Broca's area and the language instinct

Mariacristina Musso[1], Andrea Moro[2], Volkmar Glauche[1], Michel Rijntjes[1], Jürgen Reichenbach[3], Christian Büchel[1] & Cornelius Weiller[1]

Language acquisition in humans relies on abilities like abstraction and use of syntactic rules, which are absent in other animals. The neural correlate of acquiring new linguistic competence was investigated with two functional magnetic resonance imaging (fMRI) studies. German native speakers learned a sample of 'real' grammatical rules of different languages (Italian or Japanese), which, although parametrically different, follow the universal principles of grammar (UG). Activity during this task was compared with that during a task that involved learning 'unreal' rules of language. 'Unreal' rules were obtained manipulating the original two languages; they used the same lexicon as Italian or Japanese, but were linguistically illegal, as they violated the principles of UG. Increase of activation over time in Broca's area was specific for 'real' language acquisition only, independent of the kind of language. Thus, in Broca's area, biological constraints and language experience interact to enable linguistic competence for a new language.

The ability to acquire a language is a unique and essential human trait. Darwin argued that language is an instinct, like the upright posture[1]. It is well known that children acquire their mental grammar spontaneously from their parents' speech. Forty years ago, Chomsky proposed that for generalizing from a sample of sentences to language as a whole, an innate set of mental computations is required[2]. On the basis of linguistic analyses of sentence structure, he argued that a common design, called universal grammar (UG), underlies "the Babel of languages"[3,4]. This universal plan of all languages suggests a predetermined brain system[5]. Several functional neuroimaging studies have shown that in people who acquired two different languages before a 'critical age'[6], an overlapping cortical representation is used for both languages. The same result has been shown for semantic processing in late bilinguals, who have an equally high proficiency for both languages[7].

In the present study, we investigated the system underlying the acquisition of new linguistic competence of two, albeit parametrically different[8], languages: Italian and Japanese. When postulating an epigenetic role of a brain system in language learning, the acquisition of linguistic competence should involve this brain system only when the new language (whether Italian or Japanese or any other 'real' language) is based on the principles of UG. Conversely, learning an artificial language that does not follow the principles of UG should depend on other brain systems[9]. Whether or not acquisition of a new language in adults depends on a general learning ability is controversial, however. Some claim that nonspecific learning mechanisms, which are not associated with particular cognitive domains, underlie the acquisition of new linguistic competence[10,11]. According to this perspective, 'unreal' and 'real' languages should involve the same brain systems.

In the first of two fMRI studies, 12 native German speakers who had never been exposed to Italian or any other Romance language

learned three grammatical rules of Italian and three artificial rules of an unreal language using Italian lexicon (**Table 1**). The first grammatical rule concerned the so-called 'null-subject' parameter[8]; in German and closely related languages, the subject is obligatorily and overtly expressed, whereas in Italian it is not. For example, the German sentence *Ich esse eine Pizza* ("I eat a pizza") corresponds to Italian *Mangio una pizza*, where the subject *io*, or "I," is not overtly expressed. The second rule concerned the passive construction in which the object of a transitive verb (sometimes referred to as the 'patient') becomes the subject and the subject (referred to as the 'agent') either becomes a prepositional phrase or is suspended. For the example "Mario buys a newspaper," or in German, "*Mario* [S, subject] *kauft* [V, verb] *die Zeitung* [O, object]," is transformed into the passive form "*Die Zeitung* [S] *wird* (*von Mario*) [P, prepositional phrase] *gekauft* [V]," meaning "The newspaper is bought (by Mario)." In Italian this is translated as "*Il giornale* [S] *è comprato* [V] (*da Mario* [P])." The third rule concerned subordinate declarative constructions. Italian maintains the same subject-verb-object (SVO) order as in the main-clause phrase; in contrast, German typically uses the SOV order. For example, "*Maria sagt, dass Mario* [S] *die Zeitung* [O] *kauft* [V]," meaning "Maria says that Mario buys the newspaper" in German, would be "*Maria dice che Mario* [S] *compra* [V] *il giornale* [O]" in Italian. Although the order of the elements in passive and subordinate phrases is different in Italian versus German, in every natural language grammar (including Italian and German), the noun phrases and the verb phrase within a clause typically receive their grammatical role (*e.g.*, subject or object) by means of hierarchical relations[8] rather than through the bare linear order of the words in a string. (Linear order can, however, be modified to affect meaning according to UG)[12]. These absolute principles define the design characteristics of language[8] and are therefore responsible for some

core similarities across languages. Thus, these three Italian grammatical rules, as well as their German counterparts, represent examples of real rules of language.

The unreal language that we was used in a control task was constructed by manipulating Italian. It makes use of the Italian lexicon, but does not entirely reproduce Italian syntax. In the unreal grammar learning task, the subjects could not relate the nominal and verbal elements by means of any hierarchical order, as the new rules defined a mere linear order of the single words. A similar paradigm was previously designed to test a 'language savant' who could master different real languages, but not the unreal one[13]. In the first rule, negative sentences were built by putting the negation word *no* always after the third word of the phrase. For example, "*Maria* [1] *compra* [2] *il* [3] *caffè* [4]," or "Maria buys the coffee," becomes "*Maria* [1] *compra* [2] *il* [3] *no caffè* [4]." The second rule required that the interrogative construction be built by inverting the linear sequence of the words of a sentence For example, "*I* [1] *bambini* [2] *amano* [3] *il* [4] *gelato* [5]," or "The children love ice cream," becomes "*Gelato* [5] *il* [4] *amano* [3] *bambini* [2] *i* [1]." The third rule arbitrarily emphasized a specific word position for choosing the correct indefinite article (*un* or *uno* for masculine (m.); *una* for feminine (f.)). In the unreal Italian, indefinite articles within a sentence always agree with the last noun of the phrase. For example, "a girl loves a boy," in which "girl" is a feminine noun and "boy" is a masculine noun, becomes "*Un* (m.) *ragazza* (f.) *ama un* (m.) *ragazzo* (m.)," rather than "*Una* (f.) *ragazza* (f.) *ama un* (m.) *ragazzo* (m.).

