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A Dissociation Between Linguistic and Communicative Abilities in the Human Brain

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Abstract

Although language is an effective vehicle for communication, it is unclear how linguistic and communicative abilities relate to each other. Some researchers have argued that communicative message generation involves perspective taking (*mentalizing*), and—crucially—that mentalizing depends on language. We employed a verbal communication paradigm to directly test whether the generation of a communicative action relies on mentalizing and whether the cerebral bases of communicative message generation are distinct from parts of cortex sensitive to linguistic variables. We found that dorsomedial prefrontal cortex, a brain area consistently associated with mentalizing, was sensitive to the communicative intent of utterances, irrespective of linguistic difficulty. In contrast, left inferior frontal cortex, an area known to be involved in language, was sensitive to the linguistic demands of utterances, but not to communicative intent. These findings show that communicative and linguistic abilities rely on cerebrally (and computationally) distinct mechanisms.

Keywords

communication, language, mentalizing, theory of mind, neuroimaging

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Language is an enormously effective means of communication, and it might appear that human communicative abilities are just a subset of linguistic skills. In fact, the cognitive and evolutionary relation between language and communication is actively debated (Carruthers, 2002; Levinson, 2006; Newton & de Villiers, 2007; Tomasello, 2008; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Varley & Siegal, 2000). In this report, we address a crucial element of this debate, namely, whether linguistic and communicative abilities are linked by their reliance on *mentalizing*, the capacity to deal with mental states of other people (Frith & Frith, 2006; Newton & de Villiers, 2007; Varley & Siegal, 2000).

Some scholars have argued for the primacy of linguistic skills in supporting the cognitive architecture of human mentalizing abilities (Carruthers, 2002; Newton & de Villiers, 2007). For instance, Newton and de Villiers showed that performance on a mentalizing task (false-belief task) was impaired when paired with verbal shadowing, but was not impaired when paired with rhythmic finger tapping. The authors suggested that taxing the language system via verbal shadowing hindered performance on the false-belief task and that therefore language is needed for mentalizing. Contrary evidence comes from aphasic patients with severely impaired linguistic

abilities, who nonetheless perform well on mentalizing tasks (Varley & Siegal, 2000).

In this study, we contributed to this debate by asking whether the generation of communicative intentions relies on the same cognitive mechanisms that support mentalizing abilities (Frith & Frith, 2006; Levinson, 2006; Tomasello, 2008; Tomasello et al., 2005). We hypothesized that mentalizing is essential for selecting communicative actions, and more specifically, that it is essential for adapting communicative behavior to what an interlocutor knows and believes (Clark, 1996). If the mentalizing abilities used during communicative behavior are related to the language system (Carruthers, 2002; Newton & de Villiers, 2007), there should be overlap between cerebral structures supporting mentalizing and linguistic processes. Previous studies of mentalizing reported activations in language-related brain areas (Sassa et al., 2007; Tylén, Wallentin, & Roepstorff, 2009), and studies of language reported activations in the mentalizing network (Ferstl, Neumann,

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Bogler, & von Cramon, 2008; Mason & Just, 2006). However, those studies were not designed to dissociate mentalizing and linguistic effects. In our study, we independently manipulated communicative intent and linguistic processing to directly test whether the neurocognitive bases of communicative and linguistic abilities are distinct, and how they relate to mentalizing (Levinson, 2006; Tomasello, 2008; Tomasello et al., 2005).

We measured cerebral activity (with functional magnetic resonance imaging, fMRI) while healthy participants engaged in a verbal communication task. We compared brain states during the generation of utterances differing in communicative intent and investigated how these cerebral responses were modulated by linguistic difficulty. If the generation of a communicative act for a specific agent (*audience design*; Clark, 1996) involves mentalizing, then cerebral structures previously associated with mentalizing (medial prefrontal cortex; posterior superior temporal sulcus, or pSTS; and temporo-parietal junction; Frith & Frith, 2006) should be sensitive to the subjects' communicative intent. Furthermore, if linguistic abilities are dependent upon communicative abilities, then activity in these mentalizing-related structures should be modulated by linguistic difficulty. Alternatively, if communicative and linguistic capacities are supported by cognitively distinct mechanisms, then different cerebral structures should be sensitive to communicative intent and linguistic difficulty.

