



Common Brain Substrates Underlying Auditory Speech Priming and Perceived Spatial Separation

Junxian Wang^{1†}, Jing Chen^{2,3†}, Xiaodong Yang¹, Lei Liu¹, Chao Wu⁴, Lingxi Lu⁵, Liang Li^{1,3,6} and Yanhong Wu^{1,3*}

¹ School of Psychological and Cognitive Sciences and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, China, ² Department of Machine Intelligence, Peking University, Beijing, China, ³ Speech and Hearing Research Center, Key Laboratory on Machine Perception (Ministry of Education), Peking University, Beijing, China, ⁴ School of Nursing, Peking University, Beijing, China, ⁵ Center for the Cognitive Science of Language, Beijing Language and Culture University, Beijing, China, ⁶ Beijing Institute for Brain Disorders, Beijing, China

OPEN ACCESS

Edited by:

Howard Charles Nusbaum,
The University of Chicago,
United States

Reviewed by:

Xing Tian,
New York University Shanghai, China
Iiro P. Jääskeläinen,
Aalto University, Finland

*Correspondence:

Yanhong Wu
wuyh@pku.edu.cn

[†]These authors share first authorship

Specialty section:

This article was submitted to
Auditory Cognitive Neuroscience,
a section of the journal
Frontiers in Neuroscience

Received: 06 February 2021

Accepted: 10 May 2021

Published: 17 June 2021

Citation:

Wang J, Chen J, Yang X, Liu L,
Wu C, Lu L, Li L and Wu Y (2021)
Common Brain Substrates Underlying
Auditory Speech Priming
and Perceived Spatial Separation.
Front. Neurosci. 15:664985.
doi: 10.3389/fnins.2021.664985

Under a “cocktail party” environment, listeners can utilize prior knowledge of the content and voice of the target speech [i.e., auditory speech priming (ASP)] and perceived spatial separation to improve recognition of the target speech among masking speech. Previous studies suggest that these two unmasking cues are not processed independently. However, it is unclear whether the unmasking effects of these two cues are supported by common neural bases. In the current study, we aimed to first confirm that ASP and perceived spatial separation contribute to the improvement of speech recognition interactively in a multitalker condition and further investigate whether there exist intersectant brain substrates underlying both unmasking effects, by introducing these two unmasking cues in a unified paradigm and using functional magnetic resonance imaging. The results showed that neural activations by the unmasking effects of ASP and perceived separation partly overlapped in brain areas: the left pars triangularis (TrIFG) and orbitalis of the inferior frontal gyrus, left inferior parietal lobule, left supramarginal gyrus, and bilateral putamen, all of which are involved in the sensorimotor integration and the speech production. The activations of the left TrIFG were correlated with behavioral improvements caused by ASP and perceived separation. Meanwhile, ASP and perceived separation also enhanced the functional connectivity between the left IFG and brain areas related to the suppression of distractive speech signals: the anterior cingulate cortex and the left middle frontal gyrus, respectively. Therefore, these findings suggest that the motor representation of speech is important for both the unmasking effects of ASP and perceived separation and highlight the critical role of the left IFG in these unmasking effects in “cocktail party” environments.

Keywords: auditory speech priming, perceived spatial separation, speech recognition, speech motor system, common brain substrate, unmasking

Abbreviations: ACC, anterior cingulate cortex; ANSP, auditory non-speech priming; ASP, auditory speech priming; ASSN, amplitude-modulated speech-spectrum noise; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; MFG, middle frontal gyrus; nPS, ANSP and separation condition; nPC, ANSP and co-location condition; OrbIFG, pars orbitalis of IFG; PC, ASP and co-location condition; PS, ASP and separation condition; PPI, psychophysiological interaction; SMG, supramarginal gyrus; SMR, signal-to-masker ratio; TrIFG, par triangularis of IFG.

INTRODUCTION

How do our brains deal with a complex scene where listeners need to selectively detect, follow, and recognize a speaker's words (target) when multiple people are talking (masker) at the same time (i.e., the "cocktail party" problem) (Cherry, 1953; Schneider et al., 2007; McDermott, 2009; Bronkhorst, 2015)? Previous studies have shown that listeners can take advantage of diverse perceptual and/or cognitive cues, such as prior knowledge of the contents of the speech and/or the speaker's voice (Freyman et al., 2004; Yang et al., 2007), information obtained from lip reading (Wu et al., 2017b), and perceived spatial separation (Freyman et al., 1999), to improve their recognition of target speech masked by non-target sounds (i.e., release from masking or unmasking). In real-life conditions, these unmasking cues are not alone, and several cues belonging to an auditory object influence the perception at the same time. However, a majority of relevant studies usually focused on the cognitive and neural mechanisms of a single one among these unmasking cues (Zheng et al., 2016; Wu et al., 2017a,b), and very few have investigated dual unmasking cues that are closer to a real-life condition (Du et al., 2011; Lu et al., 2018). Therefore, this study employed two unmasking cues in a unified paradigm to investigate neural bases across different unmasking effects.