In the second fMRI study, another group of 11 native German speakers participated in a similar experiment; but this time the language to learn was Japanese (**Table 2**). Subjects were screened carefully to ensure that they had not previously been exposed to Japanese. The first grammatical rule concerned the construction of the main-clause phrase; Japanese normally uses the SOV order, and German the SVO order with inflected V. For example, the German sentence "*Maria* [S] *iβt* [V] *eine Pizza* [O]," meaning "Maria eats a pizza," corresponds to "*Maria wa* [S] *piza o* [O] *taberu* [V]," ("Maria a pizza eat") in Japanese. The second and third grammatical rules concerned the same structures as in the Italian experiment: passive constructions and subordinate clauses. Consider passive constructions first: unlike German and Italian, Japanese does not use modal verbs (such as "to be"—*sein* and *essere* in German and Italian, respectively), but rather a passive suffix, *–reru*, on the verb. Thus, the German passive sentence "*Das Gedicht* [S] *wird* [V (modal)] *vom Dichter* [P] *geschrieben* [V]," or "The poem is written by the poet," is translated to Japanese as "*Shi wa* [S] *sakka ni* [P] *kakareru* [V + suffix]". Japanese has various options for the subordinate clause. To simplify, we opted

for only one format: "Maria says that Paul drinks a coffee" becomes "*Maria* [S_m, subject of main clause] *sagt* [V_m, verb of main clause] *dass Paul* [S_s, subject of subordinate clause] *einen Kaffee* [O_s, object of the subordinate clause] *trinkt* [V_s, verb of subordinate clause]" in German and "*Maria wa* [S_m] *Paul ga* [S_s] *kohi o* [O_s] *nomu* [V_s] *to iu* [V_m]" in Japanese.

Paralleling the first study, the unreal language used as a control task in this experiment was not totally artificial, but resulted from the selective manipulation of some Japanese grammatical rules, rendering them linguistically illegal. Two of the artificial rules were identical to those in the experiment with Italian: the construction of the negative sentence in the manipulated Japanese was built by putting the negation word *nai* ("no") always after the third word in the linear sequence of words in all sentences. For example, "Maria does not eat a pizza" is "*Maria* [1] *wa* [2] *piza* [3] *nai o taberu*," whereas interrogative phrases were built by inverting the order of the single words: "*Taberu* [5] *o* [4] *piza* [3] *wa* [2] *Maria* [1]." Since articles (definite and indefinite) are not used in Japanese, we designed an alternative third rule to match that in the unreal

Table 1 Sample sentences used in the Italian fMRI experiment

	Italian (real language learning task)	German (native language of subjects)
Null-subject parameter	Mangio la pera "Eat the pear"	Ich esse die Birne "I eat the pear"
Passive construction	La pera è mangiata da Paolo "The pear is eaten by Paolo"	Die Birne wird von Paul gegessen "The pear is by Paul eaten"
Subordinate construction	Pia dice che Paolo mangia la pera "Pia says that Paolo eats the pear"	Pia sagt, dass Paul die Birne isst "Pia says that Paolo the pear eats"
	Unreal Italian **(artificial rules violating UG)**	
Negative construction	Paolo mangia la no pera "Paolo eats the no pear"	
Interrogative construction	Pera la mangia Paolo "Pear the eats paolo"	
Use of indefinite article	Una bambino mangia una pera "A (fem.) child (masc.) eats a (fem.) pear (fem.)"	

Table 2 Sample sentences used in the Japanese fMRI experiment

	Japanese (real language learning task)	German (native language of subjects)
Main clause construction	Paul wa nashi o taberu "Paul pear eat"	Paul iβt die Birne "Paul eats the pear"
Passive construction	Nashi wa Paul ni taberareru "Pear Paul eat-passive suffix"	Die Birne wird von Paul gegessen "The pear is by Paul eaten"
Subordinate construction	Pia wa Paul ga nashi o taberu to iu "Pia Paul pear eat that says"	Pia sagt, dass Paul die Birne isst "Pia says that Paolo the pear eats"
	Unreal Japanese **(artificial rules violating UG)**	
Negative construction	Paul wa nashi nai o taberu Paul pear eat no	
Interrogative construction	Taberu o nashi wa Paul Pear eat Paul	
Past-tense construction	Paul wa nashi o-ta taberu Paul pear-ta (suffix past) eat	
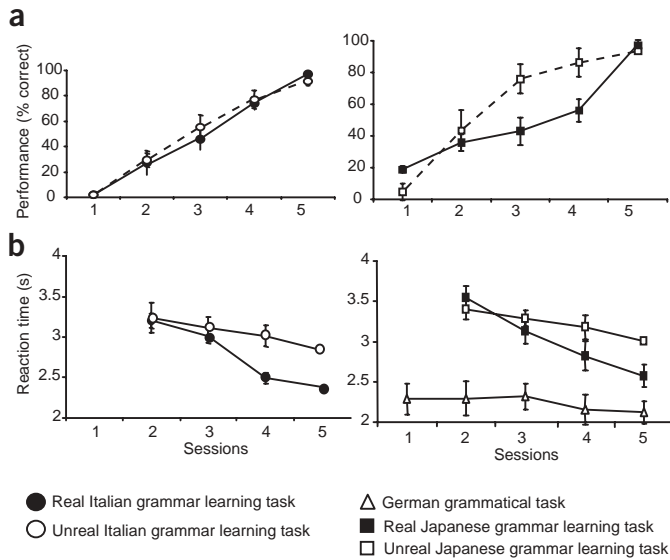
Figure 1 Behavioral measurements. (**a**) Performance (mean % correct) in judging the syntactical correctness of the sentences presented in each of the five fMRI sessions per learning task (data averaged across subjects). Performance showed an improvement across sessions during the learning tasks. Performance increase was not significantly difference between the acquisition of real versus unreal Italian (left) or Japanese (right) grammatical rules. (**b**) Mean reaction times (RT) for the correct syntactical judgment of the presented sentences in each of five fMRI sessions per task. Subjects showed a significant RT reduction ($P < 0.0001$) across sessions in all grammatical rules learning tasks. Reaction times were faster during the grammatical learning tasks (either Italian or Japanese) than during the artificial learning tasks ($P < 0.03$).

native language), Italian and Japanese—are parametrically different. For example, German is an overt subject language, whereas Italian and Japanese are null-subject languages; Japanese is an object-verb language, whereas Italian is a verb-object language. Parameter setting constitutes a fundamental aspect of language acquisition, as it captures the core differences among all human languages in classes of equivalence[8,9].

