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Spontaneous gesture and spatial language: Evidence from focal brain injury

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ABSTRACT

People often use spontaneous gestures when communicating spatial information. We investigated focal brain-injured individuals to test the hypotheses that (1) naming motion event components of manner-path (represented by verbs–prepositions in English) are impaired selectively, (2) gestures compensate for impaired naming. Patients with left or right hemisphere damage (LHD or RHD) and elderly control participants were asked to describe motion events (e.g., *running across*) depicted in brief videos. Damage to the left posterior middle frontal gyrus, left inferior frontal gyrus, and left anterior superior temporal gyrus (aSTG) produced impairments in naming paths of motion; lesions to the left caudate and adjacent white matter produced impairments in naming manners of motion. While the frequency of spontaneous gestures were low, lesions to the left aSTG significantly correlated with greater production of path gestures. These suggest that producing prepositions–verbs can be separately impaired and gesture production compensates for naming impairments when damage involves left aSTG.

1. Introduction

How do we communicate spatial information using language? What neural structures implement this type of information? We use spatial language, such as prepositions and action verbs, to describe spatial events in our environment and organize relational thinking (Chatterjee, 2001, 2008). People also use hand gestures spontaneously when they talk. Gestures, particularly *iconic* gestures are used commonly when individuals express spatial information such as giving directions or describing motion in space. These spontaneous co-speech iconic gestures that accompany verbal spatial information (Alibali, 2005) are the focus of this study.

There is growing interest in understanding the neural underpinnings of spatial language (e.g., Amorapanth, Widick, & Chatterjee, 2009; Chatterjee, 2008; Damasio et al., 2001; Kemmerer, 2006) and gesture comprehension (e.g., Dick, Goldin-Meadow, Hasson, Skipper, & Small, 2009; Dick, Goldin-Meadow, Solodkin, & Small, 2012; Holle, Gunter, Rueschemeyer, Hennenlotter, & Iacoboni, 2008; Skipper, Goldin-Meadow, Nusbaum, & Small, 2009; Willems & Hagoort, 2007; Willems, Özyürek, & Hagoort, 2007). However, little is known about the neural correlates of spontaneous gestures that naturally accompany spatial language production (but see recent papers by Marstaller & Burianova, 2015a, 2015b; Marstaller et al., 2015). In this study we test two main hypotheses. First, if spatial representations and lexical–semantic spatial information are organized similarly in the brain (Chatterjee, 2008), patients with focal brain injury to left frontal-parietal regions, known to process spatial information (e.g., Göksun, Lehet, Malykhina, & Chatterjee, 2013; Kemmerer, 2006; Kemmerer & Tranel, 2003), would have difficulty verbally describing spatial events. Second, if spatial language and spatial gestures rely on the same neural structures, then damage to areas needed for spatial language would also impair gesturing spatial events. That is, deficits of spatial knowledge would lead to deficits in both verbally and gesturally expressing spatial information. Alternatively, if spatial gestures compensate for verbal deficits without being reliant on the same neural structures, deficits in spatial language would result in a greater use of gestures.

A dynamic spatial event consists of several components that are encoded across world's languages (Talmy, 2000). The *path* and *manner* of motion describe two of these components. *Path* refers to a figure's trajectory relative to ground and *manner* refers to how the action is performed. That is, the path of motion describes an "extrinsic dynamic relation" of the movement of a figure

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relative to external landmarks and the manner of motion describes an "intrinsic dynamic relation" of the movement of figure parts relative to each other (Chatterjee, 2008). For example, in the sentence "*John is running into the room*," *running* describes the manner and *into the room* describes the path of the motion. In English, manner of motion is expressed typically by the main verb of a sentence whereas path of motion is expressed by a prepositional phrase.

In the following sections we first review the current understanding of the neural basis of spatial language, centering on dynamic spatial events. Then we discuss the relation between speech and gesture with respect to motion events before presenting the current study.

1.1. The neural correlates of spatial language: Motion events

Attention to path and manner of motion activates different neural networks (Wu, Morganti, & Chatterjee, 2008) as we demonstrated in a one-back matching task using a computer animated starfish moving with different manners and paths. In some blocks, participants attended to manner and in others to path. Within regions sensitive to motion, dorsal areas (i.e., bilateral posterior parietal and frontal areas) were preferentially activated in path conditions and relatively ventral areas (i.e., bilateral posterior inferior/middle temporal cortex) were preferentially activated in manner conditions.

The neural parsing of attention to these perceptual components of dynamic events parallels the linguistic parsing of path and manner represented by prepositions and verbs. Comprehending verbs correlates with activation in the posterior middle temporal gyrus (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002; Kemmerer et al., 2008) whereas comprehending prepositions correlates with activation in the left posterior inferior parietal and prefrontal cortices (Amorapanth et al., 2009; Baciu et al., 1999; Noordzij, Neggers, Ramsey, & Postma, 2008). Neuropsychological and other imaging studies confirm the role of these areas and anatomic division of processing verbs and prepositions (Amorapanth et al., 2009; Damasio et al., 2001; Emmorey et al., 2002; Kemmerer, 2006; Göksun et al., 2013; Kemmerer, 2006; Kemmerer & Tranel, 2003; Kemmerer et al., 2012; MacSweeney et al., 2002; Tranel & Kemmerer, 2004; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003; Tranel, Manzel, Asp, & Kemmerer, 2008).

Together, these findings are consistent with Chatterjee's (2008) suggestion that spatial perception and language have an analogous organizational structure within the brain. That is, the left hemisphere contains a perceptual to verbal gradient, in which perceptual nodes serve as points of entry for their lexical correspondences that are shifted toward peri-Sylvian cortex (Chatterjee, 2008).

Here we examine the neural segregation of path and manner of motion by testing focal brain injured individuals' production of motion event sentences using voxel-based lesion symptom mapping (VLSM) analysis. In VLSM patients are not classified based on lesion site, clinical diagnosis or behavioral performance. The inferential strengths of lesion methods offer an important constraint on neural hypotheses generated by functional neuroimaging methods (Chatterjee, 2005; Fellows et al., 2005).

1.2. Gesture as a compensatory strategy for impaired speech

Speech and gesture form a tightly integrated communication system; either part of one system or two highly interrelated systems (Alibali, Kita, & Young, 2000; Goldin-Meadow, 2003; Kita & Özyürek, 2003; McNeill, 1992; McNeill, 2005; for opposing views see Krauss, Chen, & Gottesman, 2000). Although most theories agree that spontaneous gesture production relates to speech production, the proposed nature of this relationship differs (e.g., Alibali, 2005; Butterworth & Hadar, 1989; De Ruiter, 2007; Hostetter & Alibali, 2008; Kita, 2000; Kita & Özyürek, 2003; McNeill, 1992, 2005). Some argue that speech and gesture originate from the same representational system, in which gesture carries a global-synthetic image of an utterance and speech carries the linear-segmented hierarchical linguistic structure of an utterance (McNeill, 1992, 2005) or that gestures are generated during subprocesses of speech production (Butterworth & Hadar, 1989).

Others claim that speech and gesture are generated by two separate but interrelated systems (e.g., Alibali et al., 2000; Kita, 2000; Kita & Özyürek, 2003; Krauss et al., 2000). For example, Krauss' *Lexical Gesture Process Model* proposes that gestures are generated from spatial imagery in working memory. These gestures prime lexical items, increase their activation, and facilitate their access to speech (Krauss et al., 2000). In this model, gestures are formed before speech processes occur. Another view, the *Interface Model* suggests that speech and gesture are generated by two separate, but bidirectionally related systems. A message generator plans speech whereas an action generator plans gesture, originating from an interface representation between spatial thinking and speech (Kita & Özyürek, 2003). This model is also compatible with the *information-packaging hypothesis,* which argues that gestures help speakers to organize and package spatial information into units that are compatible with the speech (Kita, 2000).