Among multiple unmasking cues, the prior knowledge of the content and voice of the target speech [i.e., auditory speech priming (ASP)] and perceived spatial separation are two typical and effective cues. The ASP refers to a segment of the target phrase spoken by the target speaker, which is presented without interferences before a target-masker mixture, and it can improve recognition of the last keyword in the target speech, even though the last keyword does not appear in the segment (Freyman et al., 2004; Wu et al., 2012a,b, 2017a). The perceived spatial separation represents spatially separating sound images of target speech from those of competing speech, which can cause even larger unmasking effect on speech recognition (Freyman et al., 1999, 2004; Li et al., 2004; Bronkhorst, 2015). Studies of patients with schizophrenia suggest that ASP and perceived separation share some common features. Even though patients with schizophrenia exhibit deficiencies in speech perception and increased vulnerability to masking stimuli, they retain the ability of using ASP and perceived separation to improve their recognition of the target speech masked by two-talker speech (Wu et al., 2012, 2017a). Similarly, despite age-related declines in hearing, older adults can utilize ASP and perceived separation to improve their recognition of the targets under a noisy environment just as well as do younger adults (Li et al., 2004; Ezzatian et al., 2011). These studies propose that certain top-down auditory mechanisms underlying the unmasking effects of ASP and perceived separation are preserved in patients with schizophrenia and older adults (Li et al., 2004; Ezzatian et al., 2011; Wu et al., 2012, 2017a). Researchers have claimed that the ASP helps listeners maintain the target's voice and content in working memory and may facilitate grouping the target speech to enhance the listener's selective attention to the target (Freyman et al., 2004; Schneider et al., 2007; McDermott, 2009; Ezzatian et al., 2011; Wu et al., 2012a,b; Carlile, 2015; Wang et al., 2019).

The perceived separation mainly works via the head-shadowing effect increasing the signal-to-masker ratio (SMR) in the ear close to the target, and/or the neurophysiological effect of disparity in interaural time between targets and maskers, both of which enhance selective attention to the target speech (Freyman et al., 1999; Li et al., 2004). Accordingly, the unmasking effects of ASP and perceived separation may both contribute to the high-level processing, such as enhanced selective attention to the target speech. Moreover, the selective attention might allocate more cognitive resources to the motor representation of speech that is beneficial for speech recognition under "cocktail party" listening conditions (Wu et al., 2014). The intersecting processing of the unmasking effects induced by ASP and perceived separation is predicted to occur in the high-level processing.

Previous studies have no consensus on whether two unmasking cues are processed independently or interdependently. If an additive effect was observed, i.e., the combined effect of two cues is equivalent to the sum of their individual effects, researchers conclude that these two cues are processed independently in separate brain regions (Bronkhorst, 2015). Otherwise, the non-additive effect indicates intersecting processing of these cues in overlapping brain regions. Studies have shown varied additives of two cues; for instance, Du et al. (2011) found an additive effect of the differences in fundamental frequency and spatial location during speech segregation. Lu et al. (2018) found an additive effect of emotional learning (of the target voice) and perceived separation on improving speech recognition. Despite this, Darwin et al. (2003) found that the effect of the differences in fundamental frequency and vocal-tract length is larger than the sum of their individual effects during speech recognition. Freyman et al. (2004) found that the benefit of ASP was more significant when the target and maskers were perceived to be co-located than when they were perceived to be separated, indicating the non-additive effect of ASP and perceived separation. These suggest that the combinations of different cues result in varied additive effects. In the case of ASP and perceived separation, their benefits to speech recognition cannot be added, suggesting the existence of intersections of their neural underpinnings. The present study aims to investigate how ASP and perceived separation improve the recognition of the target speech in a complex scene and reveal the neural bases underlying their unmasking effects.

Despite a lack of studies on neural mechanisms underlying dual unmasking effects, some researchers have separately investigated neural bases of the unmasking effects of ASP and perceived spatial separation. They have found that ASP and perceived separation mainly activated the ventral and dorsal pathways in the auditory system, respectively. Notably, both of them activate the left inferior frontal gyrus (IFG) (Zheng et al., 2016; Wu et al., 2017a). In addition, ASP and perceived separation both enhance the functional connectivity between the IFG and specific brain substrates, such as the left superior temporal gyrus and left posterior middle temporal gyrus for the ASP, and the superior parietal lobule for the perceived separation (Zheng et al., 2016; Wu et al., 2017a). This suggests that the speech motor system, especially the IFG (Du et al., 2014), may be the common brain area that is activated by both the

unmasking effects of ASP and perceived separation. The left IFG is thought to be the speech-related area involved in both speech production and perception (Hickok and Poeppel, 2004; Liakakis et al., 2011). It exchanges information with other brain substrates located in the ventral and dorsal pathways in the auditory system (Friederici, 2012), and it is involved in unification operations during speech comprehension (Acheson and Hagoort, 2013). Moreover, the par triangularis of the IFG (TriIFG) is a junction in the IFG (Friederici, 2012; Frühholz and Grandjean, 2013). A dual stream model for auditory processing suggests that auditory information transferred via both ventral and dorsal streams terminates in the TriIFG (Frühholz and Grandjean, 2013). The TriIFG is thought to be the main locus of speech intelligibility in the IFG (Abrams et al., 2013), and it is especially important in the retrieval or selection of semantic information under adverse listening conditions (Skipper et al., 2007). The present study predicts that the speech motor system plays a critical role in the unmasking effects of ASP and perceived separation. In particular, the TriIFG is the interested brain substrate, and it is predicted to correlate with recognition accuracy of the target speech in a multitalker condition.