Method

Participants

Twenty healthy right-handed participants (16 female and 4 male; mean age = 22 years, range = 18–30) without known neurological history, dyslexia, or hearing complaints, and with normal or corrected-to-normal vision, took part in the study. All participants had Dutch as their mother tongue.

Procedure

Participants (*senders*) were asked to describe concepts (*target words*; e.g., “beard”) to another person (the *receiver*, a confederate) by using a single sentence and avoiding prespecified words (*taboo words*; e.g., “chin,” “man,” “hair,” “shave”). The sender and receiver could clearly hear each other's utterances (by means of magnetic-resonance-imaging-compatible headphones). The receiver inferred target words on the basis of the utterances generated by the sender, who was lying in an MRI scanner.

Experimental design

We independently manipulated communicative intent and linguistic difficulty in a 2×2 factorial design. The first factor was *communicative setting*, which involved a manipulation of the communicative intent of the speaker. Communicative intent was operationalized as the presence or absence of the need to convey a specific concept to a specific agent. In

targeted trials, the sender was told that the receiver did not know the target word. In *nontargeted* trials, the sender was told that the receiver already knew the target word. In fact, in both trial types, the receiver was a confederate with previous knowledge of the target word. The second factor was *linguistic difficulty*. In *difficult* trials, the taboo words were semantically closely related to the target word, and the sender needed to build an utterance by searching distant portions of the semantic space surrounding the target word. In *easy* trials, there was a large semantic distance between target and taboo words, and the sender could use the semantic space adjacent to the target word. For instance, an easy trial could contain target word “rainbow” with taboo words “violet,” “four-leaf clover,” “poem,” “sound,” and “water.” (Fig. 1a shows a difficult trial.)

The experiment was run in two consecutive sessions: one session of targeted trials and one session of nontargeted trials, the order of which was counterbalanced across participants. Each session contained 30 task trials (15 easy and 15 difficult) and 30 control trials, in which the sender was presented a list of words to be read and uttered out loud.

Lexical frequency of taboo and target words was matched between all conditions (using CELEX; Baayen, Piepenbrock, & van Rijn, 1993). Stimulus lists were pseudorandomized to avoid having participants describe the same target word in targeted and nontargeted trials. All materials were in Dutch.

Task trials consisted of five phases (Fig. 1b). First, senders were presented with taboo and target words and were required to plan their utterance. Second, senders uttered their one-sentence description, which they had to do within at most 10 s. Third, the receiver planned his answer, and fourth, he uttered the answer. Fifth, the experimenter provided feedback by presenting a green (correct) or red (incorrect) square. In targeted trials, the receiver (confederate) gave wrong answers on a prescribed set (30%) of trials. A red square was presented after these trials, and each such trial was immediately repeated to give the sender a second chance to describe the target word (*repeat trials*). Repeat trials were modeled in the fMRI analysis, but were not used for statistical inference. In nontargeted trials, the receiver did not utter a response, and hence, there was no Phase 3 in which the sender listened to the receiver's response (Fig. 1b). Feedback in nontargeted trials was always a green square (correct).

The sender and receiver pressed a button to proceed from one phase of a trial to the next. In the fMRI analysis, we distinguished the planning phase (Phase 1, of interest) from the other phases (not of interest; Noordzij et al., 2009; Toni, Schluter, Josephs, Friston, & Passingham, 1999). This allowed us to isolate cerebral responses associated with the planning of an utterance from artifacts linked to speech production. Participants were familiarized with the paradigm by means of five practice trials in each communicative setting.