Evidence for the Interface Model comes from cross-linguistic studies of gesture production. For instance, when an English speaker expresses a "roll down" event, the one-clause sentence (e.g., he *rolled down*) accompanies a gesture that conflates path and manner information (e.g., index finger makes circles while moving down). In contrast, Turkish or Japanese speakers express the same event in two clauses (e.g., he descended as he rolled) and use two separate gestures for path and manner (e.g., one for moving down and the other for circular movement). Nevertheless, when English speakers use two separate clauses for manner and path of motion, their gestures are similar to those of Turkish speakers (Kita et al., 2007). These findings suggest that spontaneous gestures are synchronized with speech and influenced by the form of sentences used, regardless of the surface properties a particular language (Kita et al., 2007; Kita & Özyürek, 2003). Additionally, healthy people often gesture when they communicate spatial information verbally (Alibali, 2005; Alibali, Heath, & Myers, 2001; Feyereisen & Havard, 1999).

Only recently neurocognitive research has started to investigate the neural correlations of co-speech gestures, suggesting that co-speech gestures and speech processing probably engage overlapping areas in the left inferior frontal gyrus (BA 45), superior temporal sulcus, and posterior middle temporal gyrus (Dick et al., 2009, 2012; Holle et al., 2008; Willems & Hagoort, 2007; Willems et al., 2007; Willems, Özyürek, & Hagoort, 2009). In two recent studies, Marstaller and Burianova (2015a, 2015b) examined neural underpinnings of co-speech gestures. One was an fMRI study, showing that co-speech gesture production engaged areas that were associated with language production such as left inferior frontal gyrus, anterior superior temporal gyrus, bilateral posterior superior temporal sulcus, left hippocampus, parahippocampus, ventral and dorsal premotor areas, and primary motor cortex (Marstaller et al., 2015a).

Neuropsychological evidence of neural correlates of gesture production comes from studies with aphasic patients (e.g., Ahlsen, 1991; Cicone, Wapner, Foldi, Zurif, & Gardner, 1979; Cocks, Dipper, Middleton, & Morgan, 2011; Cocks, Sautin, Kita, Morgan, & Zlotowitz, 2009; Dipper, Cocks, Rowe, & Morgan, 2011; Feyereisen, 1983; Friederici, 1981, 1982; Glosser, Wiener, & Kaplan, 1986; Hadar, Burstein, Krauss, & Soroker, 1998; Kemmerer, Chandrasekaran, & Tranel, 2007; Le May, David, &

Thomas, 1988), patients with Parkinson's disease (e.g., Cleary, Poliakoff, Galpin, Dick, & Holler, 2011), and split-brain patients (e.g., Kita & Lausberg, 2008; Lausberg, Kita, Zaidel, & Ptito, 2003). The key question raised by this research is whether verbal impairments lead to gestural impairments. The evidence to date is mixed. If speech and gesture originate from the same representational system (McNeill, 1992, 2005), problems in speech would parallel problems in gesture execution. Some studies support this hypothesis (Cicone et al., 1979; Glosser et al., 1986; Goodglass & Kaplan, 1963; McNeill, 1985). For example, Cicone et al. (1979) reported that Broca's aphasics' gestures did not clarify their incomplete sentences. Additionally, some studies suggest that damage to the right hemisphere is associated with more gesture production (e.g., Hadar & Krauss, 1999; Hadar et al., 1998; Kita & Lausberg, 2008; Lausberg, Zaidel, Cruz, & Ptito, 2007; McNeill & Pedelty, 1995). For example, McNeill and Pedelty (1995) suggested that the right hemisphere injured patients who had intact language produce many gestures because of impairment in visuo-spatial imagery.

In contrast, other findings provide evidence for separate, but interrelated gesture and speech systems as proposed by Interface Model (Kita & Özyürek, 2003). For example, Broca's aphasics gesture less per minute compared to healthy control subjects, but they also gesture more per word than control subjects (Feyereisen, 1983). Others report that aphasic patients use more iconic gestures than healthy control subjects (Hadar et al., 1998; Lanyon & Rose, 2009). Aphasic patients may produce more meaning-laden gestures when they have trouble retrieving words than when their production is fluent consistent with the idea that gestures facilitate lexical retrieval (e.g., Hadar et al., 1998; Hermann, Reichle, Lucius-Hoene, Wallesch, & Johannsen-Horbach, 1988; Lanyon & Rose, 2009; Le May et al., 1988; Marshall, Best, Cocks, et al., 2012; Pashek, 1998; Raymer et al., 2006; Rose & Douglas, 2001, 2008; Rose, Douglas, & Matyas, 2002).

Even though gestures may compensate for impaired verbal communication (e.g., Ahlsen, 1991; Fex & Mansson, 1998; Feyereisen, 1983; Kemmerer et al., 2007; Rodriguez, Raymer, & Rothi, 2006), less is known about how brain-injured individuals produce spatial gestures spontaneously to accompany their speech. If speech and gesture are generated by different but related systems, and co-speech gestures originate from an interface representation between spatial thinking and speech (Kita & Özyürek, 2003), how do brain-injured patients who have verbal problems depict spatial information in gestures? In one case study, Kemmerer et al. (2007) examined verbal and gestural descriptions of motion events of a severely anomic patient who had a lesion affecting the fronto-parietal and superior temporal parts of peri-Sylvian cortex. Despite having deficits in describing motion events, this patient used informative spontaneous gestures to communicate his knowledge about motion events. For example, when describing a swinging event, he made an arc movement to represent the 'swinging' action even when he did not use a proper verb. We recently found that even though spontaneous gesture production correlated positively with degree of deficits in naming spatial prepositions, patients with damage to the left posterior middle frontal gyrus and the left inferior frontal gyrus, gestured spatial information less often than expected (Göksun et al., 2013). Thus, despite online coupling between gesture and speech, in cases where information cannot be presented verbally, spontaneous gestures might step into express intact spatial knowledge.

1.3. The current study

In this study, by testing focal brain injured patients, we investigate (1) the neural organization of spatial motion event expressions in English, and (2) the relation between verbal and spontaneous gestural information in describing these events. The first question is whether spatial motion components of path and manner can be selectively impaired. If comprehension and production of spatial words are tightly linked, we predicted that patients who have damage in left peri-Sylvian fronto-parietal regions would have impairments in correctly producing words that describe paths of motion (i.e., preposition). In contrast, patients who have damage to the left posterior inferior/middle temporal gyrus would have problems in correctly producing words that describe manners of motion (i.e., verbs). Thus, patients with left-hemisphere damage would have problems in naming both paths and manners; but the specific neural correlates with each would differ. Right hemisphere damaged patients served as another control group and we predicted that they would not have problems with speech (no impairment in naming) and would look alike to healthy controls.

For the relationship between speech and spontaneous gestures, if spatial language and spatial gestures share tightly intertwined neural networks, deficits in the use of spatial prepositions and verbs should lead to deficits in the use of gestures depicting path and manner of motion, respectively. That is, left hemisphere damaged patients who have difficulty in naming path or manner of motion would also have trouble generating analogous spontaneous spatial gestures. In this case, the naming deficits could reflect a conceptual deficit with downstream consequences regardless of whether the output is verbal or gestural. However, if patients do not have a conceptual problem, spontaneous spatial gestures might be produced to compensate for deficits in retrieving words to describe paths and/or manners of motion. Finally, for right hemisphere damaged patients who do not have speech problems, in line with the Interface Model (Kita & Özyürek, 2003), we do not expect to see compensatory gesture production.