In summary, previous studies inconsistently suggest the existence of intersecting processing of dual unmasking cues. In the present study, we introduced ASP and perceived spatial separation in a “cocktail party” listening condition and combined them in a unified paradigm. We aim to first verify that the unmasking effects of ASP and perceived separation are not processed independently and further investigate the existence of their common neural bases, by using functional magnetic resonance imaging (fMRI). The existence of overlapping brain substrates is thought to be a primary investigation of the commonality of neural mechanisms underlying two unmasking effects. In the light of past results, we hypothesized that the unmasking effects of ASP and perceived separation intersect in the high-level processing, and the left IFG is the shared brain substrate critically involved in these unmasking effects.

MATERIALS AND METHODS

Participants

Thirty-six participants (21 females, 15 males; mean age = 22.06 years, SD = 1.94 years; $Min_{age} = 19$ years, $Max_{age} = 27$ years) took part in the behavioral testing, and 27 of them (15 females, 12 males; mean age = 22 years, SD = 1.94 years; $Min_{age} = 19$ years, $Max_{age} = 27$ years) voluntarily participated in the follow-up fMRI testing. All participants were right-handed university students who spoke Mandarin. All of them had normal pure-tone hearing thresholds (≤ 25 dB HL) in each ear and had bilaterally symmetric hearing (≤ 15 dB HL). The hearing thresholds were measured by an audiometer (Aurical, 60645-1, Denmark) at frequencies of 125, 250, 500, 1,000, 2,000, 4,000, 6,000, and 8,000 Hz for 22 participants. The hearing thresholds of the remaining participants were measured by Apple iOS-based automated audiometry (Xing et al., 2016) at frequencies of 250, 500, 1,000, 2,000, 3,000, 4,000, 6,000, and 8,000 Hz in a sound booth. All participants gave their

informed consent before the experiment and received a certain monetary compensation. The experimental procedures were approved by the Committee for Protecting Human and Animal Subjects in the School of Psychological and Cognitive Sciences, Peking University.

