistics. The images in (b) show results for conjunction and interaction analyses of peripheral processes. The colored regions are areas where the number of syllables in a sentence had a greater effect in speaking than in listening or a greater effect in listening than in speaking; the light gray regions are areas identified by the conjunction analysis of the effect of number of syllables across modality ($p < .05$ cluster-level, family-wise-error corrected, voxel-wise threshold of $p < .001$, uncorrected). See Table S2 in the Supplemental Material for coordinates and statistics.

Linguistic processes

The conjunction analyses for repetition of linguistic processes across experiments all demonstrated overlap of brain areas showing response adaptation to repetition of semantic, lexical, and syntactic content across speech production and speech comprehension (Fig. 4a). For semantic repetition, significant suppression effects in both comprehension and production were found in bilateral posterior middle temporal gyrus and right precuneus. For lexical repetition, left posterior inferior/middle temporal gyrus, left anterior middle temporal gyrus, right fusiform gyrus, left precuneus, left frontal superior medial gyrus, and left inferior frontal gyrus (Brodmann's area, BA, 45/47) showed suppression in both modalities. Right inferior parietal lobe (BA 40/39), the orbital part of bilateral middle frontal gyri (BA 47/46), and the superior parts of right middle frontal gyrus and right inferior frontal gyrus (BA 9/44/45) showed enhancement after repetition of words in both production and comprehension. Syntactic repetition yielded significant suppression effects in left inferior frontal gyrus (BA 44/6) and left posterior middle temporal gyrus, but no enhancement effects.

For the differences between speech production and speech comprehension, we looked for brain areas showing an interaction between modality and the relevant factors (semantics, words, syntax) while also showing an adaptation effect for the relevant factor only in one modality (i.e., there was no detectable effect in the other modality at $p < .50$). For semantic and syntactic repetition, no areas met either of those criteria, indicating that there were no areas reacting differently to semantic or syntactic repetition in production and comprehension. For repetition of words, however, there was one cluster meeting both criteria: A cluster centered around right precuneus showed repetition suppression for words in production but not in comprehension (Fig. 4a; see also Table S1 and Fig. S1 in the Supplemental Material).

Peripheral processes

The conjunction of the effect of number of syllables in sentences across modality yielded five significant clusters: left supplementary motor area, left inferior frontal gyrus (BA 44), two clusters in bilateral middle superior temporal gyri, and one cluster stretching from left precentral gyrus across middle frontal gyrus to rolandic operculum (Fig. 4b).

There were also areas showing a differential response in production and in comprehension (Fig. 4b): Bilateral pre- and postcentral gyri (BA 3 and BA 4; primary motor cortex) as well as right globus pallidum showed an interaction between modality and the effect of the number of syllables in a sentence. Furthermore, these areas showed an effect of number of syllables only in production.

Because sentence length varied as a function of both number of syllables and syntactic structure, we performed a follow-up conjunction analysis to investigate what drove the effect of sentence length. In this analysis, we looked at the conjunction of the effects of two different factors, sentence length and syntactic repetition, across modalities. The three left-lateralized brain areas that showed an effect of sentence length were also sensitive to syntactic repetition. Bilateral middle temporal gyri, however, were sensitive to sentence length but not to syntactic repetition (Fig. 4b; see also Table S2 and Fig. S2 in the Supplemental Material).

Discussion

In the study reported here, we investigated whether linguistic processes in the modalities of speech production and speech comprehension use the same neuronal infrastructure by comparing fMRI adaptation effects for semantic, lexical, and syntactic repetition across speaking and listening. The same brain areas were sensitive to semantic, lexical, and syntactic repetition in production and in comprehension, and almost no brain areas showed different response-adaptation effects to repetition of meaning, words, and syntax in these two language modalities. Bilateral posterior middle temporal gyri were involved in sentence-level semantic processing. Left posterior and anterior middle temporal gyrus, left inferior and middle frontal gyrus, and the homologous areas on the right were involved in lexical processing. Left posterior middle temporal gyrus and left inferior frontal gyrus were involved in syntactic processing. The only area that showed a difference between modalities for any of these effects was right precuneus, which was sensitive to lexical repetition in production but not in comprehension.

Though the studies are very different, our data are largely consistent with, and provide interpretations for, results from two other studies on speaking and listening (Awad et al., 2007; Stephens et al., 2010). In those studies, the bilateral temporo-parietal junction was activated in both modalities (Awad et al., 2007) or correlated between them (Stephens et al., 2010). In our study, this region was sensitive to repetition of sentence-level semantic structure in speaking and listening. Awad et al. (2007) also found that anterior temporal lobe was activated in both modalities. In our study, temporal lobe was sensitive to word repetition (though our region was more posterior). However, unlike us, Awad et al. did not find any inferior frontal activation. This is surprising in its own right given the robust nature of Broca's area's involvement in language processing and the very low-level baselines that Awad et al. used. Stephens et al. found speaker-listener coupling in early auditory areas, which we found to be sensitive to processing load in both modalities, as well as in inferior frontal gyrus, which in our study was sensitive to repetition of words. Stephens et al. furthermore found correlation in response patterns in insula, right anterior superior temporal gyrus, and right parietal lobule, where we did not find foci of overlapping adaptation effects. This discrepancy may be due to the very different nature of the materials. Both production and comprehension of the story content in Stephens et al.'s study may have triggered processes such as attention and empathy.