2. Methods

2.1. Participants

We recruited 32 patients with chronic unilateral lesions from the Focal Lesion Subject Database at the University of Pennsylvania (Fellows, Stark, Berg, & Chatterjee, 2008). Sixteen patients had unilateral left hemisphere damage (LHD) and 16 patients had unilateral right hemisphere damage (RHD). The database excludes patients with a history of other neurological disorders, psychiatric disorders, or substance abuse. We did not select patients based on specific lesion locations or behavioral criteria. VLSM analyses are more useful in patient populations with different lesion locations. LHD patients ranged in age from 37 to 79 ($M = 64.69$, SD = 11.49, 10 females) and RHD patients ranged in age from 45 to 87 ($M = 63.50$, SD = 11.99, 11 females). The average years of education for LHD ($M = 13.6$, SD = 2.02) and RHD patients ($M = 15.1$, SD = 3.44) were comparable. Fourteen age-matched (range: 38–77, $M = 60.85$, SD = 11.05, 9 females) and education-matched ($M = 16$, SD = 2.12) elderly healthy adults served as a control group (HC). The three groups did not differ in age or years of education, $ps > .05$. Additionally, LHD and RHD patients did not differ in lesion size, $p > .05$. Fig. 1 displays lesion overlap maps of patients. All participants were right-handed, native English-speakers, had normal or corrected to normal vision, and no hearing loss. They provided written, informed consent in accordance with the policies of the University of Pennsylvania's Institutional Review Board. Participants received $15/h for volunteering their time. Table 1 presents demographic data for each patient.

2.2. Tasks and stimuli

2.2.1. Neuropsychological tasks

Patients were administered the language comprehension and language production subtests of the Western Aphasia Battery

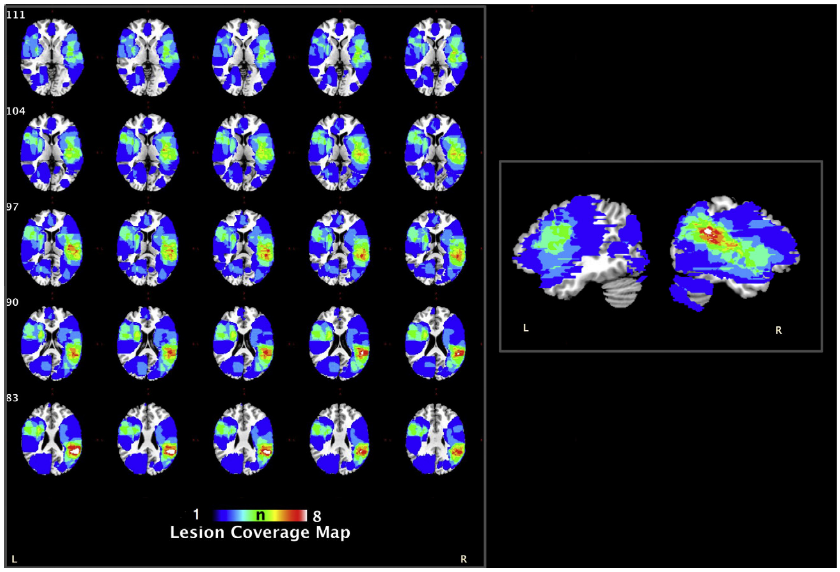

Fig. 1. Coverage map indicating the lesion locations for all participants. The colored scale represents the number of patients with a lesion in that pixel.

Table 1
Patient demographic and neuropsychological data.

Patient	Gender	Age	Education (years)	Lesion Side	Location	Lesion size (# of voxels)	Cause	Chronicity (months)	WAB (AQ)	OANB (Action)	OANB (Object)
LT_85	F	63	15	L	I	13,079	Stroke	177	98.8	100	98.8
CD_141	F	52	16	L	T	21,605	Stroke	143	98.8	100	96
KG_215	M	61	14	L	F	17,422	Stroke	145	94.4	96	93.8
TO_221	F	77	13	L	O	5886	Stroke	160	100	100	100
BC_236	M	65	18	L	FP	155,982	Stroke	210	80.8	88	94
XK_342	F	57	12	L	OT	42,144	Stroke	125	91.4	94	93
TD_360	M	58	12	L	T BG	38,063	Stroke	118	65.3	52	28
IG_363	M	74	16	L	F	16,845	Stroke	117	91.4	96	95
KD_493	M	68	14	L	T	22,404	Aneurysm	101	92.1	98	95
DR_529	F	66	12	L	PA F	8969	Stroke	100	94.9	94	90.1
DR_565	F	53	12	L	PA F	14,517	Aneurysm	103	99.8	98	97.5
MC_577	F	79	11	L	C	4191	Stroke	50	85.3	82	79
NS_604	F	37	12	L	PO	79,231	AVM	113	100	100	98
UD_618	M	77	15	L	F	48,743	Stroke	47	89.4	76	85
KM_642	M	77	12	L	P	7996	Stroke	109	96.8	94	98
CC_749	F	71	12	L	P	34,266	Stroke	50	88.8	–	–
FC_83	M	70	12	R	FTP	8040	Stroke	169	99.8	96	98
MB_101	F	58	18	R	T BG	10,543	Stroke	426	98.4	98	98
NC_112	F	48	16	R	O	4733	Stroke	178	100	98	–
RT_309	F	66	21	R	T	79,691	Hematoma	128	–	–	–
DF_316	F	87	12	R	P	2981	Stroke	126	97.1	88	93
DC_392	M	56	10	R	PT	39,068	Stroke	108	97.6	98	95
DX_444	F	80	12	R	PT	41,172	Stroke	106	95.5	94	93
TS_474	F	51	11	R	P	22,208	Stroke	100	95.1	98	95
NS_569	F	72	18	R	FT BG	37,366	Stroke	77	100	100	99
DG_592	F	45	12	R	PT	130,552	Stroke	127	97.8	98	98
KG_593	F	49	12	R	FTP BG	170,128	Stroke	58	100	90	95
KS_605	M	63	18	R	C	23,217	Stroke	76	98.8	100	100
ND_640	F	70	18	R	PT	64,603	Stroke	54	96.8	100	100
CS_657	M	75	18	R	PO	33,568	Stroke	43	99.2	98	100
KN_675	M	64	18	R	FT	23,779	Stroke	32	–	–	–
MN_738	F	62	16	R	C	32,154	Stroke	25	98.4	100	100

Key: F: frontal; T: temporal; P: parietal; O: occipital; BG: basal ganglia; C: cerebellum; I: insula; PA: pericallosal artery. WAB-AQ indicates a composite language score with a maximum possible score of 100. OANB (action) and OANB (object) demonstrate knowledge of verbs and nouns with a maximum possible score of 100.

(WAB; Kertesz, 1982). They were also administered the Object and Action Naming Battery (OANB; Druks, 2000). This task included 50 pictures of actions and 81 pictures of objects. The scores from these neuropsychological tests are presented in Table 1.

2.2.2. Experimental tasks

The experimental task consisted of 22 dynamic movie clips, depicting different motion events. Different combinations of 10 manners (hop, skip, walk, run, cartwheel, crawl, jump, twirl, March, step) and 9 paths (through, to, out of, under, over, in front of, around, across, into) were used. All actions in the video were performed by a woman outdoors. The movies were created with a Sony digital camera and were edited using iMovie (see Fig. 2 for sample stimulus). Each movie lasted for 3–4 s. The final set of 22 was selected from 32 movies based on ratings of familiarity and descriptions of the actions (both path and manner) by 18 native English speakers with a mean age of 21.88 (range: 18–27, SD = 2.76). After watching each movie clip, they first rated the familiarity of the action in the clip on a 5-point scale (1 = not familiar at all, 5 = very familiar). Then, they described what the woman was doing in each clip. For example, when the participants saw the woman running across the street, they first rated the familiarity of action by simply hitting 1–5 on the keyboard. Then, they described the action by saying something like "the woman ran across the street." Two practice trials were presented before the start of the task. Stimuli were presented on a Macbook Air computer using MATLAB version 7.5.0., 2007 Psychtoolbox. The final set of 22 movie clips was selected based on the agreement among the participants. Movie clips with an average of at least 3.5 familiarity rating and 99% naming agreement were used.