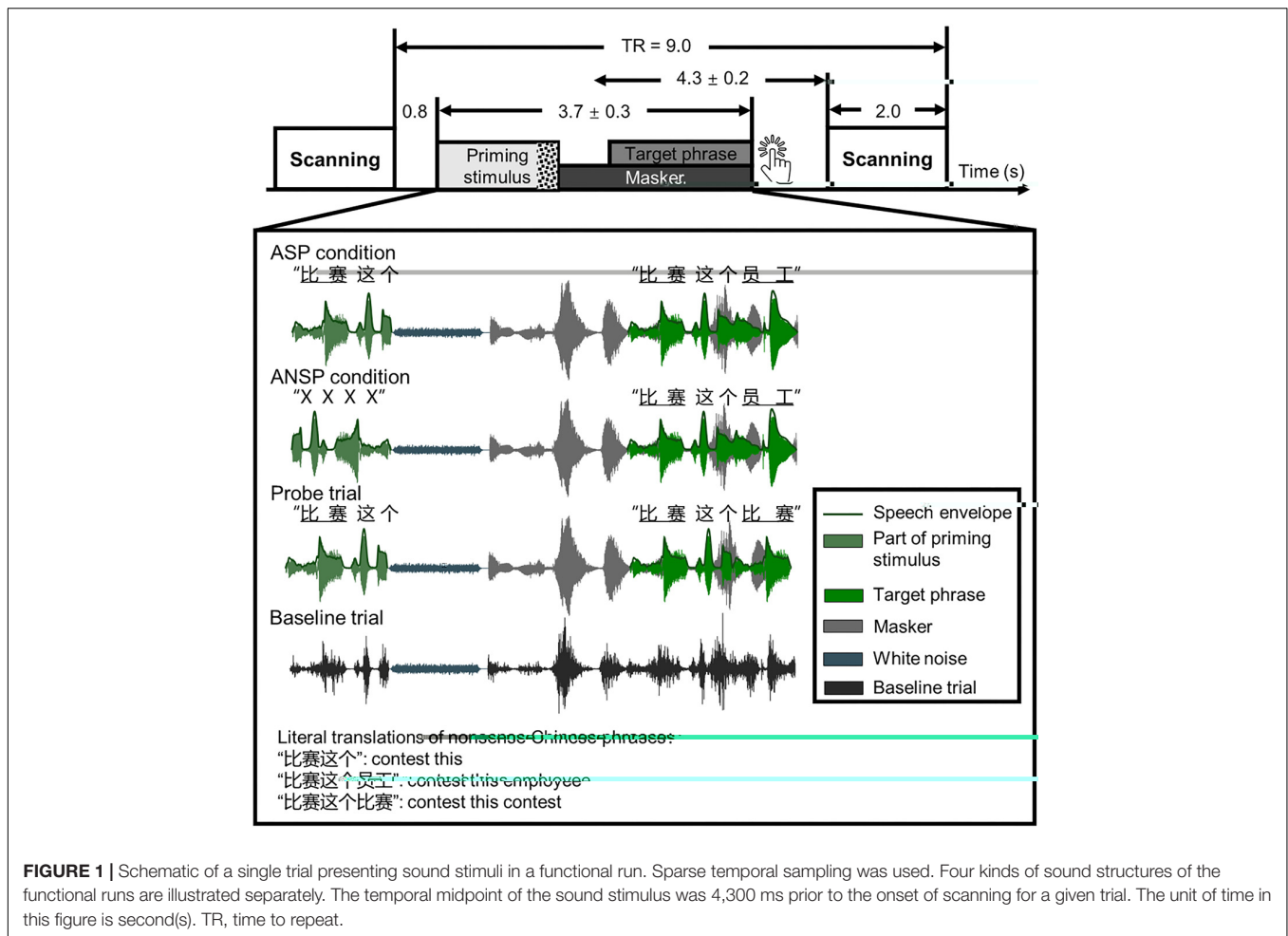
Stimuli and Procedures

The mean duration of a sound stimulus was $3,711 \pm 341$ ms. Each speech stimulus comprised three parts: a priming stimulus [of the ASP condition or auditory non-speech priming (ANSP) condition], a target phrase, and a two-talker speech masker. It started with a priming stimulus, following which a target phrase mixed with a two-talker speech masker was presented. The speech stimuli were processed by head-related transfer functions (Qu et al., 2009) to simulate sounds from one of three azimuth angles (i.e., -90° , 0° , 90°) 30 cm from the center of the listeners' heads in the horizontal plane. The target phrases and the two-talker speech masker were “non-sense” sentences in Chinese that were syntactically, but not semantically, correct. The target phrases, spoken by a young female (talker A), were three-word phrases. Each word of the target phrase contained two syllables. For example, one target phrase translated into English was “contest this employee” (keywords are underlined). The structure of these target phrases did not support any context for recognizing the keywords. There was no overlap in target phrases between behavioral and fMRI tests for each participant. In the fMRI testing, we used a minority of response trials as probes to monitor whether participants were doing a speech-recognition task. Target phrases of these response trials were modified by substituting the last keyword of the original target phrase with the first keyword of it, so that the first and the last keywords were identical.

Considering that the benefits of ASP and perceived separation are more significant when masked by the two-talker speech masker than other types of maskers (Freyman et al., 2004; Lu et al., 2018), we used the two-talker speech masker as the distractive sounds. The masker was a 47-s loop of a digitally combined continuous recording of Chinese non-sense sentences spoken by two young females (talkers B and C). No keyword in the speech masker appeared in target phrases. In the behavioral testing, the sound pressure level of the target phrases was fixed at 56 dBA SPL, and the sound levels of the maskers were adjusted to produce four SMRs: -12 , -8 , -4 , and 0 dB. In the fMRI testing, the SMR was fixed at -4 dB (Wu et al., 2017a,b). All sound pressure levels were measured by an Audiometer Calibration and Electroacoustic Testing System (AUDit and System 824; Larson Davis, Provo, UT, United States). The SMRs were calibrated before applying the head-related transfer function.

The priming stimuli were manipulated differently in the ASP and the ANSP conditions (see the illustration in **Figure 1**). In the ASP condition, a priming stimulus was identical to a target phrase except that the last keyword of the target was replaced by a piece of white noise. The duration of the white noise matched that of the longest last keyword across all target phrases. The sound pressure level of the white noise was 10 dB lower than that of the corresponding target phrase (following Freyman et al., 2004) to ensure its perceived loudness being consistent. In the ANSP

condition, a priming stimulus was produced as follows: The target



Random-Effects Analysis and *Post hoc* Tests

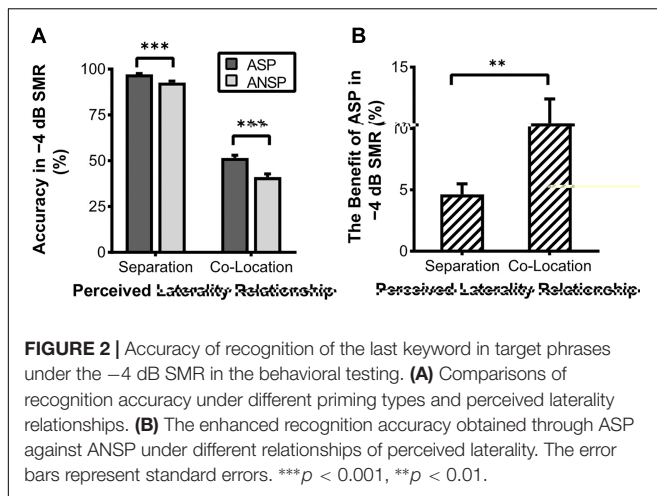
The first-level general linear model for each participant contained seven regressors in total: five for the listening conditions (PS, PC, nPS, nPC, and baseline), one for blank trials, and one for uninteresting/irrelevant response trials. Six realignment parameters of head movements were entered to account for residual movement-related effects. The blood oxygenation level-dependent response for each event was modeled using the canonical hemodynamic response function. Contrast images of “PS > baseline,” “PC > baseline,” “nPS > baseline,” and “nPC > baseline” for each participant, were entered into a 2 (priming type: ASP, ANSP) × 2 (perceived laterality relationship: separation, co-location) repeated-measure analysis of variance (ANOVA). Only clusters passing the cluster-level family wise error correction for multiple comparisons (we set at FWE corrected cluster-level threshold of $p_{FWE} < 0.05$) were entered into the *post hoc* tests. To identify the causes of main effects, *post hoc* paired-samples *t* tests were conducted by inclusively masking specific *t*-contrast images with the corresponding *F* contrasts ($p < 0.001$ at the voxel level, uncorrected). We calculated the ASP effect (i.e., “ASP > ANSP” contrast) by the formula $(PS + PC) > (nPS + nPC)$ and the spatial unmasking effect (i.e., “perceived separation > perceived co-location”

contrast) by the formula $(PS + nPS) > (PC + nPC)$. Moreover, referring to the method in Wild et al. (2012a), we calculated the logical intersections of clusters activated by both the ASP effect and the spatial unmasking effect. Overlapping clusters containing more than 10 voxels were reported and used as regions of interest for behavioral–neural correlation analyses.