Data acquisition and analysis

Echo-planar images were acquired with an eight-channel head coil on a 3-T Siemens magnetic resonance imaging

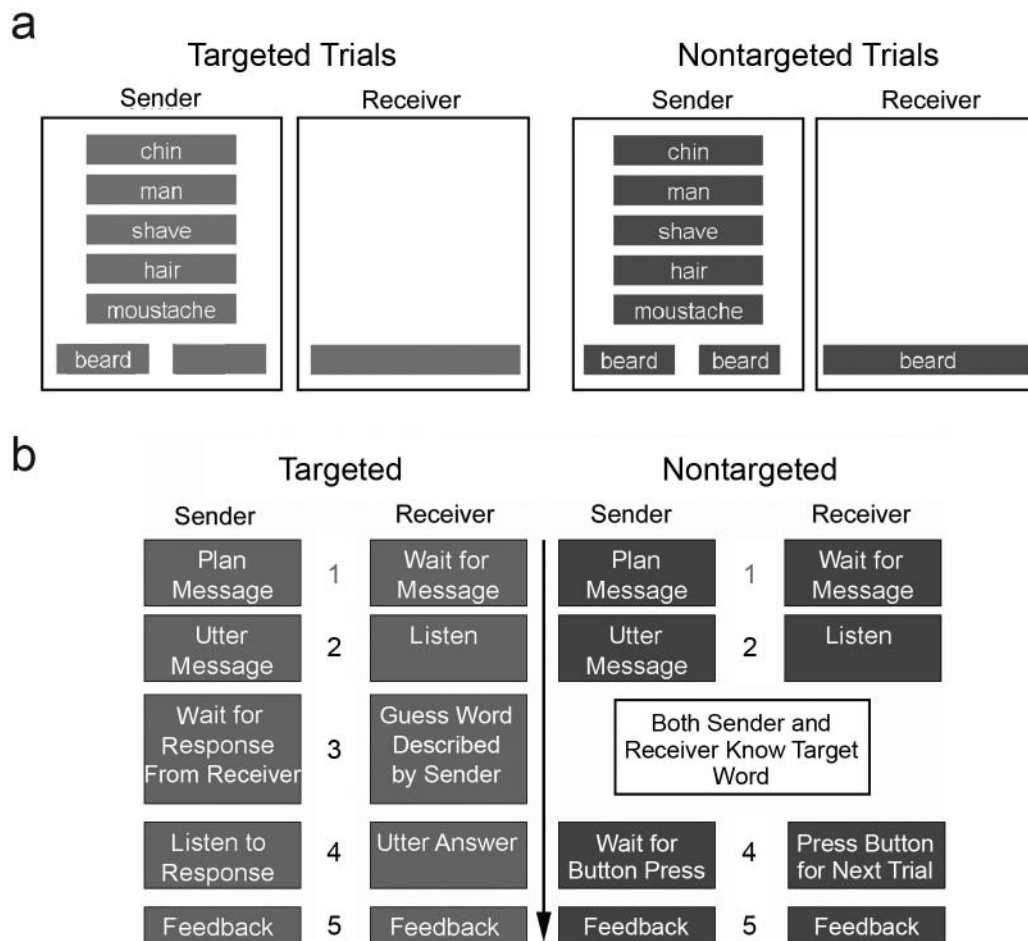


Fig. 1. Stimuli and experimental design. An example of a stimulus is shown in (a). In the nontargeted setting, the receiver knew the target word ("beard"), and the sender was reminded of that fact by the repetition of the target word on the sender's screen. In the targeted setting, the sender was told that the receiver did not know the target word. The illustration of the time course of a trial (b) shows the tasks of the sender and receiver during the five phases of a task trial. All functional magnetic resonance imaging analysis focused on the planning phases (Phase 1), in which the sender generated a communicative act. All materials were in Dutch.

system (repetition time = 2,060 ms; echo time = 30 ms; flip angle = 85°, field of view = 224 mm; 31 transversal slices; voxel size = 3.5 × 3.5 × 3.5 mm). Preprocessing involved realignment by means of rigid body registration, slice timing correction to the onset of the first slice, normalization to Montreal Neurological Institute (MNI) space, interpolation to 2 × 2 × 2-mm voxels, and spatial smoothing (8 mm full-width at half-maximum).

First-level analysis was done in the context of the general linear model and involved a multiple regression analysis with regressors describing the planning phases of the different trial types (easy, difficult, control) and the speaking and listening phases of the sender. Regressors describing repeat trials (in targeted setting only) were also included. Magnetic resonance disturbances induced by speaking were accounted for by including the full Volterra expansions of the scan-by-scan estimated head motion and scan-by-scan average signals from outside the brain, white matter, and cerebrospinal fluid as

regressors (Verhagen, Grol, Dijkerman, & Toni, 2006). Head motion never exceeded 3 mm, or 3°.