2.3. Procedure

Participants were tested individually in the laboratory or in their homes. After 2 practice trials, each participant received 22 test trials in a random order. After watching the short movie clip on the screen, the experimenter asked the participants to describe what the woman did in the clip. The experimenter presented the movie clips on a Macbook Air computer using Matlab, 2007 and advanced to the next trial when the participant was ready. The session was videotaped for further transcriptions of speech and gesture. The experimenter did not mention gestures to the participants or encourage their gesturing during the tasks. The neuropsychological tasks were administered on a different testing session either before or after the experimental tasks.

2.3.1. Coding

2.3.1.1. Speech. Native English speakers transcribed all speech verbatim for participants' responses to each trial. First, speech for each trial was coded for the correct use of manner (how the action was performed) and path (the trajectory of action) information based on what the participant said in each trial. That is, we coded the accuracy of verb (manner) and preposition (path) in each trial. We categorized each response into three categories: (1) manner only (2) path only and (3) manner + path together. For example, for the event in which the woman was running around a tree, *manner only* response would be "she was running" (i.e., running is the manner of the action). In contrast, the same event could be described as "she went around the tree," which omits the manner and mentions only the path of the action (i.e., around). Finally, the description "she ran around the tree" constitutes both *manner* (i.e., run) and *path* (i.e., around) information.

2.3.1.2. Gesture. We transcribed the participants' spontaneous use of gestures for each trial. A change in the shape of the hand or motion signaled the end of a gesture. For each trial, the coders initially decided whether at least one gesture was produced or not. The gestures in each trial were then classified as (1) static or (2) dynamic. *Static* gestures referred either to objects or to locations. These gestures included pointing to the objects, depicting a property of the objects, or illustrating the location of an object (e.g., pointing to the right side to refer to the location of an action). *Dynamic* gestures involved the movement of the hand in one directional axis (e.g., from left to right or back and forth) or circular movements of the hand. We focused on dynamic gestures that were *iconic*. For the purposes of this study, we further classified each dynamic gesture into three types: (1) manner only, (2) path only, and (3) manner + path together. *Manner only* gestures depicted the manner of motion without depicting path (e.g., repetitive up and down movement of index and middle fingers without any forward motion to represent walking). *Path only* gestures depicted changes of location without depicting manner (e.g., palm faces down moves straight from left to right to represent across). *Manner + path* together gestures encoded both of these components simultaneously (e.g., moving a hand forward while repetitively moving the index and middle fingers to represent 'walk over').

After classifying each gesture into a category, we coded whether patients produced *complementary* gestures (same information in gesture as in speech) or *additional/compensatory* gestures (appropriate gesture with inaccurate or absent path-manner verbal information; or gesture and speech contain different information for path and manner). For each sentence type in speech (manner only, path only, manner + path, and no dynamic information), we recorded the frequency with which LHD and RHD patients produced different types of gestures (manner only, path only, manner + path).

2.4. Reliability

To establish the reliability of the coding system, we conducted two types of reliability by a second person. First, the second coder randomly chose and independently coded 20% participants' all responses both for speech and gesture. That is, she fully coded the speech and gesture for 9 participants. For speech, agreement between coders was 93.4% (n = 198 trials) in assigning manner only, path only, manner + path categories to the descriptions. For gesture, agreement between coders was 92.1% (n = 198 trials) for gesture identification, 94.3% for gesture category (static vs.

Fig. 2. Sample stimuli from the experimental task. The pictures are still frames from two motion events: jump over (left side) and walk across (right side). The yellow arrows indicate the direction of the person's movement. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

dynamic, $n = 198$ trials), and 91.0% ($n = 198$ trials) for coding gestures that involved manner only, path only, and manner + path.

Second, she randomly chose and coded 20% of each patient's responses both for speech and gesture ($n = 184$ trials in total, 4 trials from each person). For speech, agreement between coders was 93.6% in assigning manner only, path only, manner + path categories to the descriptions. For gesture, agreement between coders was 97.8% for gesture identification, 97.6% for gesture category (static vs. dynamic), and 93.7% for assigning gestures as involving manner only, path only, and manner + path.

2.5. Analyses

2.5.1. Behavioral analyses

For speech, the dependent variable was the naming of manner and path information in the video clips. First, for each trial we coded whether a participant named the manner (verb) and/or path (prepositions) of the specific video clip correctly. We next calculated the percentage of trials for the use of manners (verbs) and paths (prepositions). Then, for each trial, we categorized whether a participant named manner only, path only or both (manner + path) in a given trial. The percentages of manner only, path only, and manner + path together responses were calculated for each patient. In addition to these coding, we computed whether speech was absent (no word related to an action) or whether manner only and path only sentences contained errors (e.g., in manner only, path is incorrect). For gestures, first, the percentage of static vs. dynamic gestures to the overall gesture use was calculated. Then, the percentage of trials in which participants produced at least one dynamic iconic gesture was calculated. We categorized these dynamic gestures as manner only, path only, and manner + path together. As in speech, the percentage of trials in which participants produced manner only, path only, and manner + path together was calculated. We also calculated the frequency of using complementary and additional/compensatory gestures for different types of gestures (manner only, path only, manner + path).

2.5.2. Neuroanatomical analyses

Clinical CT or MRI scans for all patients were rendered to a common anatomical space (Colin27; http://imaging.mrccbu.cam.ac.uk/downloads/Colin). In our database, all lesions are drawn manually on a slice-by-slice basis by two senior neurologists, each with over 25 years of experience. Distortions caused by chronic large vascular lesions, which result in focal areas of atrophy, and ventricular dilation *ex vacuo* are compensated for by aligning lesions with preserved neuroanatomic landmarks in non-lesioned parts of the brain. We then conducted voxel-based lesion symptom mapping (VLSM; Bates et al., 2003) analyses, using Voxbo brain-imaging analysis software developed at the University of Pennsylvania (http://www.nitrc.org/projects/voxbo/). VLSM assessed the relation between behavioral measures and brain lesions on a voxel by voxel basis. We restricted the analyses to the voxels in which at least 2 patients had lesions. The analyses resulted in statistical *t*-maps of lesioned brain areas that were significantly related to impaired behavioral performances. The *t*-map for each analysis was thresholded at $q < .05$ using the False Discovery Rate (FDR) to control for multiple comparisons (Benjamini & Hochberg, 1995; Genovese, Lazar, & Nichols, 2002). We conducted VLSM analyses for speech and gesture dependent variables separately. One-tailed *t*-tests for speech accuracy and two-tailed *t*-tests for gesture production compared behavioral scores between patients with and without lesions at every voxel.

3. Results

3.1. Neuropsychological tests

Even though most of these patients were not severely impaired, WAB scores were lower for the LHD patients compared to the RHD patients, $F(1,27) = 4.713$, $p = .039$, $\eta^2 = .17$ ($M = 92.62$ and $M = 98.18$, LHD and RHD, respectively). For naming objects and actions, the groups did not differ significantly, $ps > .05$ (see Table 1).