Correlation Analysis

To identify the correlation between brain activations and behavioral improvements by the ASP effect and the spatial unmasking effect, we conducted Spearman correlation analyses by using the IBM SPSS.20 software. As we have introduced in the *Introduction*, the left TriIFG is important in semantic processing of speech under adverse listening conditions. We used the left TriIFG that was activated by both unmasking effects as the region of interest in the correlation analyses and extracted contrast values within this overlapping cluster by the MarsBar toolbox (version 0.44²). The correlations for four contrasts (i.e., “PS > nPS,” “PC > nPC,” “PS > PC,” and “nPS > nPC”) were examined by using corresponding contrast values and behavioral improvements at the -4 dB SMR.

²<http://marsbar.sourceforge.net/>



Psychophysiological Interaction Analysis

We conducted generalized form of context-dependent psychophysiological interaction (PPI) analyses (McLaren et al., 2012) to identify brain regions showing significant functional connectivity with the brain substrates of interest (i.e., the left IFG), by using the gPPI Toolbox (version 7.12³, based on SPM8). Each seed region was defined as a sphere with a 6-mm radius centered at the peak voxel. The first-level generalized PPI model contained all regressors in a first-level general linear model, additional PPI regressors (for the PS, PC, nPS, and nPC conditions, noise baseline trials, blank trials, and response trials), time courses of the seed region, and a constant (McLaren et al., 2012). Single-participant contrast images (“PS > nPS,” “PC > nPC,” “PS > PC,” and “nPS > nPC” contrasts) of the first-level generalized PPI model were subjected to second-level one-sample t tests to identify brain regions showing increased coactivation with the seed region due to corresponding contrasts. The level of significance was set at $p < 0.001$ uncorrected with an extent threshold with minimum cluster size of 20 voxels (Wandschneider et al., 2014).

Behavioral Testing

Behavioral testing was conducted before the fMRI testing, and it featured three intraparticipant variables: (1) priming type (ASP, ANSP), (2) perceived laterality relationship (separation, co-location), and (3) SMR (-12, -8, -4, 0 dB). Variables for the priming type and perceived laterality relationship were the same as in the fMRI testing.

In each trial, a speech stimulus started with a priming stimulus, following which a target phrase mixed with a two-talker speech masker was presented. The onset of the target phrase was $1,000 \pm 200$ ms later than that of the masker, and they were terminated simultaneously. Participants started each trial by themselves, and they were instructed to verbally repeat the entire target phrase as much as possible when the sounds ended in each trial. The experimenter scored and calculated the number of correctly recognized syllables of the last keywords (participants

were not aware that only the last keywords were scored). Each syllable of the last keyword was counted as one point. Before the formal testing, a training session was conducted to ensure that participants had understood the task of the behavioral testing.

Four combinations of priming types and perceived laterality relationships were assigned to four blocks, and their orders of presentation were counterbalanced across participants by using the Latin square order. The four SMRs were randomly ordered in each block. For each participant, 12 trials (12 target phrases) were conducted for each of 16 conditions. Sounds were binaurally presented to participants via the headphones (HD 650, Sennheiser electronic GmbH & Co., KG, Germany), driven by Presentation software (version 0.70).

RESULTS

Behavioral Improvements Due to ASP and Perceived Spatial Separation

In the behavioral testing, the 2 (priming type: ASP, ANSP) \times 2 (perceived laterality relationship: separation, co-location) \times 4 (SMR: -12, -8, -4, 0 dB) repeated-measured ANOVA showed significant main effects of priming type ($F_{1, 35} = 34.98$, $p < 0.001$, $\eta_p^2 = 0.50$), perceived laterality relationship ($F_{1, 35} = 2,539.91$, $p < 0.001$, $\eta_p^2 = 0.99$), and SMR ($F_{3, 105} = 1,127.50$, $p < 0.001$, $\eta_p^2 = 0.97$). Their interaction was also significant ($F_{3, 105} = 7.33$, $p < 0.001$, $\eta_p^2 = 0.17$). Simple-effect analyses (Bonferroni-corrected) showed that the ASP effect was not consistently significant between the two perceived laterality relationships (detailed results are provided in **Supplementary Table 1**). Only when the SMR was -4 dB did the ASP contrast to ANSP improve the recognition of the target under both the perceived separation (PS: 0.97 ± 0.02 , nPS: 0.93 ± 0.05 , $F_{1, 35} = 29.05$, $p < 0.001$) and the perceived co-location (PC: 0.51 ± 0.09 , nPC: 0.41 ± 0.10 , $F_{1, 35} = 27.44$, $p < 0.001$) conditions (see **Figure 2A**). In the -4 dB SMR, the benefits of ASP (recognition accuracy of ASP minus that of ANSP) between the two perceived laterality relationships were compared by paired-sample t tests. The results showed that the benefit of ASP under the perceived co-location condition (i.e., recognition accuracy of PC minus that of nPC; the benefit of ASP: 0.10 ± 0.12) was greater than that under the perceived separation condition (i.e., recognition accuracy of PS minus nPS; the benefit of ASP: 0.05 ± 0.05) ($t_{35} = 3$, $p = 0.005$, see **Figure 2B**). These results indicate that the unmasking effect of ASP decreases when the perceived spatial separation helps improve the recognition of the target speech.