The second-level group analysis was a factorial design with the factors of communicative setting (targeted, nontargeted) and linguistic difficulty (easy, difficult). This analysis was based on four contrast images from the planning stage for each subject: "easy > control" and "difficult > control" independently estimated for targeted and nontargeted trials. Correction for violation of the sphericity assumption was applied when appropriate. All results were corrected for multiple comparisons by combining a $p < .001$ voxel-level threshold with a cluster extent threshold to obtain a $p < .05$ whole-brain-corrected significance level (Friston, Holmes, Poline, Price, & Frith, 1996). Given our previous work, we assessed the contribution of pSTS (15-mm spherical region of interest with MNI coordinates of [50 -42 14] and [-50 -42 14]; Noordzij et al., 2009) by masking the simple main effect of semantic difficulty during targeted trials with the Communicative Setting ×

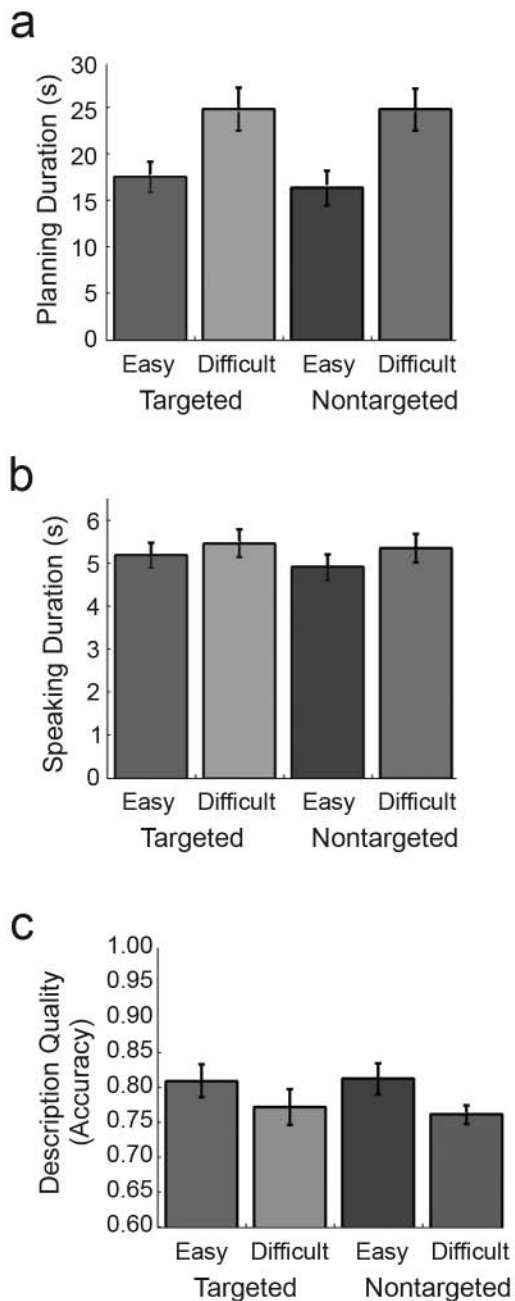


Fig. 2. Behavioral results: mean planning duration (a), speaking duration (b), and quality of descriptions as determined by the posttest (c), as a function of communicative setting (targeted and nontargeted) and linguistic difficulty (easy and difficult). For results of statistical analyses, see Table 1. Error bars represent standard errors of the mean.

Linguistic Difficulty interaction, using small-volume correction at $p < .05$.

Behavioral data analysis involved repeated measures analysis of variance on planning duration, speaking duration, and the number of words per description. The factors in these analyses were communicative setting (targeted, nontargeted) and linguistic difficulty (easy, difficult).

