



Shared neural correlates for language and tool use in Broca's area

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Functional magnetic resonance imaging was used to test predictions from a theory of the origin of human language. The gradual theory suggests that human language and tool-use skills have a similar hierarchical structure, and proposes that tool-manipulation skills are related to the origin and evolution of human language. Our results show an overlap of brain activity for perceiving language and using tools in Broca's area. The location of this overlap suggests that language and tool use share computational principles for processing complex hierarchical structures common to these two abilities. The involvement of monkeys' homologous region during tool use suggests that neural processes for computation of complex hierarchical structures exist in primates without language, and could have been exapted to support human

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Introduction

The evolutionary origin of language remains a controversial issue. Did it emerge suddenly in humans or arose slowly through the adaptation of existing primate ability(ies), such as manual skills? One prominent gradual theory supposes that tool-use and tool-making skills are related to language evolution, as both abilities have similar hierarchical organization [1]. Language has a hierarchical structure, that is, grammar, a set of rules for combining words in a meaningful order. Tool use has a similar hierarchical structure, in which simple hand movements are combined in a certain order to achieve appropriate object manipulation. These combination rules exist for different tools and have been called 'action grammar' by Greenfield [1]. For example, when cutting paper with scissors, one hand holds the piece of paper, and the other hand opens and closes the scissors repeatedly, during which time a process of adaptation occurs regarding the relative positions of the piece of paper and scissors.

Behavioural experiments showed that non-human primates can acquire simple grammar skills, but are unable to master the 'phrase structure grammar level', which is characteristic of human languages [2]. Human functional neuroimaging showed a dissociation between the involvement of different parts of the inferior frontal gyrus (Broca's area) in language: a part posterior to the pars opercularis for simple grammar, and an anterior part in Brodmann area 44 (BA44) for complex grammar processing [3]. Considering the central role of Broca's area in language, one can hypothesize that the anterior part

of BA44 specifically evolved for grammatical aspects of human language.

This issue has recently been revived by the discovery of mirror neurons [4]. Mirror neurons in area F5 of the monkey ventral premotor cortex discharge both when the monkey performs a particular action and when it observes another individual doing a similar action [5]. Functional magnetic resonance imaging (fMRI) and positron emission tomography experiments in these monkeys show that both action observation [6] and tool use [7] activate the arcuate sulcus in the inferior frontal cortex of these animals, a region thought to be the homologue of Broca's area in humans [8]. In humans, neuroimaging studies established that a mirror system exists in Broca's area [5] and homology of monkey F5 and human BA44 had been suggested from several imaging studies [9]. It has been argued that mirror systems provide a bridge between action and communication and could have formed the substrate of language evolution [4].

F5 mirror neurons have been found to respond to the use of a tool by macaque monkeys after training [10], and then it follows that if human language is functionally based on the primates' neural substrate for tool-use [1], the same neural computations within Broca's area, the human homologue of F5, could be involved in both language and tool use. In contrast, if human language processing, particularly the processing of complex syntactic structures for sentence comprehension, is a unique human specialization without any counterparts in other animals [11], there should be no activity related to the

use of tools in the pars opercularis region, BA44, involved in complex grammar processing. To distinguish between these two hypotheses, brain correlates of language and of tool-use tasks were measured in the same participants using fMRI, and the analysis focused on the overlap between the two tasks in Broca's area.

Methods

Participants

Sixteen healthy (seven females and nine males, age range 18–35 years), right-handed [12], volunteers participated in this study, which was approved by the ethics committees of the Advanced Telecommunications Research Institute. They gave their written informed consent to the experimental procedure and signed a participation agreement. All participants were native Japanese speakers.

Design and experimental conditions

The fMRI experiment consisted of five conditions (EXECUTION, IMAGERY, HOLD, STORY and REVERSE). Participants practiced the experimental tasks outside the MRI scanner before actual scanning. As participants were highly familiar with tools used in the experiment, they all reported being able to perform the tool-use EXECUTION and tool-use IMAGERY without difficulty. The tasks used to investigate language (STORY and REVERSE) did not entail any difficulties requiring training.