Brain Regions Activated by ASP and Perceived Spatial Separation

A 2 (priming type: ASP, ANSP) \times 2 (perceived laterality relationship: separation, co-location) repeated-measured ANOVA was conducted, and no suprathreshold cluster was activated by the interaction. We marked out clusters activated by the ASP effect (i.e., “ASP > ANSP”) from these by the main effect of priming type, using a voxel-wise threshold of

³<http://www.nitrc.org/projects/gppi/>

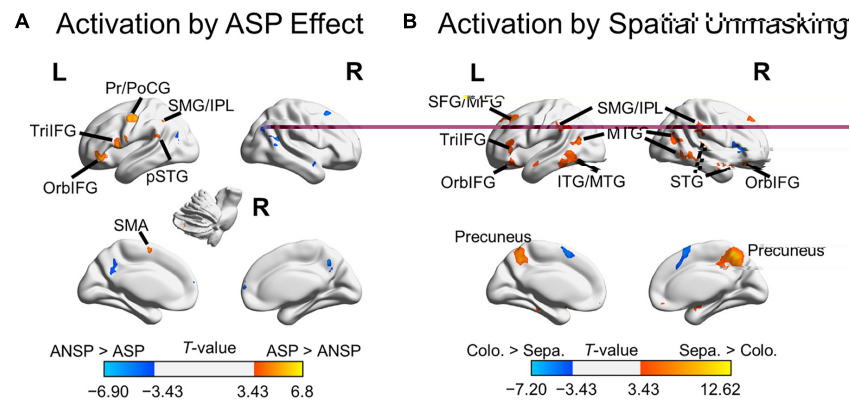


FIGURE 3 | Areas of the brain activated by the ASP effect and spatial unmasking effect. **(A)** Clusters activated by the "ASP > ANSP" contrast (i.e., the ASP effect, the warm color) and by the "ANSP > ASP" contrast (the cold color). **(B)** Clusters activated by the "perceived separation > perceived co-location" contrast (i.e., spatial unmasking effect, the warm color) and by the "perceived co-location > perceived separation" contrast (the cold color). ITG, inferior temporal gyrus; MTG, middle temporal gyrus; PrCG, precentral gyrus; PoCG, postcentral gyrus; SFG, superior frontal gyrus; SMA, supplementary motor area; STG, superior temporal gyrus; pSTG, posterior STG. L, left; R, right.

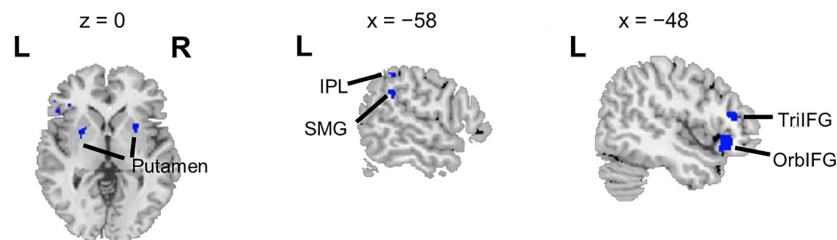


FIGURE 4 | Overlapping brain areas activated by both the ASP effect and the spatial unmasking effect. L, left; R, right. Negative values of the x axis (the coronal axis) denote the left hemisphere. The variable z denotes the vertical axis.

$p < 0.001$, uncorrected (clusters activated by the main effect of priming type are in both warm and cold colors in **Figure 3A**). The ASP effect activated the left motor cortex, left IFG, left posterior superior temporal gyrus, left inferior parietal region, bilateral putamen, and the right cerebellum (as shown in warm color clusters in **Figure 3A**). Meanwhile, we marked out clusters activated by the spatial unmasking effect (i.e., "perceived separation > perceived co-location") from these by the main effect of perceived laterality relationship, using a voxel-wise threshold of $p < 0.001$, uncorrected (clusters activated by the main effect of perceived laterality relationship are in both warm and cold colors in **Figure 3B**). The spatial unmasking effect activated the bilateral precuneus, bilateral IFG, bilateral middle temporal gyrus, bilateral superior frontal gyrus extending into middle frontal gyrus (MFG), bilateral inferior parietal region, bilateral superior temporal gyrus, and bilateral putamen (as shown in warm color clusters in **Figure 3B**). The detailed results are also shown in **Supplementary Table 2**.