Posttest

In a separate posttest, we assessed whether the quality of senders' descriptions was influenced by communicative setting or linguistic difficulty. Sixteen new participants listened to 192 utterances (equally distributed across conditions) from senders in the fMRI experiment, and guessed which word was described in each utterance. Semantic distance between their answer and the target word was computed using a distributional-proximity-based method on a large corpus of written Dutch (Van der Plas, 2008). The computation of semantic distance gave a number indicating the amount of overlap between two words (from 0, indicating no overlap, to 1, indicating perfect semantic overlap). This additional analysis allowed us to assess whether the quality of senders' descriptions varied by communicative setting or linguistic difficulty.

Results

There were no behavioral differences between targeted and nontargeted trials, as indexed by planning times, speaking times, or number of words used in the utterances (Figs. 2a and 2b; Table 1). Moreover, the posttest on the quality of the descriptions showed that there was no effect of communicative setting on quality of description (Fig. 2c; Table 1). Table 1 presents the results of analyses of variance on these behavioral measures.

Despite this behavioral equivalence for targeted and nontargeted trials, targeted trials evoked stronger responses than nontargeted trials in a confined portion of the dorsomedial prefrontal cortex (Fig. 3a; Table 2), a region known to be involved in tasks requiring mentalizing (Frith & Frith, 2006; Northoff et al., 2006), including making inferences about mental states of agents different from oneself (Mitchell, Macrae, & Banaji, 2006). We show that the same area is involved in the generation of a communicative utterance provided that the recipient of that utterance is believed not to have the same knowledge as the speaker.¹ No areas were sensitive to the opposite contrast (nontargeted > targeted trials). Table 2 shows the contrasts from a fMRI whole-brain analysis.

As expected, it took senders longer to plan their utterances in the difficult trials than in the easy trials (Fig. 2a; Table 1). Also, participants in the posttest guessed the target-word descriptions from the easy trials more accurately than those from the difficult trials (Fig. 2c; Table 1). Activation levels in bilateral, but strongly left-lateralized, inferior frontal cortex (LIFC, including Brodmann's areas 44 and 45; Eickhoff et al., 2005) and bilateral inferior parietal cortex likewise showed stronger activation for difficult as compared with easy trials (Fig. 3b; Table 2). LIFC is known to be involved in a wide variety of language production and comprehension tasks (Hagoort, 2005; Vigneau et al., 2006). The opposite contrast (easy > difficult trials) led to increased activation levels in left dorsal precentral sulcus and left inferior occipital gyrus. We had no a priori hypothesis about this comparison and

Table 1. Behavioral Results

Measure and effect	<i>F</i>	<i>df</i>	<i>MSE</i>	<i>p</i>	<i>p_{rep}</i>	η_p^2
Planning time						
Communicative setting	< 1	1, 19	28.69	n.s.	.41	.01
Linguistic difficulty	57.81	1, 19	21.32	< .001	> .99	.75
Communicative Setting × Linguistic Difficulty	< 1	1, 19	7.35	n.s.	.60	.05
Speaking time						
Communicative setting	1.35	1, 19	0.53	.26	.68	.07
Linguistic difficulty	10.55	1, 19	0.25	.004	.97	.36
Communicative Setting × Linguistic Difficulty	< 1	1, 19	0.38	n.s.	.58	.04
Number of words						
Communicative setting	2.64	1, 19	4.29	.12	.79	.12
Linguistic difficulty	1.95	1, 19	0.75	.18	.74	.09
Communicative Setting × Linguistic Difficulty	1.16	1, 19	1.11	.30	.65	.06
Quality of descriptions						
Communicative setting	< 1	1, 15	0.006	n.s.	.26	.004
Linguistic difficulty	4.54	1, 15	0.007	.050	.88	.23
Communicative Setting × Linguistic Difficulty	< 1	1, 15	0.001	n.s.	.34	.009

Note: For a graphical representation, see Figure 2.

interpretation of these findings does not add to understanding of the main findings.

Finally, the left pSTS showed a supra-additive response when semantically difficult communicative problems needed to be solved (Communicative Setting × Linguistic Difficulty interaction; see Fig. 3c).