RESULTS
Behavioral results

We analyzed data from eight subjects in each experiment. They were unaware of the nature of the different rules before learning (see Methods). They obtained equally high accuracy (% correct) at the end of the experiment in all syntactic tasks (real Italian, 97 ± 4.1% (mean ± s.d.); unreal Italian, 91.6 ± 10%; real Japanese, 97 ± 3.2%; unreal Japanese, 94 ± 4.68%). The learning curves for each condition (real and unreal grammatical learning tasks) were not linear (**Fig. 1a**). In the third session of the Japanese experiment

Italian. For this, we manipulated the morphosyntactic rule regarding past tense. In the unreal Japanese, the past tense was built by adding the suffix *-ta*, not on the verb element as in real Japanese, but on the second word, counting from right to left, in all sentences. For example, the present-tense sentence "*Maria* [5] *wa* [4] *piza* [3] *o* [2] *taberu* [1]" becomes "*Maria* [5] *wa* [4] *piza* [3] *o-ta* [2] *taberu* [1]."
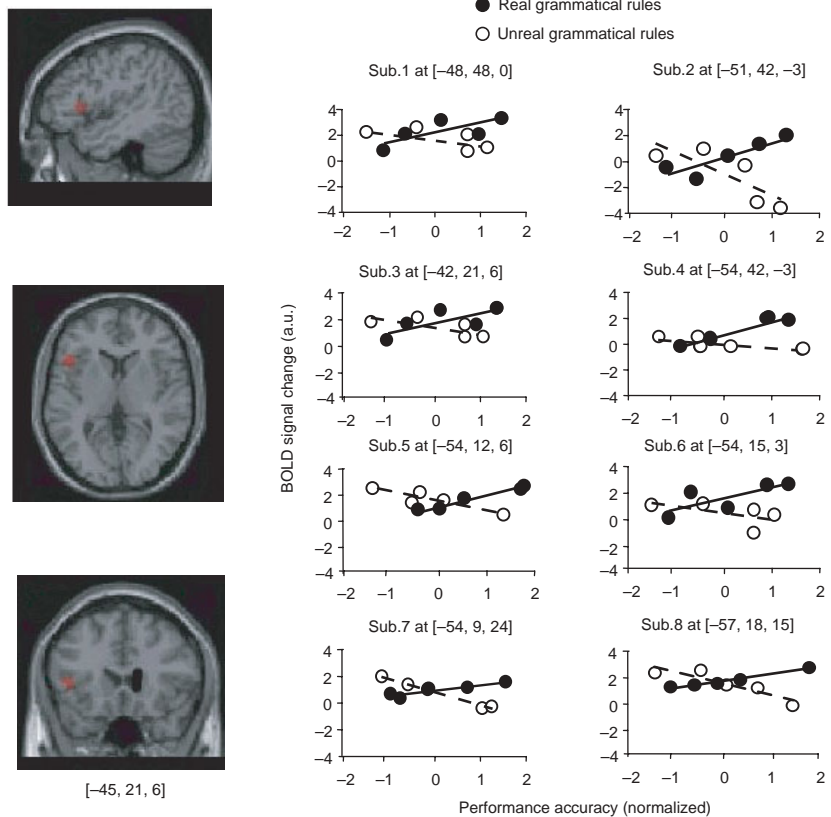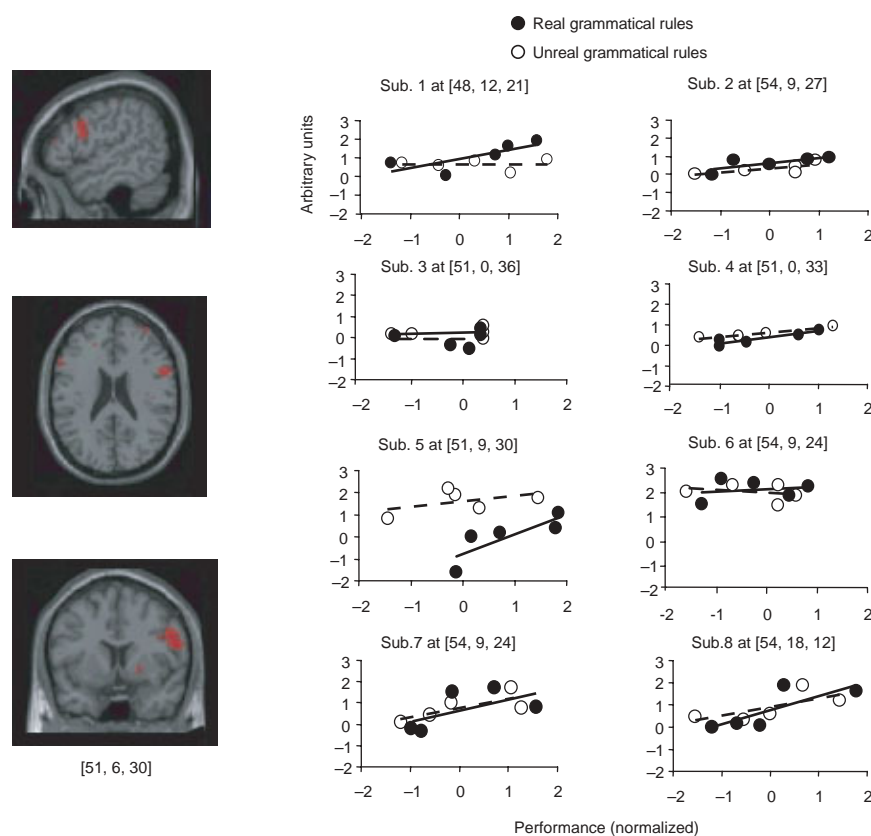
Using fMRI, we tested for differences in brain activity between acquisition of real and unreal grammars (both foreign to the German subjects). The unreal grammars were not entirely artificial as in previous studies of language acquisition in adults[14–16], but rather resulted from the selective manipulation of Italian or Japanese grammatical rules, rendering them linguistically illegal. Crucially, only experiments using real languages can include all components of grammar (morphology, semantics, syntax, phonology mediated by written language) and also involve parameter setting. The three real languages used here—German (subjects'

Figure 2 Result of the interaction between performance and type of rule learning (real versus unreal Italian). Left, the activation specific to real language acquisition resulting from the random effects analysis is displayed on selected slices of the MRI template available in SPM99. The threshold was set at $P < 0.05$ (corrected for multiple comparisons). Right, plots of changes in BOLD (blood oxygen-level dependent) signal in the left inferior frontal gyrus (Talairach coordinates *x, y, z*: –45, 21, 6) for the five sessions containing 'real grammatical rule' trials and the five sessions with 'unreal grammatical rule' trials are shown as a function of accuracy within sessions. The distances between individual subjects' peak voxel and the peak voxel derived from the group analysis using a random model were 28, 23, 3, 24, 13, 11, 23 and 15 mm, respectively, for subjects 1–8. See **Supplementary Fig. 1** online for individual data plotted by session.