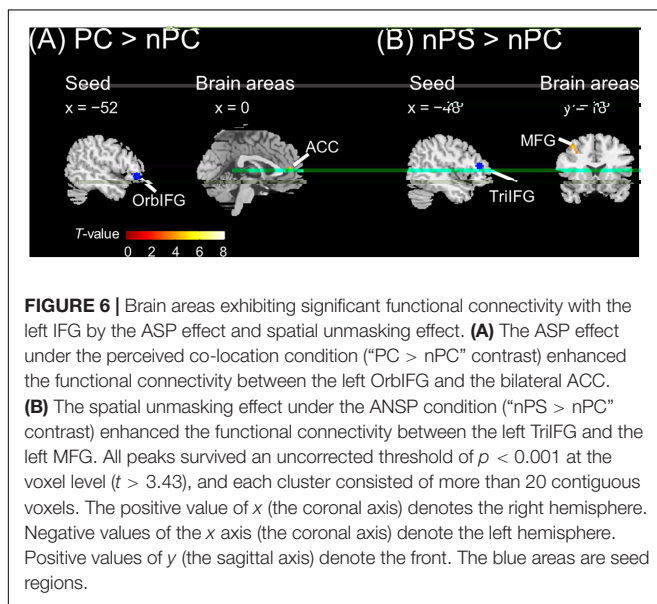
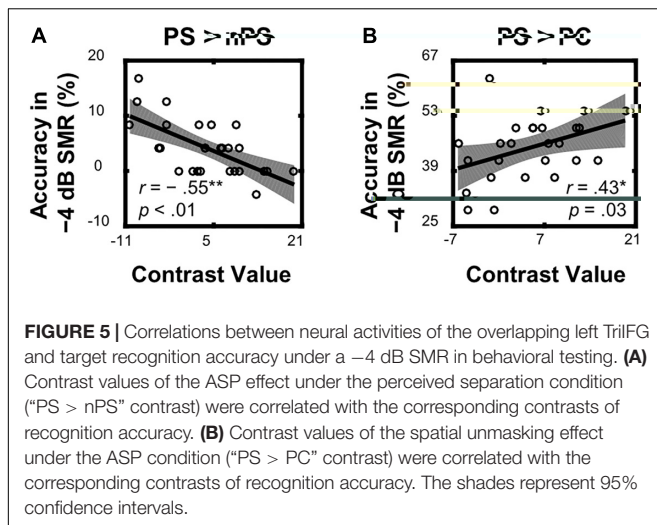
Overlapping brain areas activated by both the ASP effect and the spatial unmasking effect were the bilateral putamen, left inferior parietal lobule (IPL), left supramarginal gyrus (SMG), left pars orbitalis of the IFG (OrbIFG), and left TriIFG (**Figure 4**), revealing shared neural bases of the unmasking effects of ASP and perceived separation.

Correlations Between Brain Activation and Behavioral Improvement Due to ASP and Perceived Spatial Separation

Within the left TriIFG, the overlapping brain area activated by both the ASP effect and the spatial unmasking effect, the Spearman correlation analyses showed that contrast values for the ASP effect under the perceived separation condition (i.e., "PS > nPS" contrast) were significantly correlated with behavioral improvements for the corresponding contrast ($r = -0.55$, $p < 0.01$, **Figure 5A**), and contrast values for the spatial unmasking effect under the ASP condition (i.e., "PS > PC" contrasts) were also significantly correlated with behavioral improvements for the corresponding contrast (PS > PC: $r = 0.43$, $p = 0.03$, **Figure 5B**). The sizes of these correlations were moderate. No significant correlation was observed for the ASP effect under the perceived co-location condition (i.e., "PC > nPC" contrast) or the spatial unmasking effect under the ANSP condition (i.e., "nPS > nPC" contrast).

Enhanced Functional Connectivity Due to ASP and Perceived Spatial Separation

The seed regions were located in the left IFG. As shown in **Figure 6A** and **Table 1**, the ASP effect under the perceived



co-location condition (i.e., “PC > nPC” contrast) enhanced the functional connectivity of the left OrbIFG [the seed locus at $(-52, 38, -6)$] with the bilateral anterior cingulate cortex (ACC). Meanwhile, the spatial unmasking effect under the ANSP condition (i.e., “nPS > nPC” contrast) enhanced the functional connectivity of the left TriIFG [the seed locus at $(-48, 36, 14)$] with the left MFG (**Figure 6B** and **Table 1**). Clusters that survived an uncorrected threshold of $p < 0.001$ at the voxel level with more than 20 contiguous voxels are reported.

DISCUSSION

In the present study, we introduced ASP and perceived spatial separation to investigate how they improve recognition of the target speech in a “cocktail party” environment. The behavioral results showed that the benefits of ASP and perceived separation for speech recognition cannot be added. Neuroimaging results

showed that neural underpinnings underlying the unmasking effects of ASP and perceived separation partly overlapped in brain areas related to the speech motor system, especially in the left IFG. These findings suggest the intersection of neural bases underlying two unmasking effects.

The behavioral results were consistent with previous findings that recognizing the target speech masked by two-talker speech can be improved by the prior knowledge of an early segment of the target speech and the perceived spatial separation (Freyman et al., 1999, 2004; Li et al., 2004; Wu et al., 2005, 2012, 2017a; Yang et al., 2007; Ezzatian et al., 2011; Zheng et al., 2016). Moreover, even though ASP improved the speech recognition in two perceived laterality relationships under a moderate degree of masking (such as the -4 dB in this study), the benefit of ASP was more significant when the maskers were perceived to be co-located with the target than when they were perceived to be separated from the target (Freyman et al., 2004). That is, we observed the non-additive benefits of ASP and perceived separation to speech recognition. Considering the additive effect of two cues suggesting independent processing of them (Du et al., 2011; Bronkhorst, 2015; Lu et al., 2018), the behavioral results suggest intersecting processing of ASP and perceived spatial separation.