3.2. Speech

We first calculated participants' overall performance for producing verbs (manners) and prepositions (paths). Univariate ANOVAs with the group (LHD, RHD, and HC) as the between-subject variable and the correct use of verbs and prepositions as the dependent variables revealed main effects of group, $F(2,43) = 8.01$, $p < .001$, $\eta^2 = .27$ and $F(2,43) = 25.07$, $p < .001$, $\eta^2 = .54$. As shown in Fig. 3, the LHD patients were less accurate than both the RHD patients and HC participants in both naming manners and paths (Scheffé, $ps < .05$). Further comparisons indicated that the LHD patients were worse in naming paths (prepositions) than manners (verbs), $t(15) = 3.91$, $p < .001$. No difference was found for other groups. WAB scores also correlated with naming paths (prepositions) and manners (verbs), $r = .73$ and $r = .60$, $ps < .01$. Results remained the same when we controlled for age and chronicity.

Second, we analyzed whether participants named manner only, path only, or manner + path together in their description of the events. As displayed in Fig. 4, the LHD patients produced fewer correct manner + path together sentences than both the RHD patients and HC participants, $F(2,43) = 5.26$, $p < .01$, $\eta^2 = .20$. Additional descriptive analyses showed that LHD patients omitted path expressions more than other groups and produced only the manner expressions. For every trial, patients produced some words (there was no absent speech). Yet, in 14% of the trials LHD patients did not produce any motion verbs or prepositions (see Table 2 for the number of trials in each category).

We found significant lesion-symptom relations for deficits in producing manners expressions (verbs) and path expressions (prepositions). The FDR corrected *t*-statistic thresholds with a significance level of $q = .05$ were 3.05 and 3.41 for paths and manners, respectively. As displayed in Fig. 5a, lesions to the left posterior middle frontal gyrus, the left inferior frontal gyrus, and the left

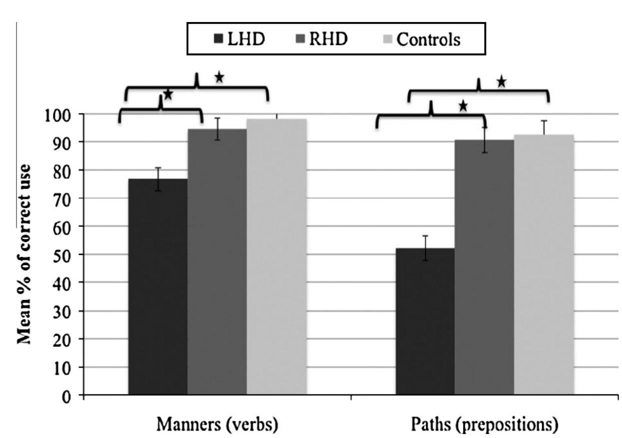

Fig. 3. The percentage of trials on which LHD patients, RHD patients and HC participants correctly named manners (verbs) and paths (prepositions). * $p < .05$; error bars referred to the standard error of mean.

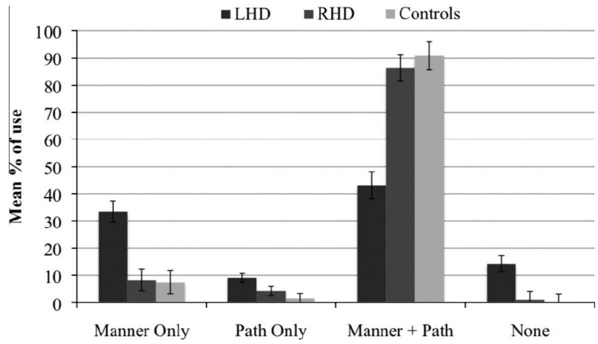

Fig. 4. The percentage of trials on which LHD patients, RHD patients and HC participants correctly named manner only, path only, manner + path together, and none. Error bars referred to the standard error of mean.

anterior superior temporal gyrus were associated with impairments in naming path of motion. Lesions to the left caudate and white matter underlying middle frontal gyrus were related to impairments in naming manners (Fig. 5b).

To contrast the neural bases particularly for naming manner and path, we used VLSM analyses of residual scores (Amorapanth et al., 2012). We calculated the residual scores of one dependent variable (e.g., path) regressed onto another (e.g., manner) and paired these scores with lesion data in VLSM analyses. Similar to the fMRI analyses,

VLSM residual analyses would present a contrast between two dependent variables while accounting for the shared lesions between variables. Based on these analyses, we retrieved the FDR corrected t-statistic thresholds (with a significance level of $q = .05$) of 3.68 and 4.71 for manner > path and path > manner residual analyses, respectively. As shown in Fig. 6, lesions to the left posterior middle frontal gyrus, the left inferior frontal gyrus were critical for naming path of motion (beyond what might be expected with a deficit in naming manners of motion) while lesions to the left caudate and white matter underlying middle frontal gyrus were critical for impairments in naming manners.

3.3. Gesture analyses

As a group LHD patients produced gestures in significantly more trials (67 trials, $M = 19\%$, 81 gestures) than RHD patients (21 trials, 5.9%, 26 gestures) and HC (17 trails, 5.5%, 40 gestures), $F(2,43) = 3.12$, $p < .05$. $\eta^2 = .13$. All path and manner gestures were accurate for the specific trial. Participants also produced a few static gestures that referred to objects in the actions (LHD = 14 gestures, RHD = 2 gestures, and HC = 2 gestures).

We then examined whether groups differed in using manner only, path only, or manner + path together in their gestures. No reliable differences were found in terms of how often each group produced these types of gestures (see Fig. 7). However, we found significant lesion-symptom relations for producing path only gestures that occurred with speech. The FDR corrected t-statistic thresholds with a significance level of $q = .05$ was 3.29 for path only gesture production. In particular, as displayed in Fig. 8,

Table 2
The number of trials each group used manner only, path only, and manner + path expressions or the number of trials neither component was correct (error).

	Manner only	Path only	Manner + path	Errors
LHD (n = 352 trials)	118	32	152	50
RHD (n = 352 trials)	29	15	304	4
Controls (n = 308 trials)	23	5	280	0

patients with lesions to the left anterior superior temporal gyrus and underlying white matter significantly produced more path only gestures than those that did not have lesions in this location. As no lesions were correlated to manner gestures and the use of manner was low in number, we did not run residual analyses for gesture production.

3.4. Speech-gesture relations

For patients, the use of spatial gestures correlated negatively with the accuracy in naming manners and paths, $rs = -.37$ and $rs = -.23$, $ps < .001$. For HC, spatial gestures correlated negatively only with the accuracy in naming paths, $r = -.39$, $p < .001$.

To further analyze whether patients produced *complementary* gestures (same information in speech and gesture) or *compensatory* gestures (inaccurate or absent path-manner information in speech and appropriate gesture), for each sentence type in speech (manner only, path only, manner + path, and no dynamic information) we counted how frequently LHD and RHD patients produced different types of gestures (manner only, path only, manner + path).

The total number of complementary and compensatory gesture was low in the whole group. Nonetheless, LHD patients produced complementary gestures in 42% of the trials (28 out of 67 gesture trials) and compensatory gestures in 58% of the trials (38 out of 67). Seven different patients produced at least 1 compensatory gesture (range: 1–8). Among the compensatory gestures LHD patients used mostly path only information (44%) – the other types (manner only and manner + path) were used in the rest of the trials (28% each). In contrast, RHD patients' gestures were mostly complementary (90.5%, 19 out of 21 trials) and compensatory gestures were used only in 9.5% of their gesture trials (2 out 21 trials). RHD patients' gesture production was similar to HC, who produced compensatory gestures only in 5.8% of their gesture trials (1 out 17 trials) and the rest was complementary gestures. Six different RHD patients and 5 different HC produced complementary gestures at least in one trial.