● Real grammatical rules
○ Unreal grammatical rules

Sub. 1 at [48, 12, 21]   Sub. 2 at [54, 9, 27]

Sub. 3 at [51, 0, 36]   Sub. 4 at [51, 0, 33]

Sub. 5 at [51, 9, 30]   Sub. 6 at [54, 9, 24]

Sub.7 at [54, 9, 24]   Sub.8 at [54, 18, 12]

Arbitrary units

Performance (normalized)

[51, 6, 30]

Figure 3 Results of the conjunction analysis of the real and unreal Italian learning experiment. Left, the common patterns of activation are shown on slices from the MRI template used for the normalization. The threshold was set at $P < 0.05$ (corrected for multiple comparisons). Right, plots of changes in BOLD signal in the right inferior frontal gyrus (*x, y, z*: 51, 6, 30) are shown as a function of performance during acquisition of grammatical rules of either real Italian or of an unreal language. The distances between single-subject activation and main-group activation in the conjunction analysis were about: 11, 5, 8, 6, 3, 7, 7 and 21 mm, respectively, for subjects 1–8. See **Supplementary Fig. 2** online for individual data plotted by session.

in particular, there was an inflection in performance on the real versus unreal grammatical tasks. There was no significant difference in performance across sessions between real and unreal language learning tasks ($t_7 = 0.1$, $P = 0.57$ in the first fMRI experiment and $t_7 = 0.5$, $P = 0.32$ in the second; **Fig. 1a**).

We also analyzed reaction times (RTs), measured as latency from the appearance of the written sentence to the correct button-press response with the left hand (**Fig. 1b**). Subjects showed a significant reduction in RT and improvement in accuracy over the course of the sessions. In each of the four experiments—real and unreal Italian, real and unreal Japanese—the reduction in RT (comparing performance in first vs. last session) was significant ($t_7 = 0.79$, $P < 0.0001$). In addition, the grammatical judgments during the real (Japanese or Italian) grammatical learning tasks were faster than during the unreal ones (real versus unreal Italian, $t_7 = 0.79$, $P < 0.0001$; real versus unreal Japanese, $t_7 = 1.9$, $P < 0.03$).

Functional imaging results

Concerning the fMRI data, the overall main effect of performing the classification task (judging grammatical correctness of sentences) compared to the baseline task (looking at the black screen) showed activation in widely distributed areas, including prefrontal, parietal, anterior cingulate, occipital cortex, inferior and middle temporal gyrus and the cerebellum on both hemispheres ($P < 0.05$, corrected for multiple comparisons).

We used a random-effects model to identify the activation pattern specific to the interaction between change in blood oxygen–level dependent (BOLD) signal and type of rule learning (real versus unreal), as reflected by the individual accuracy of performance for each session. We used this regression analysis because task performance is directly linked to behavior in this case[17]. No specific pattern of

brain activation was found for unreal grammatical acquisition (Italian or Japanese). An interaction between real and unreal grammatical acquisition was evident in two different parts of the pars triangularis of the left inferior frontal gyrus (Broca's area, corresponding to Brodmann's area 45). The relative distance between the activation resulting from learning Italian and Japanese was about 12 mm (**Fig. 4**). Increase of BOLD signal in this area correlated with the increase in accuracy during the acquisition of natural rules (Italian or Japanese) (**Figs. 2** and **4**).

The correlation coefficient between parameter estimates in Broca's area and accuracy of performance within sessions showed: (i) a significant positive correlation between BOLD signal and accuracy in the real grammatical task (Italian experiment, $r = 0.66$, $P < 0.001$; Japanese experiment, $r = 0.47$, $P < 0.001$), (ii) a significant negative correlation between parameter estimates and learning unreal rules (Italian experiment, $r = -0.50$, $P < 0.001$; Japanese experiment, $r = -0.32$, $P = 0.021$).

The common anatomical substrate for learning either grammatical or artificial rules was identified using a random effects model and a conjunction analysis. In this analysis, a significant increase in BOLD signal, parallel to the improvement in performance in both tasks, was found in two different parts of the right inferior frontal gyrus, anterior to the precentral sulcus (**Figs. 3** and **5**). Additional activation was found in the left lingual gyrus. In the Japanese study, the conjunction analysis showed a further activation in the left cingulate, right insula, right supramarginal gyrus and left cerebellum.

The correlation coefficient for the group between parameter estimates in right inferior frontal gyrus and accuracy within sessions (**Figs. 3** and **5**) showed a significantly positive correlation between BOLD signal and accuracy of performance for both the real grammatical tasks (Italian, $r = 0.37$, $P = 0.008$; Japanese, $r = 0.21$, $P = 0.009$) and the unreal grammatical tasks (Italian, $r = 0.33$, $P = 0.01$; Japanese, $r = 0.040$; $P = 0.004$).

DISCUSSION

Our results showed a significant correlation between the increase in BOLD signal in the left inferior frontal gyrus and the on-line performance for the real, but not for the unreal language learning tasks. This stands as neurophysiological evidence that the acquisition of new linguistic competence in adults involves a brain system that is different from that involved in learning grammar rules

Figure 4 Results of the interaction between performance and type of rule learning (real Italian versus unreal Italian in yellow; real versus unreal Japanese in red) resulting from the random effects analysis are shown on selected slices of the T1 template, thresholded at $P < 0.001$ (uncorrected) for visualization. Right, plots of individual changes in BOLD signal in the left inferior frontal gyrus during the acquisition of grammatical rules of either real or unreal Japanese are shown as a function of accuracy within sessions The distances between individual subjects' peak voxel and the peak voxel derived from the group analysis using a random model were 12, 21, 25, 9, 9, 9, 6 and 11 mm, respectively, for subjects 1–8. See **Supplementary Fig. 3** online for individual data plotted by session.