Discussion

Our results shed light on two issues concerning the relationship between communicative and linguistic abilities. First, we have shown that generating a targeted communicative message for a specific other relies on mentalizing capacities. This

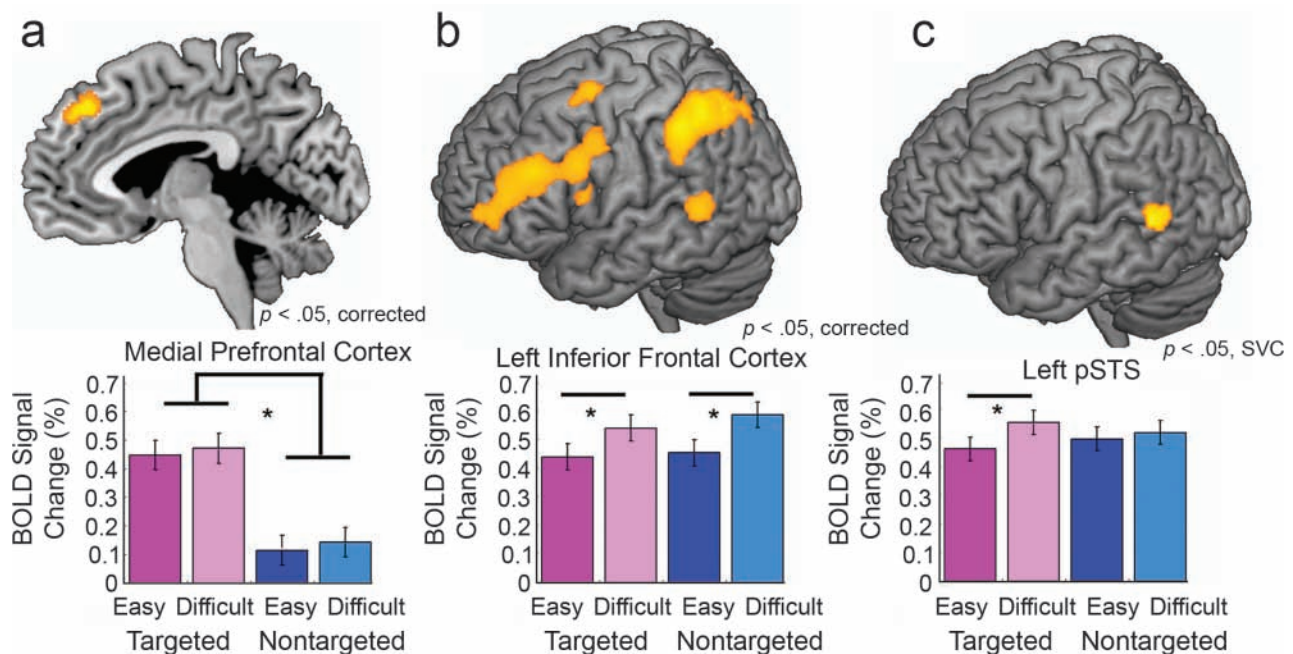


Fig. 3. Imaging results: brain areas showing differential activity for targeted versus nontargeted trials (a) and difficult versus easy trials (b), and the effect of the interaction between communicative setting and linguistic difficulty (c). The accompanying graphs depict the percentage of blood-oxygenation-level-dependent (BOLD) signal change for task trials relative to control trials. Error bars represent standard errors of the mean. Asterisks indicate a significant difference in activation. pSTS = posterior superior temporal sulcus; SVC = small volume correction. All results are corrected for multiple comparisons at the $p < .05$ level.

Table 2. Results of Functional Magnetic Resonance Imaging Whole-Brain Analysis

Contrast and area	Coordinates			t (max)	Number of voxels
	x	y	z		
Targeted > nontargeted					
Dorsomedial prefrontal cortex	-2	38	44	4.91	217
Difficult > easy					
Left inferior frontal sulcus	-42	34	26	6.07	1,664
Right inferior frontal sulcus	50	8	24	4.95	233
Left inferior parietal lobe	-34	-50	46	8.25	3,658
Right inferior parietal lobe	50	-36	46	6.06	1,678
Left middle frontal sulcus	-26	2	60	5.25	211
Left posterior superior temporal sulcus	-64	-46	8	5.02	328
Easy > difficult					
Left dorsal precentral sulcus	-32	-24	48	3.86	195
Left inferior occipital gyrus	-10	-80	-2	4.41	339