In addition to the trial analyses, we counted how each patient group used speech and gesture combinations for manners and paths. As presented on Table 3, LHD patients produced many additional or compensatory gestures either presenting one component in speech and one in gesture, or gesturing about the path or manner of action without relevant speech. In contrast, RHD patients' gestures involved the same components in both speech and gesture.

4. Discussion

To evaluate the neural organization of spatial language and spontaneous spatial gestures, we examined focal brain injured individuals' descriptions of events that contained *path* and *manner* motion components. Two main hypotheses framed our investigation. First, if the neural organization of perceiving and producing path (preposition) and manner (verb) of motion information are aligned, patients who have damage in left peri-Sylvian fronto-parietal regions would also have problems in naming paths (i.e., preposition) in speech whereas patients who have damage to the left posterior inferior/middle temporal gyrus would have problems in naming manners (i.e., verbs). Thus, even though LHD patients would have more naming problems compared to RHD and HC, producing path (preposition) and manner (verb) of motion words could be selectively impaired. Second, if spatial language and spatial gestures share tightly intertwined neural networks, deficits in the use of spatial prepositions and verbs should lead to deficits in the use of gestures depicting path and manner of motion, respectively. In contrast, if speech and gesture are generated by

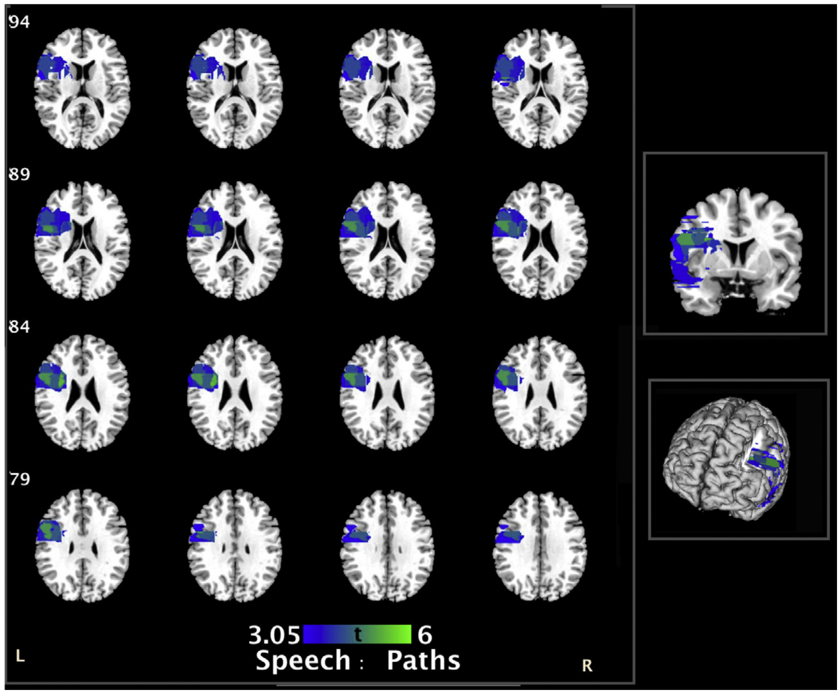

Fig. 5a. Representative slices from VLSM analyses for naming path of motion (prepositions). The maps show significant *t*-scores with a FDR of $q = .05$.

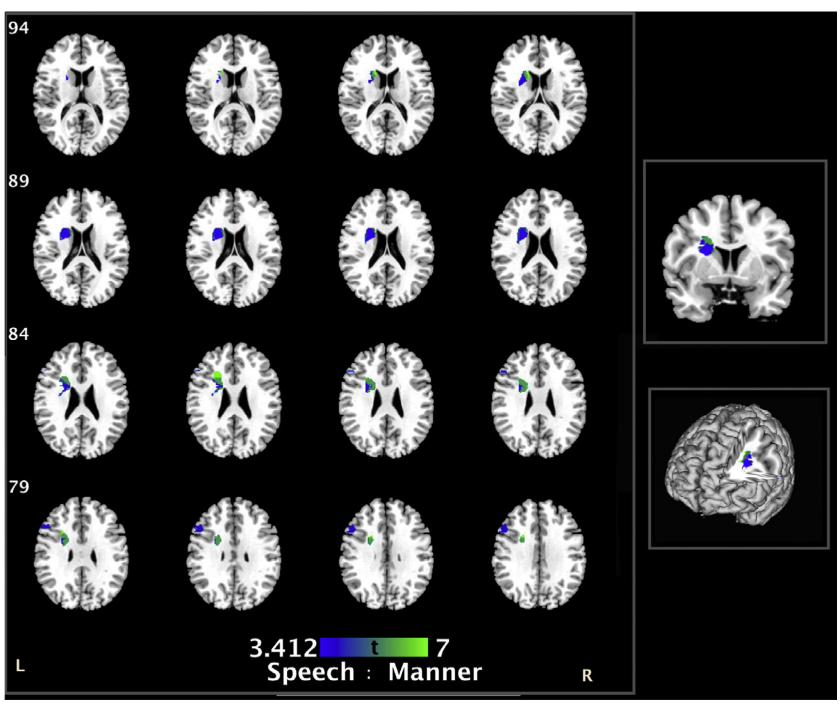

Fig. 5b. Representative slices from VLSM analyses for naming manner of motion (verbs). The maps show significant *t*-scores with a FDR of $q = .05$.

two different but related systems (Kita & Özyürek, 2003), problems in naming prepositions and verbs would not necessarily lead to deficits in gesture use; rather gesture use might increase with lexical access deficits.

We found that LHD patients performed worse than RHD patients and healthy controls in naming paths and manners of motion in dynamic events. LHD patients were less accurate in naming paths than manners, thus, had problems producing full manner + path sentences. Lesions to the left posterior middle frontal gyrus, the left inferior frontal gyrus, and the left anterior superior temporal gyrus impaired the ability to produce prepositions describing paths of motion. Lesions to the left caudate and adjacent white matter impaired the ability to produce verbs describing manners of motion. Although the groups did not produce many spontaneous gestures, gesture analyses showed that LHD patients, as a group, produced more spatial gestures than other groups. Intriguingly, LHD patients who had lesions to the left superior temporal gyrus produced significantly more path gestures

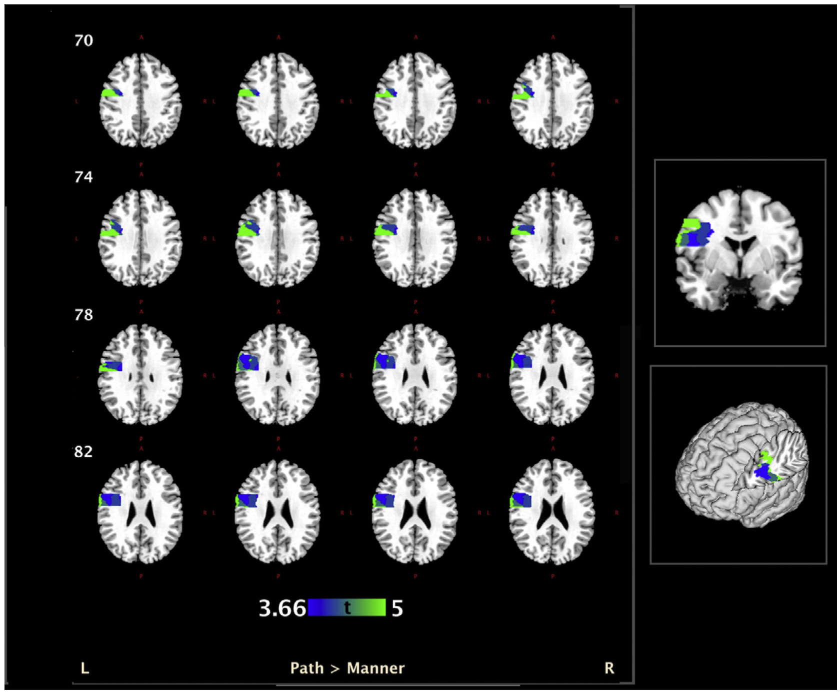

Fig. 6a. Representative slices from VLSM residual analyses for naming impairment of path > manner. The maps show significant *t*-scores with a FDR of $q = .05$.