Participants in the scanner were instructed about the condition in the coming trial by sound stimuli made of beeps varying in number and pitch. Conditions were repeated three times within each session and each condition lasted for 40 s except HOLD, which was repeated six times and lasted for 20 s. The order of the conditions was randomized within each repetition (except HOLD, a control condition that occurred in the second and fifth positions in each session for the participants to rest after every two conditions except the first in the session. See lower panel of Fig. 1).

Tool-use EXECUTION condition (see Fig. 1, upper panel): the participants were asked to manipulate appropriately one of three common tools (pencil, scissors and chopsticks) with their right hand while their hand rested on an arm rest to prevent head movement. Participants were able to see their hands, position of a piece of paper or beads and the tools through two mirrors without image reversal. In the pencil task, participants were given a piece of paper that had lines printed with a 2 cm gap between each line and asked to draw a spiral continuously between two adjacent lines with a pencil. In the scissors task, participants were given a piece of paper that had lines printed with a 6 mm gap between each line and were asked to cut along one line at a time with

the scissors. In the chopsticks task, participants were given several 5-mm sized round shaped beads suspended on a thread and instructed to pick up one of the beads and move it to the other side with chopsticks. These three tools were chosen as examples of sequential behaviour. In the case of the scissor task, the action of opening and closing the hand to cut is defined as a single stroke, repeating such stroke equates to a sequence. As only one tool was used per session, participants underwent three sessions, with the tool order randomized across participants.

Tool-use IMAGERY condition: participants were asked to imagine that they were manipulating the tools as they did in the EXECUTION condition while they held the appropriate tool and looked at its target (e.g. paper). This condition was used to isolate cognitive aspects of tool use, such as planning (present in IMAGERY and EXECUTION) from purely motor aspects that should not be active in IMAGERY.

Tool-use HOLD condition: the participants were asked to hold the tool and look at the target object without imagining using the tool.

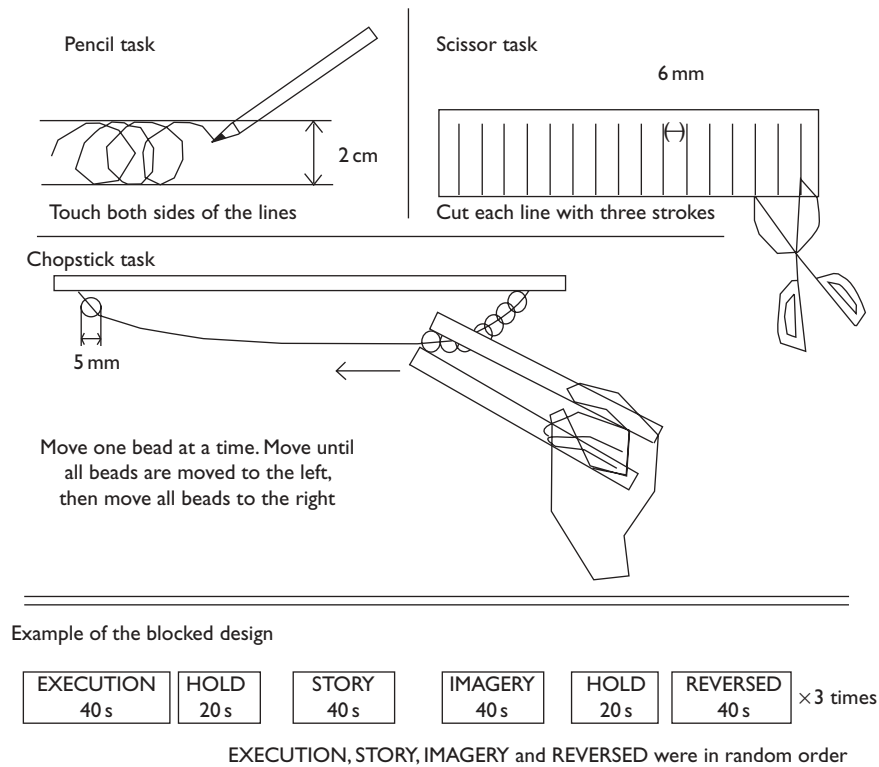
STORY condition: participants listened to a famous Japanese fairy-tale and to explanations of the story narrated by a professional Japanese storyteller. All participants knew the story and each STORY trial consisted of a different part of the story or explanations.