[–45, 21, 6] Italian experiment (yellow)
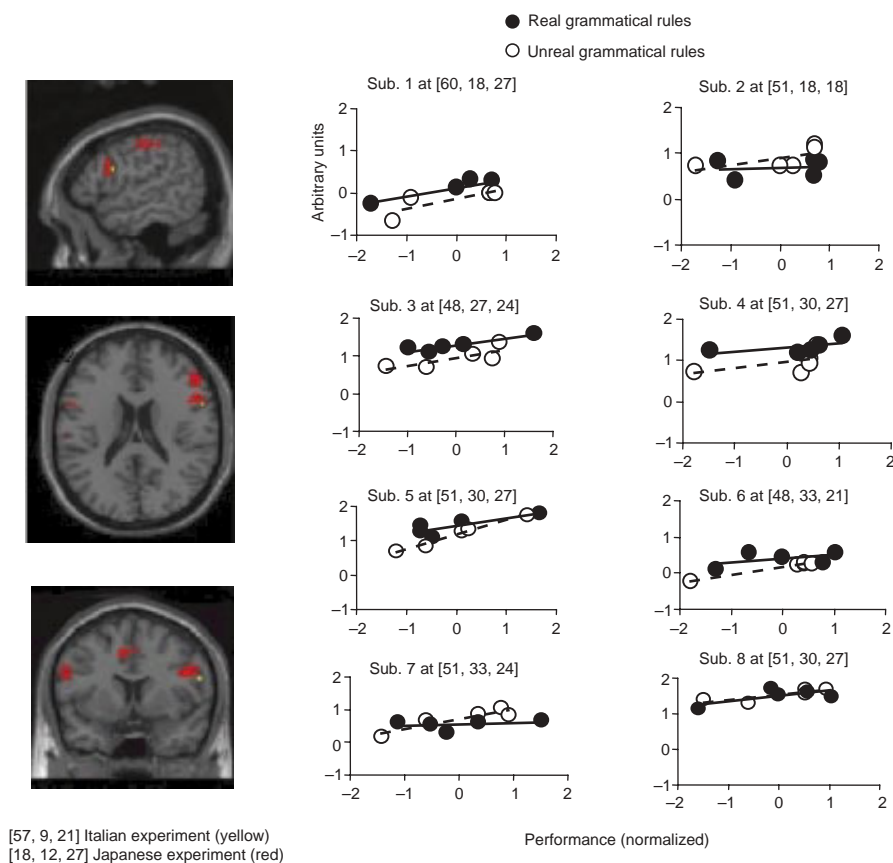[–45, 33, 3] Japanese experiement (red)
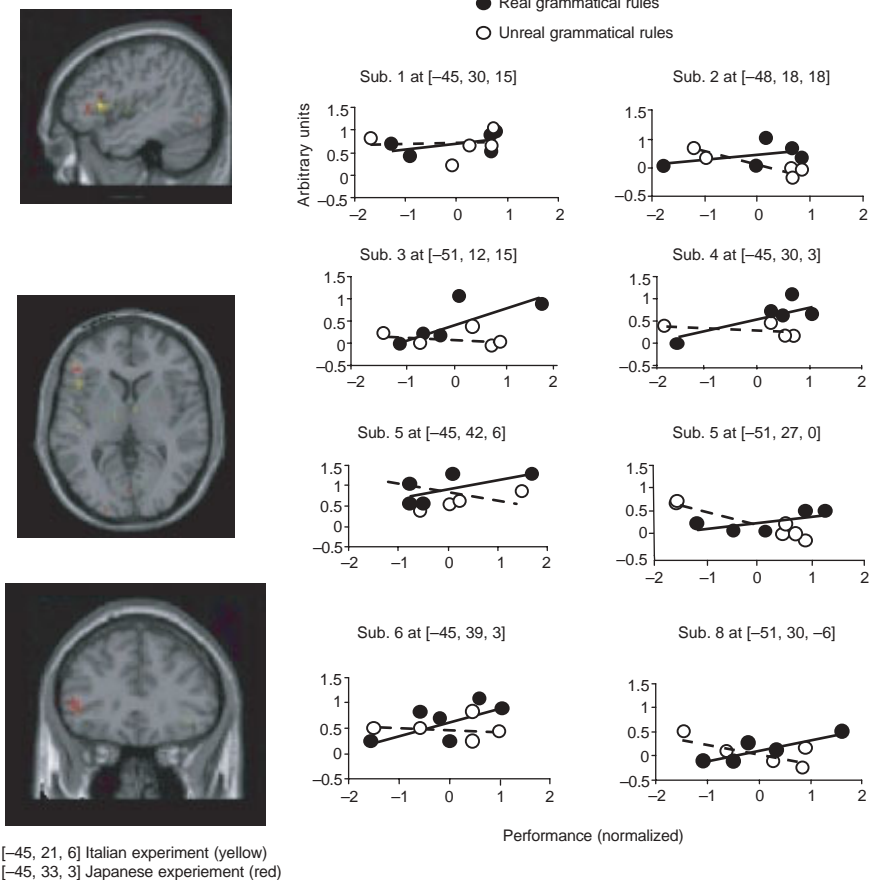
that violate UG. More specifically, our results show that Broca's area has a key role in the acquisition of 'real' rules of language, independent of the linguistic family to which the language belongs. Thus, the investigation of parametrically different languages, such as Italian and Japanese, allows relevant statements about the mechanisms of language acquisition in general.

Unlike children, adults acquire a new language by learning explicit information about the rules of a foreign grammar, as our subjects did during both learning tasks. A common activation for both conditions was found in the right inferior frontal gyrus (**Figs. 3** and **5**). Several functional imaging studies have shown that right prefrontal cortical regions, including the frontal pole (Brodmann's area 10), the inferior frontal gyrus and the lateral dorsal frontal areas, are part of an extensive neuronal system that subserves episodic memory retrieval[18–25]. Humans and monkeys with frontal lesions can perform normally on recognition memory tasks (reporting whether stimuli were previously seen or not), but they are severely impaired in tasks requiring monitoring of selections[23,25]. A putative role of the right inferior frontal gyrus in the acquisition of both kinds of rules (real and unreal) is to monitor each kind of information independent of its character; that is, to retrieve hierarchical or linear information from episodic memory to make an appropriate response. Thus, explicit retrieval of information seems to be insufficient to obtain new linguistic competence.