The above inference is supported by remarkable neuroimaging results, which showed overlaps in neural underpinnings underlying the unmasking effects of ASP and perceived spatial separation. These intersectant brain areas included bilateral putamen, left IPL, left SMG, left OrbIFG, and left TriIFG. The common feature of these brain substrates is their involvement in the speech motor representation (for putamen, Abutalebi et al., 2013; for SMG, Deschamps et al., 2014; for IPL, Hickok and Poeppel, 2000; Shum et al., 2011; for IFG, Klaus and Hartwigsen, 2019), indicating a notable and common role of the speech motor representation for different unmasking effects in a noisy environment. This finding is in accordance with the idea that the auditory-to-motor transformation is important for speech perception in challenging listening situations (Price, 2010; D’Ausilio et al., 2012; Wu et al., 2014) and suggests that the enhancement of the speech motor representation is possibly the common neural mechanism underlying both the unmasking effects of ASP and perceived separation in a multitalker condition. Specifically, the inferior parietal region, containing the IPL and the SMG, is an important component of the network for the sensorimotor integration of speech. The sensorimotor integration is likely to be an emulation process for speech perception in challenging scenarios (Nuttall et al., 2016). It is assumed that covert emulation is processed in parallel with external events through the generation of top-down predictions of ongoing listening events, and perceptual processing is modulated by the feedback generated by these predictions (Wilson and Knoblich, 2005; Hickok et al., 2011; Nuttall et al., 2016). Interestingly, previous studies have discovered mirror neurons in the IPL and the left IFG, even though these studies focused on how actions are processed (Fogassi et al., 2005; Chong et al., 2008; Kilner et al., 2009). In consideration of the roles of IPL and IFG in this study, it can be proposed that the assumed perceptual emulator beneficial for challenging speech perception

TABLE 1 | Areas of the brain exhibiting significant functional connectivity associated with the ASP effect under the perceived co-location condition ("PC > nPC" contrast) and with the spatial unmasking effect under the ANSP condition ("nPS > nPC" contrast).

Contrast	Seed	MNI coordinates (mm)			Statistics				Location
		x	y	z	k	t	z value	p _{unc}	
PC > nPC	L. OrbIFG	-2	48	10	26	5.24	4.29	9.02E-06	L. ACC
nPS > nPC	L. TrilIFG	-38	18	48	66	4.98	4.14	1.77E-05	L. MFG
		-34	20	38					

The activation reported here survived an uncorrected threshold of $p < 0.001$ at the voxel level ($t > 3.43$), and the clusters consisted of more than 20 contiguous voxels. The MNI coordinates, k (the number of voxels), t value, z score, and uncorrected p values are provided. L, left.

(Wilson and Knoblich, 2005) may be also in these two areas. In short, the involvement of inferior parietal region (i.e., the IPL and the SMG) in both the unmasking effects of ASP and perceived separation suggests that the two unmasking cues might improve

Freyman, R. L., Helfer, K. S., McCall, D. D., and Clifton, R. K. (1999). The role of perceived spatial separation in the unmasking of speech.

- Wu, C. T., Weissman, D. H., Roberts, K. C., and Woldorff, M. G. (2007). The neural circuitry underlying the executive control of auditory spatial attention. *Brain Res.* 1134, 187–198. doi: 10.1016/j.brainres.2006.11.088
- Wu, M., Li, H., Gao, Y., Lei, M., Teng, X., Wu, X., et al. (2012a). Adding irrelevant information to the content prime reduces the prime-induced unmasking effect on speech recognition. *Hear. Res.* 283, 136–143. doi: 10.1016/j.heares.2011.11.001
- Wu, M., Li, H., Hong, Z., Xian, X., Li, J., Wu, X., et al. (2012b). Effects of aging on the ability to benefit from prior knowledge of message content in masked speech recognition. *Speech Commun.* 54, 529–542. doi: 10.1016/j.specom.2011.11.003
- Wu, X., Wang, C., Chen, J., Qu, H., and Li, W. (2005). The effect of perceived spatial separation on informational masking of Chinese speech. *Hear. Res.* 199, 1–10. doi: 10.1016/j.heares.2004.03.010
- Wu, Z. M., Chen, M. L., Wu, X. H., and Li, L. (2014). Interaction between auditory and motor systems in speech perception. *Neurosci. Bull.* 30, 490–496. doi: 10.1007/s12264-013-1428-6
- Xing, Y., Fu, Z., Wu, X., and Chen, J. (2016). "Evaluation of Apple iOS-based automated audiometry." In *Proceedings of the 22nd International Congress on Acoustics*, (Rome: ICA).
- Yang, Z., Chen, J., Huang, Q., Wu, X., Wu, Y., Schneider, B. A., et al. (2007). The effect of voice cuing on releasing Chinese speech from informational masking. *Speech Commun.* 49, 892–904. doi: 10.1016/j.specom.2007.05.005
- Zheng, Y., Wu, C., Li, J., Wu, H., She, S., Liu, S., et al. (2016). Brain substrates of perceived spatial separation between speech sources under simulated reverberant listening conditions in schizophrenia. *Psychol. Med.* 46, 477–491. doi: 10.1017/S0033291715001828
- Zündorf, I. C., Lewald, J., and Karnath, H. O. (2013). Neural correlates of sound localization in complex acoustic environments. *PLoS One* 8:e64259. doi: 10.1371/journal.pone.0064259

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2021 Wang, Chen, Yang, Liu, Wu, Lu, Li and Wu. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.