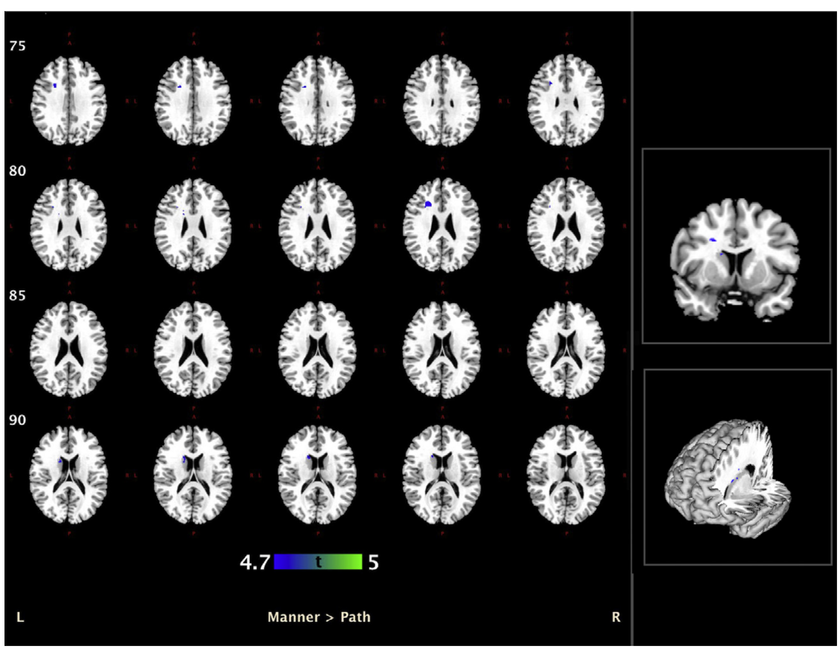

Fig. 6b. Representative slices from VLSM residual analyses for naming impairment of manner > path. The maps show significant *t*-scores with a FDR of $q = .05$.

than other patients. In line with the *Interface Model*, these observations suggest that spatial language and spatial gestures can be selectively impaired and speech and gesture are generated by two separate, but related systems (Kita & Özyürek, 2003).

4.1. The neural correlates of producing words for motion events

Chatterjee (2008) suggested that spatial perception and language have an analogous organizational structure within the brain. Our predictions about the functional anatomy of producing prepositions (the path) and verbs (the manner) of dynamic events were partially confirmed. As a group, LHD patients had more impaired naming of motion components compared to RHD and HC. Naming path and manner of motion in dynamic events can also be dissociated and have different neural underpinnings. However, perceiving and naming these spatial components share related but not identical neural organization.

Paths of motion are verbally represented by prepositions in English and our findings are consistent with the previous research on both naming and comprehending prepositions (Amorapanth et al., 2009; Damasio et al., 2001; Kemmerer & Tranel, 2003; Noordzij et al., 2008; Tranel & Kemmerer, 2004). In particular,

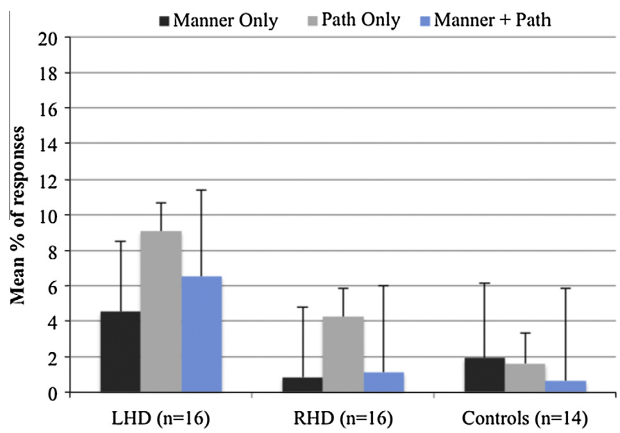

Fig. 7. The percentage of trials on which LHD patients, RHD patients and HC participants produced manner only, path only, manner + path together gestures. Error bars referred to the standard error of mean.

these studies as well as research with Broca's aphasics (e.g., Friederici, 1981, 1982; Kemmerer & Tranel, 2003; Tesak & Hummer, 1994) report the involvement of frontal regions in processing prepositions. These findings are also consistent with the view that the left hemisphere is dominant for spatial processing when the kind of spatial information is categorical and can be named (Amorapanth et al., 2009; Kosslyn, Thompson, Gitelman, & Alpert, 1998).

We provide additional evidence suggesting that the left anterior superior temporal gyrus (aSTG) is involved in producing prepositions. This is consistent with our previous study that shows the involvement of left aSTG in producing spatial static and dynamic prepositions such as the book is *on* the table and the book is moving *over* the table (Göksun et al., 2013). Additionally, categorical spatial relation deficits are associated with lesions in the white matter undercutting the left aSTG (Amorapanth et al., 2009) and impairments in matching locative prepositions to the proper pictures were linked to damage to the left aSTG (Wu et al., 2007).

The aSTG and parts of the dorsolateral prefrontal cortex are connected by the temporo-frontal extreme capsular fasciculus. The importance of this pathway for language, while anticipated by Wernicke as quoted in Petrides (2013), has not been emphasized in neurolinguistics research. First described by Petrides and Pandya (1988, 2009) in the macaque, the analog of this fasciculus has been confirmed in humans (Frey, Campbell, Pike, & Petrides, 2008; Petrides, 2013). We propose that the temporo-frontal fasciculus helps organize the aSTG with ventral prefrontal cortices into a functional unit. One function of this unit is to express path information in speech (and integrate it with gesture as we comment on below).

Manners of motion are encoded by verbs in English. We detected poor performance in naming manners of motion in patients with lesions to the left caudate and adjacent white matter. Left subcortical damage can be associated with agrammatism (Mega & Alexander, 1994) and monitoring lexical and semantic aspects of language (Crosson, 1992; Fabbro, Clarici, & Bava, 1996; Wallesch & Papagno, 1988). Additionally, in an fMRI study, Grossman et al. (2002) found bilateral caudate activation when people processed motion verbs. We suggest that left caudate might also be involved in producing motion verbs.