We found that the acquisition of linguistic competence selectively involved Broca's area. This activation should not be related to explicit memory systems associated with unspecific cognitive domains. This system was equally involved in learning real and unreal rules, which were all novel for our subject and were learned during the fMRI experiment (see Methods). The behavioral analysis of the response times showed that subjects answered progressively faster during the real grammatical tasks than during the 'unreal' grammatical tasks (**Fig. 1b**). A possible explanation of this result could be that proceduralization of rule-knowledge occurred during the 'real' grammatical learning task[26]. The progressive consolidation of knowledge could be transferred to other sentence material, resulting in a shorter time required to give the correct answer[18]. Several authors assume, even in language learning, a single, instead of dual, learning system that is neither exclusively explicit nor implicit, but for which the level of awareness ranges from explicit to implicit states on a continuum[27]. Thus, it does not mean that the activation of Broca's area relates selectively to memory processing. The contribution of this brain region to memory is, in fact, disputable and may have been downplayed previously because of its interdependent role in active language processing[18]. Rather, these behavioral results support the automatic and implicit character of the activation of Broca's area[28–30].

An indisputable and essential function of this, albeit heterogeneous and polymodal, brain region (particularly the pars triangularis) is the processing of syntactic aspects of language[29–33]. Activation of Broca's area is independent of the language (English, Chinese, German, Italian or Japanese) of subjects[29–33], suggesting a universal syntactic specialization of this area among 'real' languages[33]. On the basis of these previous and present results, we posit that this brain region is specialized for the acquisition and processing of hierarchical (rather than linear) structures, which represent the common character of every known grammar. The negative correlation between the BOLD signal in Broca's area and learning unreal grammatical rules adds additional support to the idea that this area is specialized for identifying natural principles of language. We speculate that in learning an unreal grammar, Broca's area is progressively disengaged. Moreover, it could well be the case that the hierarchical structure is typical but may not be specific for language, in accord with studies on musical harmony, which also found activation of Broca's area[28,34]. Our data show, however, that in adults the ability to learn and to individuate hierarchical struc-

Figure 5 Conjunction analysis of the real-unreal Japanese (red) and Italian (yellow) learning experiment. Left, common patterns of activation are shown on slices of the MRI template. The threshold was set at $P < 0.05$ (corrected for multiple comparisons). Right, plots of changes in BOLD signal in the right inferior frontal gyrus are shown as a function of performance during acquisition of grammatical rules of real or unreal Japanese. The distances between single-subject activation and main-group activation in the conjunction analysis were about 15, 5, 0, 0, 0, 7, 4 and 0 mm, respectively, for subjects 1–8. See **Supplementary Fig. 4** online for individual data plotted by session.

show the crucially non-recursive syntactic abilities that characterize human language. Signs produced by apes are not coordinated into well-defined motion contours of American Sign Language, and they are not inflected for aspect and agreement[5,42]. On the other hand, *FOXP2* in humans seems to be the target of selection during recent human evolution[39]. According to anatomical studies, monkeys show a human-like left-hemisphere asymmetry[43] and a cellular and functional inhomogeneity[40,41,44], but the caudal part of the left inferior frontal lobe has less cellular density and is less differentiated than in humans[41,45].

Our results indicate that the left inferior frontal gyrus is centrally involved in the acquisition of new linguistic competence, but only when the new language is based on principles of UG. The anatomical and functional features of Broca's area allow us to speculate that the differentiation of this area may represent an evolutionary development of great significance, differentiating humans from other primates.

METHODS

Subjects and stimuli. In the Italian learning study, we tested 12 German native speakers, but only 8 (4 women and 4 men, mean age 24.3) could be included in the data analysis. Three subjects were excluded because of technical problems during fMRI (the response device failed), and one did not significantly improve in performance in both tasks. In the Japanese experiment, we tested 11 subjects, but included only 8 in the analysis (4 women and 4 men, mean age 22.6). Two could not be used because of technical problems and one because of performance. All had no history of neurological or psychiatric disease and were right-handed[46]. The subjects in the Italian learning experiment were born and raised in East Germany, former German Democratic Republic, and had not learned any romance languages or English at school. The subjects taking part in the Japanese learning study did not have any knowledge of Japanese or other Asian languages. All participants reportedly had normal language development and no difficulties at school, particularly in language learning. All subjects showed normal verbal memory abilities and intelligence as tested by the California Verbal Learning Test[47] and the Intelligenz Struktur Analyse[48]. Subjects were recruited on a voluntary basis and gave their written informed consent to participate. The study was approved by the local ethics committee at FSU Jena. During the fMRI experiment, subjects learned three real grammatical rules of Italian or Japanese and three artificial rules of an 'unreal' language, which also used Italian or Japanese vocabulary. The capacity to learn and retain new words is the result of learning through memory abilities that are not specific for language[49]. Thus, before the fMRI experiment, the volunteers received a list containing all the words used in the experimental tasks (33 substantives with their relative definite

tural rules selective for a foreign language is localized in Broca's area. The acquisition of new real linguistic competence seems to have an implicit character, as indicated by our behavioral results. Several authors consider syntax processing (in native language[29] and in music[28]) in the left inferior frontal gyrus to be automatic and involuntary. A recent study shows that adults who, like our subjects, reached a high accuracy after training on an artificial language that follows real grammatical rules, show a left early anterior negativity[16], an event-related brain potential (ERP) reflecting highly automatic parsing processes[29,30].

The central role of Broca's area in acquiring a language with high proficiency is also demonstrated by the presence of functional and structural abnormalities in left prefrontal cortex, including Broca's area, in dysphasic members of the KE family[35]. Despite normal intelligence, these individuals show speech and language impairments, including a selective deficit in constructing the grammatical categories of number and tense[36]. It is unlikely that this deficit selectively affects language, as these subjects also seem to be deficient in perception and production of rhythm in both vocal and manual modalities[37]. Damage to a specific gene (*FOXP2*) is reportedly responsible for the disorders of the affected members of the KE family[38]. Whatever the exact function of this gene is, this study is consistent with multiple linguistic observations that specific language impairments not only run in families but are more concordant in identical than in fraternal twins[5]. These studies show that genetic material influences language ability[5,38,39], although the relation between syntax and genetics has not yet been understood.