REVERSE condition: participants listened to the same story played backwards. This condition, that has the same amplitude spectrum of the waveform than the narration, but no meaning, was used as a control condition for STORY.

Data acquisition

A 1.5 T MRI scanner (Shimadzu-Marconi Magnex ECLIPSE 1.5 T, Shimadzu Corp., Kyoto, Japan) located at the Advanced Telecommunications Research Institute Brain Imaging Center was used to obtain blood-oxygen level-dependent contrast functional images. Images weighted with their apparent transverse relaxation time ($T2^*$) were obtained with an echo-planar imaging (EPI) sequence (repetition time = 5 s, echo time = 50 ms, flip angle = 90°). A total of 369 image volumes ($64 \times 64 \times 64$ voxels at 3-mm isotropic resolutions that gave a total field-of-view $192 \times 192 \text{ mm}^2$) were acquired over 30 min. In a separate session, high-resolution whole-brain images were acquired from each participant to improve the localization of activation foci using a T1-weighted three-dimensional radio frequency spoiled Fourier-acquired steady-state technique (RF spoiled FAST) covering the whole brain.

Fig. 1



Top panel: task instructions in the EXECUTION condition (scissor, pencil and chopstick). Bottom panel: organization of scanning sessions.

Data processing and statistics

Statistical Parametric Mapping (SPM) 2 software [13] was used for image processing and statistical analysis. The first three volumes of each session were discarded to allow for T1 equilibration, whereas the remaining 120 image volumes were unwrapped [14] and realigned to the first volume; these realigned volumes were used to create a mean image. Estimated head movements did not exceed the acquired voxel size. T2 and T1 structural images were aligned to the mean EPI image and then spatially normalized to the Montreal Neurological Institute (MNI; Montreal, Canada) reference brain. The normalized images of $2 \times 2 \times 2 \text{ mm}^3$ were spatially smoothed for the group analysis using the full-width-half-maximum 6 mm Gaussian kernel. Though the exact location of Broca's area cannot be resolved, it is generally agreed that it includes the dysgranular region of BA44 and granular BA45. To focus on activity in Broca's area, EPI images were thus restricted to all voxels included in a cytoarchitectonically defined probabilistic map of BA44 and BA45 in the left hemisphere [15]. We did not apply smoothing to these EPI images in order to identify task-related activity voxelwise for individual participant analysis.

Parameter estimates for the EXECUTION, IMAGERY, HOLD, STORY and REVERSE trials were determined by fixed-effect analysis for each participant using a box-car

function convolved with a hemodynamic response function and high-pass filtering (cut-off frequency 400 ms). Significance was assessed using voxel-wise *t*-statistics assembled into statistical parametric maps.

Results

Three contrasts of interest were computed [EX: EXECUTION-HOLD, IM: IMAGERY-HOLD and LG (for language): STORY-REVERSE]. The resulting contrast images for each participant were used to compute a random-effect analysis of variance (Table 1 and Fig. 2) to identify voxels that were activated during language perception (LG), tool use (conjunction between EX and IM) and both language perception and tool use (conjunction between EX, IM and LG). The experimental conditions and contrasts were chosen to control for effects because of motor planning, imagery and control, sensory feedback, internal verbalization and auditory sensation. Conjunctions were computed as the minimum statistical value of the contrast images [16], that is, all individual contrasts used for calculating the conjunction are significant at the threshold used. As this implementation of conjunction is conservative and provided our strong hypotheses on the involvement of regions within the left inferior frontal gyrus in the tasks used, all contrasts were thresholded at a *P* value of less than 0.001 uncorrected. In addition, most of the activated