Note: Coordinates are in Montreal Neurological Institute space. The *t* value listed for each area is the value for the maximally activated voxel in that area. Voxels were $2 \times 2 \times 2$ mm. No areas had greater activation in nontargeted than in targeted trials. Displayed are statistically significant differences, corrected for multiple comparisons. See Figure 3 for visualization of the results.

is evidence against the notion that communication involves a reflex-like mirroring mechanism rooted in the motor system (Rizzolatti & Craighero, 2004). Rather, our results support the notion that planning an effective communicative act involves the generation of social constructs (what an agent supposes his or her interlocutors know and believe) that guide selection of an appropriate communicative action (Frith & Frith, 2006; Levinson, 2006; Toni, de Lange, Noordzij, & Hagoort, 2008). Future research should establish that activations in the mentalizing network are necessary for planning communicative acts, and should research the scope of communicative acts that is related to the activation of the mentalizing network.

Second, we have provided evidence that the cognitive and cerebral mechanisms involved in communication and language are distinct. The dorsomedial prefrontal area sensitive to communicative intent was not sensitive to linguistic difficulty. An opposite pattern of response was observed in inferior frontal and inferior parietal cortex, which were indifferent to the communicative intent of the utterances being processed (Fig. 3b). Given the well-known role of LIFC in language (Hagoort, 2005; Vigneau et al., 2006; Willems, Özyürek, & Hagoort, 2007), it is likely that LIFC activation in our study reflected increased semantic processing load, phonological processing load, or both.² This interpretation is strengthened by the left-hemispheric lateralization in our participants, who were right-handed (Knecht et al., 2000). The bilateral inferior parietal cortex activations could be related to increased attentional load in difficult trials, rather than linguistic processes per se (Corbetta & Shulman, 2002).

Our finding that distinct networks were activated by the communicative and linguistic manipulations is not compatible with the notion that communicative and mentalizing abilities are ultimately dependent upon language (Carruthers, 2002). The present findings might also appear at odds with a study from Newton and de Villiers (2007), which found that verbal shadowing, but not rhythmic finger tapping, interfered with performance on a

false-belief task. In fact, as suggested by the authors (p. 578), verbal shadowing could have interfered with the phonological loop, leading to reduced working memory resources. Accordingly, reduced performance in the false-belief task during verbal shadowing could have been a consequence of reduced working memory resources, rather than altered linguistic processing.

Our results confirm and extend previous results showing that severely aphasic patients can solve mentalizing tasks (Varley & Siegal, 2000). Perhaps these patient data are not decisive because the “logical form” of language was still intact in these patients (Carruthers, 2002). This argument does not apply to our findings because the language system was intact in our participants, and still we found that separate cerebral systems were sensitive to communicative and linguistic effort. Although we argue that communicative and language abilities are cerebrally and cognitively distinct, we do not deny that these systems interact closely, for instance, during discourse comprehension (Mason & Just, 2006).

Finally, we observed an interaction between communicative setting and linguistic difficulty in left pSTS. We previously observed a similar effect in right pSTS in a visuospatial communication paradigm (Noordzij et al., 2009), which suggests that pSTS is influenced by the format of communication (cf. Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004).

We conclude that the generation of communicative utterances relies on a neurocognitive system that is involved in understanding intentions of others, and that is distinct from the language system.

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Declaration of Conflicting Interests

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

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Notes

1. A feedback-related interpretation was not supported: A region-of-interest analysis indicated that this region was sensitive to negative feedback (red square), $t(19) = 2.30$, $p = .02$ (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004), but not differentially so in the two communicative settings ($F < 1$).

2. For our argument, it is not directly relevant exactly which language-related processes caused this effect. It is crucial that this area had similar activation regardless of the communicative intent of the utterances.