Our results support a common origin for human speech and some form of communication in non-human primates[39–43]. Chimpanzees and gorillas are able to learn words, but they do not

article and 6 verbs in the Italian learning experiment; 21 substantives and 4 verbs in the Japanese learning experiment), which they had to learn by heart to avoid confounding syntactic rule acquisition with word learning. They did not receive any information about phonological aspects of the words. Italian verbs were all with suffix –*are* and the helping verb *essere* (to be), and were learned in both present and past participle tenses. The Japanese verbs were learned in their present form only. Before scanning, we tested the recall ability of the complete list of the words. During the activation task of each epoch (total of 3 'activation' epochs per session; 30 for the whole fMRI experiment), the subjects read six simple sentences in the real and in the unreal language tasks and then judged their syntactic correctness (**Tables 1** and **2**). Performance during scanning was controlled by button presses with the left middle finger (correct sentence) or with the left index finger (incorrect sentence). The sentences were different in every session to avoid automatic answers, but comprised the same vocabulary.

As none of the subjects knew Italian or Japanese before the fMRI experiment, subjects learned the real and the unreal grammatical rules during pauses of 3 min (1 min for each rule) between sessions. Stimuli were presented visually to the subjects, while lying in the scanner, in the form of slides. One slide was presented describing each rule (for 30 s) with sentences to clarify the rule, followed by one slide for each rule (also for 30 s) with several examples, some of which were grammatically incorrect. Here, the subject had to judge the grammatical correctness of the stimuli. During training, response feedback was given (whether response was correct or incorrect). We used different sentences and examples for each training session. The subjects were able to ask questions during the training phase, but normally they did not ask, so that all received the same training. A pilot study using 20 subjects confirmed the effectiveness of both training programs off-line.

fMRI scanning and data analysis. Both experiments were performed on a 1.5-tesla whole-body magnetic resonance (MR) scanner (the Italian experiment took place in Jena, the Japanese study in Hamburg; both Siemens VISION scanners) by using multi-slice single-shot gradient echo-planar imaging (EPI) (40 slices, TE = 60 ms, TR = 5 s, 192 mm × 192 mm f.o.v., 64 × 64 pixel matrix and 3 × 3 × 3 mm voxels). The fMRI experiment consisted of ten sessions, with six epochs each. Between the sessions a specific training of 3 min took place without scanning. For each session, 36 whole-brain volumes were acquired, during which the activation task and a baseline condition ("look at the black display screen") were alternated three times every 30 s. The whole experiment lasted about 44 min.

Image processing was done with SPM99 (www.fil.ion.ucl.ac.uk/spm). Images were realigned to the first image to correct for interscan movements, resliced using a sinc interpolation, adjusted for residual motion-related changes and spatially normalized to a standard EPI template to allow for group comparisons. The data were smoothed with a Gaussian filter of 9 mm to account for residual intersubject differences. A high-pass filter with a cut-off of 120 s was used to remove low-frequency drifts.

Statistical analysis was performed using the general linear model as implemented in SPM99. Each experiment comprised 8 subjects, 80 sessions (10 sessions per subject) and 3 conditions (real grammatical judgment, unreal grammatical judgment and rest).

A group analysis was performed using a first and a second level analysis (*i.e.* random effects model). The threshold adopted was $P < 0.05$ (corrected for multiple comparison). For the random-effects model, a first-level analysis provided a contrast image for each comparison and each subject. We were interested in two comparisons: BOLD signal change for learning real versus unreal grammar (interaction) and the common effect of both real and unreal rule learning.

To test hypotheses about regionally specific condition effects, the parameter estimates were compared with the external variable, which best reflects the grammatical or 'unreal-grammatical' learning improvement within the experiment, as indexed by the number of correct answers in each session (**Figs. 2** and **4**). To permit a comparison with the estimates, the accuracy of the performance was expressed as normalized values, calculated by subtracting the experimental values from the mean, divided by the standard deviation (s.d.). In the conjunction analysis, we looked at the common effect resulting from the interaction between both type (real and unreal grammatical) of rule and BOLD signal recorded during grammatical and unreal grammatical trials. Again, the parameter estimates were compared with the individual performance (**Figs. 3** and **5**).

In a second-level analysis, the contrast images resulting from the first-level analysis were the basis of a multi-subject comparison (one-sample *t*-test for the first comparison and ANOVA for the conjunction analysis) with the number of degrees of freedom equal to the number of the subjects minus one[50].

To plot the effect size from the individual voxel closest to the cluster maximum, resulting from the random effects analysis of the interaction between real and unreal grammatical condition (**Figs. 2** and **4**) and of the conjunction analysis (**Figs. 3** and **5**), the individual regression values (beta values on the *y*-axis) were compared with the external variable quantifying rule-learning, the accuracy of the grammatical judgment on each trial. These values were normalized and plotted on the *x*-axis of the figures.

Note: Supplementary information is available on the Nature Neuroscience website.