Table 1 Results of the random-effect analysis

No. of voxels	Cluster		Peak				
	Cytoarchitectonic composition ^a		Coordinates (MNI)			Z-value	Cytoarchitectonic probabilities
	No. of assigned voxels	Assigned area	x	y	z		
Language							
521	255	BA45	-52	24	18	4.53	BA45 (80%), BA44 (20%)
	165	BA44					
9	4	BA45	-40	14	28	3.33	BA 44 (50%)
Tool use							
32	29	BA44	-50	2	20	3.43	BA44 (40%), BA3a (10%), BA4p (10%)
2	1	BA44	-58	10	4	3.13	BA44 (40%), BA45 (10%)
1	1	BA44	-50	6	34	3.09	BA44 (40%) BA6 (10%) BA3b (10%)
Language and tool use							
44	28	BA44	-50	8	36	4.69	BA44 (30%), BA6 (10%)
	2	BA6					

BA, Brodmann area; Language, LG; Tool use, conjunction between EX and IM; Language and tool use: conjunction between LG, IM and EX ($P < 0.001$ uncorrected).
^aNumber of voxels assigned to cytoarchitectonic area in the maximum probability maps [17]. Note that the summation is not equal to the cluster size because the maps do not cover the entire cortical surfaces.

clusters survive false discovery rate corrections for multiple comparisons at a P value of less than 0.05 (Fig. 2).

Significantly activated clusters were located using the probabilistic map of BAs [15] implemented in the SPM Anatomy toolbox [17]. Those probabilities were shown in Table 1. The group analysis identified significantly activated clusters for the contrast LG in Broca's area, both BA44 and BA45. The voxels of the larger cluster were assigned to BA44 and BA45. The probability of the assignment to BAs at the peak coordinates of LG cluster was 80% for BA45 and 20% for BA44. The conjunction analysis between EX and IM yielded significantly activated clusters related to tool use in Broca's area. The voxels of the most largely activated cluster was assigned to BA44, with no voxel assigned to BA45. The probability of the assignment to BA at the peak coordinates of this cluster was 40% for BA44, while assignment to BA3p and BA4p was as low as 10%. The conjunction between LG, EX and IM showed an overlap of activity in the dorsal part of BA44. Voxels in this cluster were assigned to BA44 (28 of 44, 64%) and BA6 (two of 44, 5%). The peak of this cluster was assigned probabilistically to BA44 (30%) and, with less probability, to BA6 (10%). Altogether, cytoarchitectonic probabilities corroborate the localization of this cluster to BA44 of Broca's area.

The image at the centre of Fig. 2a shows group mean activity rendered on the mean of individual participants' normalized T1-structural images. Bar graphs of Fig. 2a indicate percent signal changes from control conditions (IM, EX and LG) at the peaks of the three activated clusters illustrated at the centre and detailed in Table 1. The signal changes were averaged across sessions and then participants. As shown in the upper bar graph of Fig. 2a, the peak of the middle cluster ($x = -50$, $y = 8$ and $z = 36$) is significantly activated in the three