Our data highlight a hitherto neglected aspect of the discussion on overlap between speech comprehension and speech production: The neuronal infrastructure underlying sentence-level semantic, lexical, and syntactic processes in speaking and listening is largely shared. For semantic and syntactic repetition, we found no brain areas showing a differential effect between modalities. Language production and comprehension are two facets of one language system in the brain.

Federmeier (2007) proposed that production is more left-lateralized than comprehension. Our findings do not support this idea: The right hemisphere was equally recruited in comprehension and production, and this recruitment only occurred for semantic and lexical processing. Perhaps not coincidentally, most proposals on right-hemisphere contributions to language have focused on semantic processing (Bookheimer, 2002; Federmeier, 2007; Jung-Beeman, 2005).

The fact that we only found posterior areas involved in sentence-level semantic processing may look surprising in light of ideas ascribing semantic processes to anterior temporal regions (Indefrey & Levelt, 2004; Patterson, Nestor, & Rogers, 2007) or inferior frontal regions (Hagoort, 2005; Jung-Beeman, 2005). This inconsistency may lie in a particular strength of our design, the dissection of lexical processes from sentence-level semantic processes. We did find that both left anterior middle temporal gyrus and inferior frontal gyrus were involved in lexical processing—when the words were in the context of a sentence. Anterior temporal cortex activations are usually also seen in response to words presented in isolation. Inferior frontal gyrus activations, in contrast, are found when integrating word meaning into an overall semantic context becomes more difficult (Hagoort, Baggio, & Willems, 2009). Semantic integration of words might be a process captured more by our lexical repetition factor than by our semantic-structure repetition factor. The right-lateralized enhancement effect we found for lexical (and not semantic) repetition is consistent with this interpretation: Hagoort et al. (2009) have suggested that the areas showing enhancement integrate information from different sources into a coherent situation model. In our lexical-repetition condition, participants heard or spoke two subsequent sentences with the same word meanings but a different sentence meaning (e.g., "The man chases the woman," followed by either "The woman chases the man" or "The man is chased by the woman"). Repeating the same words but with different semantic integration requirements may have been harder than when both words and sentence-level semantics were different. This post hoc interpretation is subject to further research.

Our design also allowed us to look at motor involvement in language comprehension by comparing effects of processing load (number of syllables in a sentence) in production and comprehension. If speaking and listening share basic processes, then areas sensitive to processing load should show sensitivity to such a factor in both modalities. Left-hemisphere regions in frontal cortex (BA 44/6, supplementary motor area, left inferior frontal gyrus pars opercularis) and bilateral superior temporal gyri were sensitive to number of syllables across modalities.

The effect of number of syllables was confounded with the effect of syntactic structure, however, so these effects should be interpreted with caution. That being said, we still suggest that these effects are more likely due to the difference in syntactic structure between the sentences than to number of syllables in the sentences per se. First, if these areas were involved in the motor component of speaking or listening, they should have shown a bilateral pattern. Furthermore, previous research has found that these areas are involved in syntactic processing in comprehension (Bookheimer, 2002; Indefrey et al., 2001; Pallier, Devauchelle, & Dehaene, 2011; Snijders et al., 2009; Weber & Indefrey, 2009). A post hoc conjunction analysis examining syntactic repetition and number of syllables across modalities confirmed that the left-lateralized areas sensitive to number of syllables across modalities are also sensitive to syntactic repetition, but primary auditory cortex is not. The effect in auditory cortex during speaking is likely caused by participants hearing themselves speak.

Clearly, this interpretation is open to discussion because of the confound between processing load and syntactic structure. But however one wishes to interpret this factor, bilateral primary motor and somatosensory cortex, and globus pallidum, all showed different effects in speaking and listening. This factor therefore affects primary motor areas in speaking but not in listening. As a result, we found evidence for involvement of primary motor areas in language production but not in comprehension. Although this result may seem to contrast with existing data, the comparison in our experiment is different from the methodology used in other studies: We compared two speech conditions with each other, and the only difference between the two conditions was how much speech needed to be produced or understood. Our method yielded different results than comparing speech with nonspeech, and it may well be a better indicator of automatic motor activation during listening (Scott et al., 2009).

Our data sketch the contours of the brain's language system. Encoding or decoding a semantic representation recruits bilateral posterior temporal areas, at least when the semantic representation is linked to a visual scene, as in our study (but not only then; see Pallier et al., 2011). Retrieving lexical items is a left-lateralized function that involves left posterior and anterior middle temporal gyrus and left inferior frontal gyrus, though more ventrally than syntactic processing does. Left inferior frontal gyrus's contribution is possibly the result of operations of semantic unification between lexical items (Hagoort, 2005), as is the right frontal involvement in lexical processing. Left posterior middle temporal gyrus is likely involved in lexical retrieval (Hagoort, 2005; Snijders et al., 2009). Left anterior middle temporal gyrus has been shown to be commonly activated during picture and word naming and therefore postulated to be involved in the selection of lexical concepts (Indefrey & Levelt, 2004). Syntactic encoding and decoding both recruit left inferior frontal gyrus, as has previously been shown (Heim, 2008; Pallier et al., 2011; Snijders et al., 2009). Finally, speaking and listening part company in interacting with the external world, when either perceiving input or producing output: We found no evidence of primary motor cortex involvement in speech perception.

We have shown that the linguistic operations required to understand or produce an utterance are performed by the same network of brain areas. This network is left-lateralized for syntactic and lexical processes, but not for semantic processes. However, perceiving speech is not the same as articulating it, and the underlying neuronal infrastructure reflects just that.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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