References

- Baayen, R.H., Piepenbrock, R., & van Rijn, H. (1993). The CELEX lexical database. Philadelphia: University of Pennsylvania, Linguistic Data Consortium.
- Carruthers, P. (2002). The cognitive functions of language. *Behavioral & Brain Sciences*, *25*, 657–726.
- Clark, H.H. (1996). *Using language*. New York: Cambridge University Press.
- Corbetta, M., & Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.
- Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, *25*, 1325–1335.
- Ferstl, E.C., Neumann, J., Bogler, C., & von Cramon, D.Y. (2008). The extended language network: A meta-analysis of neuroimaging studies on text comprehension. *Human Brain Mapping*, *29*, 581–593.
- Friston, K.J., Holmes, A., Poline, J.B., Price, C.J., & Frith, C.D. (1996). Detecting activations in PET and fMRI: Levels of inference and power. *NeuroImage*, *4*, 223–235.
- Frith, C.D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, *50*, 531–534.
- Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, *9*, 416–423.
- Knecht, S., Drager, B., Deppe, M., Bobe, L., Lohmann, H., Floel, A., et al. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, *123*, 2512–2518.
- Levinson, S.C. (2006). On the human interactional engine. In N.J. Enfield & S.C. Levinson (Eds.), *Roots of human sociality* (pp. 39–69). New York: Berg.
- Mason, R.A., & Just, M.A. (2006). Neuroimaging contributions to the understanding of discourse processes. In M. Traxler & M.A. Gernsbacher (Eds.), *Handbook of psycholinguistics* (pp. 765–799). Amsterdam: Elsevier.
- Mitchell, J.P., Macrae, C.N., & Banaji, M.R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, *50*, 655–663.
- Newton, A.M., & de Villiers, J.G. (2007). Thinking while talking: Adults fail nonverbal false-belief reasoning. *Psychological Science*, *18*, 574–579.
- Noordzij, M.L., Newman-Norlund, S., de Ruiter, J.P., Hagoort, P., Levinson, S.C., & Toni, I. (2009). Brain mechanisms underlying human communication. *Frontiers in Human Neuroscience*, *3*. Retrieved from <http://frontiersin.org/humanneuroscience/paper/10.3389/neuro.09/014.2009/>
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain—a meta-analysis of imaging studies on the self. *NeuroImage*, *31*, 440–457.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science*, *306*, 443–447.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.
- Sassa, Y., Sugiura, M., Jeong, H., Horie, K., Sato, S., & Kawashima, R. (2007). Cortical mechanism of communicative speech production. *NeuroImage*, *37*, 985–992.
- Saxe, R., Xiao, D.K., Kovacs, G., Perrett, D.I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia*, *42*, 1435–1446.
- Tomasello, M. (2008). *Origins of human communication*. Cambridge, MA: MIT Press.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral & Brain Sciences*, *28*, 675–691.
- Toni, I., Lange, F.P., Noordzij, M.L., & Hagoort, P. (2008). Language beyond action. *Journal of Physiology Paris*, *102*, 71–79.
- Toni, I., Schluter, N.D., Josephs, O., Friston, K., & Passingham, R.E. (1999). Signal-, set- and movement-related activity in the human brain: An event-related fMRI study. *Cerebral Cortex*, *9*, 35–49.
- Tylén, K., Wallentin, M., & Roepstorff, A. (2009). Say it with flow-ers! An fMRI study of object mediated communication. *Brain & Language*, *108*, 159–166.
- Van der Plas, L. (2008). *Automatic lexico-semantic acquisition for question answering*. Unpublished doctoral dissertation, University of Groningen, Groningen, The Netherlands.
- Varley, R., & Siegal, M. (2000). Evidence for cognition without grammar from causal reasoning and “theory of mind” in an agrammatic aphasic patient. *Current Biology*, *10*, 723–726.
- Verhagen, L., Grol, M., Dijkerman, H., & Toni, I. (2006). Studying visually-guided reach-to-grasp movements in an MR-environment. *NeuroImage*, *31*, S45.
- Vigneau, M., Beaucousin, V., Herve, P.Y., Duffau, H., Crivello, F., Houde, O., et al. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, *30*, 1414–1432.
- Willems, R.M., Özyürek, A., & Hagoort, P. (2007). When language meets action: The neural integration of gesture and speech. *Cerebral Cortex*, *17*, 2322–2333.