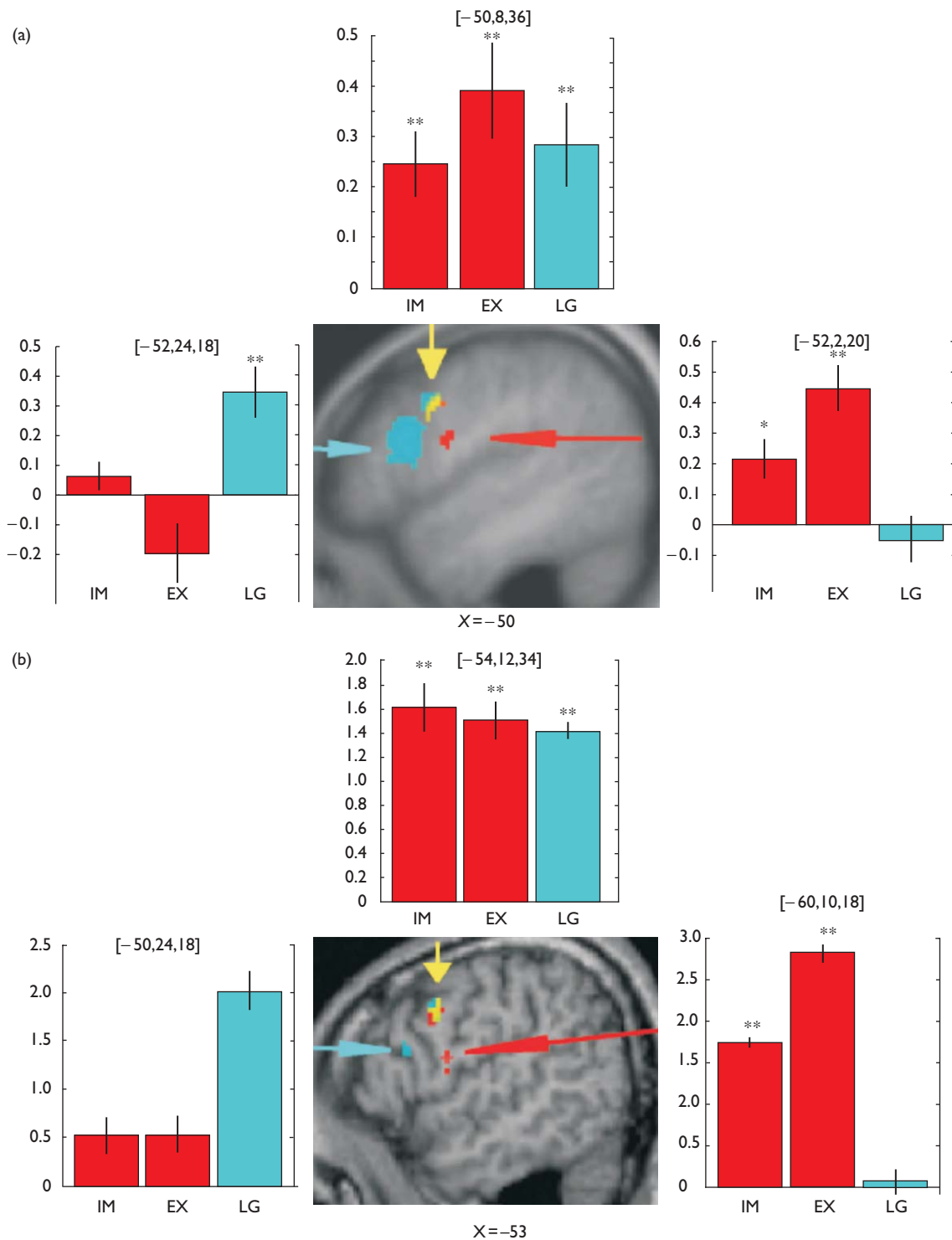
contrasts. The peak in the posterior cluster ($x = -52$, $y = 2$, $z = 20$; right graph) is significantly activated in the two contrasts related to tool use (IM and EX). In contrast, at the peak of the anterior cluster ($x = -52$, $y = 24$, $z = 18$; left graph), a significant increase in activity was only found for the contrast LG. Figure 2b shows results of a typical participant, indicating that the activity pattern is similar to the above group analysis. Out of the 16 participants in the study, eight showed significantly activated voxels for the conjunction of language and tool use (IM, EX and LG) in the posterior part of BA44 at a P value of less than 0.001 uncorrected, and 15 at P value of less than 0.01 uncorrected.