1. Darwin, C.R. *Descent of Man* (John Murray, London, 1871).
2. Chomsky, N. *Syntactic Structures* (Mouton, The Hague, Paris, 1957).
3. Chomsky, N. Knowledge of Language: its Nature, Origin and Use (Praeger, New York, 1986).
4. Pinker, S. Talks of genetics and vice versa. *Nature* **413**, 465–466 (2001).
5. Moro, A. Linguistica mendeliana ovvero quali domande su genetica e grammatica. *Lingue e Linguaggio* **1**, 39–58 (2002).
6. Kim, K.H., Relkin, N.R., Lee, K.M. & Hirsch, J. Distinct cortical areas associated with native and second languages. *Nature* **10**, 171–174 (1997).
7. Illes, J. *et al.* Convergent cortical representation of semantic processing in bilinguals. *Brain Lang.* **70**, 347–363 (1999).
8. Chomsky, N. *Lectures on Government and Binding* (Foris, Dordrecht, 1981).
9. Chomsky, N. *The Minimalist Program* (MIT press, Cambridge, Massachusetts, 1995).
10. Piattelli-Palmarini, M. *Language and Learning: the Debate Between Jean Piaget and Noam Chomsky* (Harvard Univ. Press, Cambridge, Massachusetts, 1980).
11. Anderson, M. Intelligence and Development: a Cognitive Theory (Basil Blackwell, Oxford, 1992).
12. Moro, A. *Dynamic Antisymmetry* (MIT press, Cambridge, Massachusetts, 2000).
13. Smith, N. & Tsimpli, I.A. *The Mind of a Savant* (Blackwell Publisher Ltd., Oxford, 1996).
14. Tettamanti, M. *et al.* Neural correlates for the acquisition of natural language syntax. *Neuroimage* **17**, 700–709 (2002).
15. Breitenstein, C. & Knecht, S. Development and validation of a language learning model for behavioral and functional-imaging studies. *J. Neurosci. Methods* **114**, 173–179 (2002).
16. Friederici A. D., Steinhauer, K., Pfeifer E. Brain signatures of artificial language processing: evidence challenging the critical period hypothesis. *Proc. Natl. Acad. Sci. USA* **8**, 529–534 (2002).
17. Rose M., Haider H., Weiller, C. & Buechel, C. The role of medial temporal lobe structures in implicit learning: an event-related fMRI study. *Neuron* **36**, 1221–1231 (2002).
18. Buckner, R.L. Functional neuroimaging of human memory in *The New Cognitive Neuroscience* (ed. Gazzaniga, S.) 817–828 (MIT Press, Massachusetts, 2000).
19. Lapage, M., Ghaffar, O., Nyberg, L. & Tulving, E. Prefrontal cortex and episodic memory retrieval mode. *Proc. Natl. Acad. Sci. USA* **97**, 506–511 (2000).
20. Owen, A.M. The role of the lateral frontal cortex in mnemonic processing: the contribution of functional neuroimaging. *Exp. Brain Res.* **133**, 33–43 (2000).
21. Shallice, T. *et al.* Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature* **368**, 633–635 (1994).
22. Tulving, E., Kapur, S., Craik F.I.M., Moscovitch, M. & Houle, S. Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proc. Natl. Acad. Sci. USA* **91**, 2016–2020 (1994).
23. Allan, K., Dolan, R.J., Fletcher, P.C. & Rugg, M.D. The role of the right anterior prefrontal cortex in episodic retrieval. *Neuroimage* **11**, 217–227 (2000).
24. Petrides, M. The role of the mid-dorsolateral prefrontal cortex in working memory. *Exp. Brain Res.* **133**, 44–54 (2000).
25. Henson, R.N.A., Shallice, T. & Dolan, J.R. Right prefrontal cortex and episodic mem-

ory retrieval: a functional fMRI test of the monitoring hypothesis. *Brain* **122**, 1367–1381 (1999).

26. Ullman, M.T. A neurocognitive perspective on language: the declarative/procedural model. *Nat. Rev. Neurosci.* **2**, 717–726 (2001).

27. Seger, A.C. Two forms of sequential implicit learning. *Conscious. Cogn.* **6**, 108–131 (1997).

28. Maess, B., Koelsch, S., Gunter, T.C. & Friederici, A.D. Musical syntax is processed in Broca's area: an MEG study. *Nat. Neurosci.* **4**, 540–545 (2001).

29. Hahne, A. & Friederici, A.D. Electrophysiological evidence for two steps in syntactic analysis: early automatic and late controlled processes. *J. Cogn. Neurosci.* **11**, 194–205 (1999).

30. Friederici, A.D., Meyer, M. & von Cramon, D.Y. Auditory language comprehension: an event-related fMRI study on processing of syntax and lexical information. *Brain Lang.* **74**, 289–300 (2000).

31. Embick, D., Marantz, A., Miyashita, Y., O'Neil, W. & Sakai, K.L. A syntactic specialisation for Broca's area. *Proc. Natl. Acad. Sci. USA* **23**, 6150–6154 (2000).

32. Ni, W. *et al*. An event-related neuroimaging study distinguishing form and content in sentence processing. *J. Cogn. Neurosci.* **12**, 120–133 (2000).

33. Sakai, K.L., Noguchi, Y., Takeuchi, T. & Watanabe, E. Selective priming of syntactic processing by event-related transcranial magnetic stimulation of Broca's area. *Neuron* **35**, 1177–1182 (2002).

34. Patel, A.D., Gibson, E., Ratner, J., Besson, M. & Holcomb, P.J. Processing syntactic relations in language and music: an event-related potential study. *J. Cogn. Neurosci.* **10**, 717–733 (1998).

35. Vargha-Khadem, F. *et al*. Neural basis of an inherited speech and language disorder. *Proc. Natl. Acad. Sci. USA* **95**, 12695–12700 (1998).

36. Gopnik, M. Genetic basis of grammar defect. *Nature* **347**, 715 (1990).

37. Alcock, K.J., Passingham, R.E., Watkins K. & Vargha-Khadem, F. Pitch and timing abilities in inherited speech and language impairment. *Brain Lang.* **15**, 34–46 (2000).

38. Lai, C.S., Fisher, S.E., Hurst, J.A., Vargha-Khadem, F. & Monaco, A.P. A forkhead- domain gene is mutated in a severe speech and language disorder. *Nature* **413**, 519–523 (2001).

39. Enard, W. *et al*. Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* **22**, 869–872 (2002).

40. Rizzolatti, G., Fadiga, L., Gallese, V. & Fogassi, L. Premotor cortex and the recognition of motor actions. *Brain Res. Cogn.* **3**, 131–141 (1996).

41. Rizzolatti, G. & Arbib, M.A. Language within our grasp. *Trends Neurosci.* **21**, 188–194, (1998).

42. Jensvold, M.L. & Gardner, R.A. Interactive use of sign language by cross-fostered chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **14**, 335–346 (2000).

43. Cantalupo, C., Hopkins, W.D. Asymmetric Broca's area in great apes. *Nature* **414**, 505 (2001).

44. Walker, A.E. A cytoarchitectonical study of the prefrontal area of the macaque monkey. *J. Comp. Neurol.* **262**, 256–270 (1940).

45. Petrides, M. & Pandya, D.N. Comparative architectonic analysis of the human and the macaque frontal cortex. in *Handbook of Neuropsychology* **IX** (Boller Grafman, Amsterdam, 1994).

46. Oldfield, R.C. The assessment and analysis of handiness: the Edinburgh inventory. *Neuropsychologia* **9**, 97–113 (1971).

47. Delis, K., Kramer, M., Kaplan, L. & Ober, R. *California Verbal Learning Test* (The Psychological Corporation, New York, 1987).

48. Gittler, G., Fay, F. & Trost, G. *Intelligenz-Struktur –Analyse ISA* (Swets Test Services, Frankfurt, 1998).

49. Markson, L. & Bloom, P. Evidence against a dedicated system for word learning in children. *Nature* **27**, 813–815 (1997).

50. Holmes A.P., Friston, K.J. Generalizability, random effects and population interference. *Neuroimage* **7**, S574 (1998).