Our results on the neural vulnerabilities in naming paths and manners of motion do not confirm two anatomic aspects of our predictions. Since the left posterior middle temporal gyrus is frequently associated with comprehending verbs (Kable et al., 2002, 2005; Kemmerer et al., 2008) we would have predicted that this area might also be involved in the production of words. The second area is the left inferior parietal lobule (IPL) that is associated with comprehending prepositions. One possibility is that the classic distinction between comprehension and production of language applies to these systems with posterior regions instantiating core lexical semantics linked to their production anteriorly by the relevant connecting pathways. On this view, the IPL and posterior middle temporal gyrus might be more relevant to language

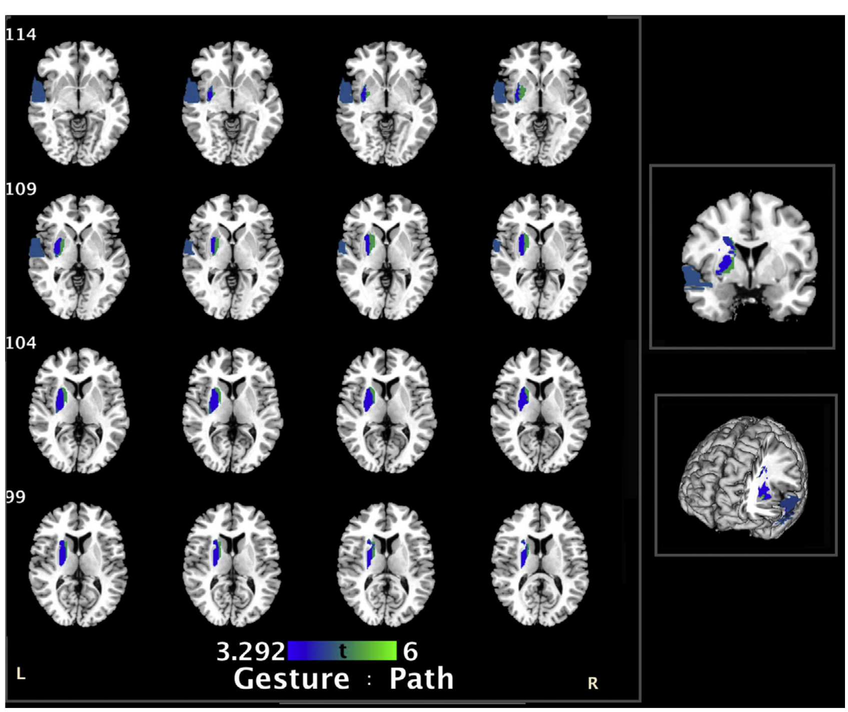

Fig. 8. Representative slices from VLSM analysis for producing path only gestures. The map shows significant *t*-scores with a FDR of q = .05.

Table 3
The number of times LHD and RHD patients produced complementary (same information in both speech and gesture) or additional/compensatory gestures (different or extra information in gesture).

	Manner S & G	Manner G + path S	Manner G (no relevant speech)
LHD	17	5	16
RHD	5	1	1
	Path S & G	Path G manner S	Path G (no relevant speech)
LHD	23	10	17
RHD	20	0	0

comprehension rather than production of words to describe path and manner information, respectively. Furthermore, their respective frontal connections through the inferior aspects of the superior longitudinal fasciculus and parts of the arcuate fasciculus may segregate within the white matter (see Frey et al., 2008, for discussion of these pathways) and in principle could be damaged selectively. Another possibility is that we may have lacked sufficient power to detect the significant effects of lesions in the IPL and posterior middle temporal gyrus.

4.2. Gesture for compensation to impaired speech

We report three key findings on the relationship between speech and spontaneous gesture. First, LHD patients produced more spatial gestures than both RHD patients and control participants. The use of spatial gestures correlated positively with the degree of impairment in naming paths and manners. Second, even though both patient groups complement their speech with gestures, only LHD patients used gestures to compensate for speech. Last, patients who had damage to the left superior temporal gyrus, seemed to produce relatively more spontaneous path gestures.

Our results show that patients use gestures for two purposes – to *complement* spatial information expressed in speech or to *compensate* for the impaired expression of spatial information. In many cases, particularly when individuals had intact speech, gesture was tightly coupled with verbal content such as making an up-down movement with right hand to represent "hopping" when saying, "she hops to the door." Yet, LHD patients also produced spatial gestures to add to or compensate for the spatial information they did not express verbally. For example, to describe the event "hopping around a tree," some make a circle in gesture to represent "around" while only saying "she hopped." More than half the LHD patients' gestures made these compensatory gestures, supporting previous findings on spontaneous gesture's role to compensate for speech problems (e.g., Ahlsen, 1991; Fex & Mansson, 1998; Feyereisen, 1983; Kemmerer et al., 2007; Rodriguez et al., 2006). Participants never produced spontaneous iconic gestures that had no meaningful relationship to the spatial characteristics of the target event.

These findings support the Interface Model (Kita & Özyürek, 2003). When the speech is intact both the message generator and action generator work in close alignment as they both originated from the same representational system. Because these two systems are different subcomponents of the same representational system, impairments in one system do not necessarily produce deficits in the other system. In our case, the representation of events could not be expressed properly in speech. The action generator is still intact and could represent the event through gestures. Thus, we suggest that these LHD patients have problems linking event representations to the message generator (lexical retrieval), but are able to express their knowledge of spatial concepts using gestures.

Our speech findings show that when individuals have lesions in the left superior temporal gyrus, their naming of paths (prepositions) is impaired. Those patients also produced more spatial gestures depicting path information. That is, brain damage in this area produces *more* rather than less, of this communicative behavior. The patients with damage to the left posterior middle frontal gyrus and the left inferior frontal gyrus, also had impairments in naming paths of motion (prepositions), but did not produce more gestures than expected. In a previous study, we found that when the patients had damage to the left posterior middle and inferior frontal gyri, they gestured less than expected (Göksun et al., 2013). We suggest that the aSTG and dorsolateral parts of prefrontal cortex form a functional unit connected by temporo-frontal extreme capsule fasciculus. One function of this unit is to organize spatial path information. However, the subcomponent of this system that instantiates the motor aspects, or spontaneous gestures of this system is localized to the prefrontal and not temporal cortices. This claim is consistent with the view proposed by Marstaller and Burianova (2015a) that the coordination of speech and gesture involves a left lateralized motor control system engaged in planning and execution of such actions. Thus, damage in the aSTG that results in difficulties producing locative terms still allows or even releases prefrontal motor control systems to express gestures in order to facilitate communication. Despite being consistent with Marstaller and Burianova's (2015a) conclusions from fMRI data, we are cautious about these claims about the role of aSTG since, the patients and HC produced relatively few gestures.

We did not assess the patients for apraxia of speech or limb apraxia. There might have been some motor deficits resulting in these impairments. Apraxia can occur at multiple levels, and spontaneous gestures vary from praxis in their explicitness and representational underpinnings (drawing on spatial relations here vs. tool knowledge/skilled movements). Future studies will need to address the link among spontaneous gesture use, limb apraxia, and apraxia of speech.

Our findings have implications for the treatment of word retrieval impairments. Studies report that using gestures with verbal treatment improves both noun and verb retrieval in patients with aphasia (e.g., Pashek, 1997; Raymer et al., 2006; Rose & Douglas, 2001). In addition, case studies indicate that making iconic gestures for objects, but not pointing to the objects, facilitates naming the objects (Rose & Douglas, 2001; Rose et al., 2002). However, others suggest that verbal treatment might still facilitate word retrieval more than gestural treatment, but the effects vary at individual levels (Marshall et al., 2012). Our study suggests that because dynamic spatial gestures can compensate for speech, specialized treatments that encourage gesturing for lexical retrieval might improve their communication abilities.

5. Conclusions

In conclusion, we investigated the neural organization of naming spatial motion event components (path and manner) and the relationship of spontaneous gestures and naming of motion components of dynamic events. Our findings suggest that naming and comprehending motion event components do not have identical neural structures. Damage to the left posterior middle frontal gyrus, the left inferior frontal gyrus, and the left anterior superior temporal gyrus produce deficits in producing spatial prepositions or naming paths of motion whereas lesions in the left caudate and white matter underlying left middle frontal gyrus produce deficits in producing action verbs or naming manners of motion. Spontaneous spatial gestures help patients communicate when they have difficulty in retrieving words for spatial information, especially when their lesions involve the anterior superior temporal gyrus. This pattern suggests that spontaneous gestures represent intact conceptual knowledge.

Acknowledgments

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