Discussion

A cluster responding to verb generation and a task usually associated with the mirror system, action observation, was previously reported in Broca's area [18]. The tasks in the present experiment are complementary, perception of language and execution of action, in order to fully assess the activity of this area during the execution and the perception in the two fields of research. The overlap of activity between tasks related to language and tool use in the dorsal part of BA44 found in the group analysis (see Fig. 2a) and also present in 15 of the 16 participants (see results from a typical participant in Fig. 2b) suggests that similar neural computations are used for both language perception and skills related to tool use.

Broca's area has an important role in unifying semantics, syntax and phonetic processes, and is important for both language production (verb generation) and comprehension (listening to a story) [19]. Both language production and comprehension rely on the sequential application of syntactic rules used to combine a finite number of symbols to form and understand meaningful sentences [20]. It was reported that the posterior part of Broca's area, comprising the dorsal part of BA44, is involved in

Fig. 2



Activity in Broca's area related to tool use and language. (a) Results of a random-effect analysis superimposed on sagittal sections of the average of our participants' normalized T1 images (cyan: LG; red: conjunction EX and IM; yellow: conjunction of LG, EX and IM.) Histograms show average percent signal change from control condition (IM, EX, LG) averaged across sessions and then participants (\pm standard error). *Significant at $P < 0.001$ uncorrected; ** $P < 0.05$ FDR corrected. (b) Activity from a typical participant superimposed on sagittal sections of the normalized individual T1 image. Histograms show the mean percent signal change averaged across the three sessions (color codes in figure and histograms and error bars follow Fig. 2a).

these syntactic aspects of language [11]. Thus, finding activity in the dorsal part of BA44 for the contrast used to show language-related activities (LG) suggests that in the present experiment, this dorsal part of BA44 is involved in these syntactic aspects of language perception. The tool-use tasks used in our study included the sequential application of learned rules, that is, 'action grammar', for the appropriate control of tool-target interactions (see Methods). It is known that observation of sequenced biological actions activates Broca's area [21]. In agreement with our hypothesis, the execution or imagination of sequential actions in the tool-use tasks used here (IM and EX) also activates Broca's area.

The cluster activated by both tool use and language (IM, EX and LG) is located in the dorsal part of BA44. This part of Broca's area was recently proposed to be devoted to grammatical aspects of language [11] and specifically to complex hierarchical sequential processing (e.g. understanding of embedded sentence), but not for simpler forms of grammar processing devoid of hierarchical structure [3]. As application of sequentially organized rules is a common feature between the tasks used in this experiment, comprehension of complex sentences and correct sequential use of common tools, the overlap of brain activity supports our hypothesis that the same neural processes are used to process these complex hierarchical structures despite the difference between their cognitive fields, language and motor control, respectively. Furthermore, these data, together with earlier findings of common activity for execution and perception of language and action [18], suggest that this region is part of a mirror system devoted to the processing of complex hierarchical structures. The homologue region in the right hemisphere is more activated for the execution of a complex form of tool making, that possess a hierarchical structure, than for a simpler form of tool-making devoid of such a structure, and this hierarchical involvement was interpreted in relation to the evolution of language [22]. In addition, the use of a common system for execution and perception of both language and action may maximize the computational power of limited neural resources.

There are similarities between language and tool use in terms of their underlying computational principles, in particular, their hierarchical structure. The overlap of brain activity reported in the present experiment in a region devoted to processing of complex grammar suggests that the same neural processes underlie these similar computational principles between language and tool use. This system could be uniquely human [20] and could have been first devoted to language before being gradually expanded and adapted for tool use. Yet, in monkeys, neural correlates of tool use include the depth of the arcuate sulcus [7], the putative homologue of human BA44 [8]. In addition, modern humans performing

the oldest form of tool making found in archaeological records activate the same left inferior frontal cortex region [23]. Thus, our finding of an overlap of activity in BA44 supports the gradual view that the neural correlates of sequentially organized behaviour, exemplified by tool use, were already present in a rudimentary form in our last common ancestors with primates, and were later exapted to support language in humans [1].

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