



## Review

## A brain perspective on language mechanisms: from discrete engrams to serial order

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### Abstract

Language is constituted by discrete building blocks, sounds and words, which can be concatenated according to serial order principles. The neurobiological organization of these building blocks, in particular words, has been illuminated by recent metabolic and neurophysiological imaging studies. When humans process words of different kinds, various sets of cortical areas have been found to become active differentially. The old concept of two language centers processing all words alike must therefore be replaced by a model according to which words are organized as *discrete distributed neuron ensembles that differ in their cortical topographies*. The meaning of a word, more precisely, aspects of its reference, may be crucial for determining which set of cortical areas becomes involved in its processing. Whereas the serial order of sounds constituting a word may be established by serially aligned sets of neurons called *synfire chains*, different mechanisms are necessary for establishing word order in sentences. The serial order of words may be organized by higher-order neuronal sets, called *sequence detectors* here, which are being activated by sequential excitation of neuronal sets representing words. Sets of sequence detectors are proposed to process aspects of the syntactic information contained in a sentence. Other syntactic rules can be related to general features of the *dynamics of cortical activation and deactivation*. These postulates about the brain mechanisms of language, which are rooted in principles known from neuroanatomy and neurophysiology, may provide a framework for theory-driven neuroscientific research on language. © 2002 Published by Elsevier Science Ltd.

### 1. Explaining language in terms of neurons

Recent advances in the neuroscientific investigation of cognition make it possible to spell out cognitive mechanisms in terms of neurons and to propose neuroscientific explanations of cognitive processes. An explanation deduces a variety of facts from a few principles or axioms. The axioms themselves must be non-disputable or well established by empirical evidence. This article shows that a few neuroscientific principles can explain important aspects of the neurophysiology of language. Four principles will be proposed and general conclusions about cortical functioning will then be grounded in electrophysiological data from single cell recordings. Specific conclusions on the representation and

processing of words in the brain will be drawn and related to recent neuroimaging data. Subsequently, questions about the brain-basis of serial order will be addressed in the light of established neuroscientific knowledge (Table 1). Three distinct brain mechanisms will be discussed as the putative neurobiological basis of serial order in language at the phonological and syntactic level.

### 2. Principles

The human cerebral cortex is a network of more than 10 billion neurons. Each neuron represents an information processor whose output is a function of the input it receives from many other neurons with which it is interwoven. The following principles are proposed to reflect universal neuroanatomical and neurophysiological properties of the human cortex:

- (I) Afferent and efferent projections are ordered. They reach, or take their origin from, well-defined areas within which the projections are organized topographically.

*Abbreviations:* ECD, equivalent current dipole; EEG, electroencephalography or electroencephalogram; ERP, event-related potential; fMRI, functional magnetic resonance imaging; MEG, magnetoencephalography or magnetoencephalogram; MMN, mismatch negativity; MMNm, magnetic correlate of the mismatch negativity; MNE, minimum-norm current estimate; PET, positron emission tomography

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Table 1

Important questions in cognitive neuroscience

- 
- (1) *Where* question: Which brain areas are critically involved in a given cognitive process?  
 (a) Activation of which brain areas is sufficient for the cognitive process?  
 (b) Which brain areas are necessary for the cognitive process?
- (2) *When* question: At which point in time does a given cognitive process take place?  
 (a) What is the time delay between stimulus delivery or behavioral response and the onset of the cognitive process?  
 (b) What is the sequence and exact time delay between different cognitive processes?
- (3) *How* question: By which neuron circuit is a particular cognitive process realized?
- (4) *Why* question: On the basis of which principles or axioms can empirical results answering aspects of Where, When and How questions be explained?
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57 (II) By way of intra-cortical connections, afferent and ef- 97  
 58 ferent information can be intermingled and merged. 98  
 59 Neighboring areas tend to be reciprocally connected, 99  
 60 and reciprocal long-range connections exist between 100  
 61 many distant areas as well. 101

62 (III) Connections between neurons are modified depending 102  
 63 on the correlation of neuronal activity. Neurons that 103  
 64 fire together strengthen their mutual connections, and 104  
 65 links between neurons that fire independently of each 105  
 66 other become weaker. 106

67 (IV) Neurons that specifically respond to spoken language 107  
 68 input or specifically contribute to language production 108  
 69 are more likely to be housed in the left hemisphere than 109  
 70 in the right. 110

71 These principles will now be qualified.

## 72 2.1. Ordered afferent and efferent projections

73 The afferent fibers transmitting information from the sen- 111  
 74 sory organs to the cortex reach well-defined areas, and the 112  
 75 efferent fibers through which the cortex controls muscle ac- 113  
 76 tivity also originate from a specific region. These are the 114  
 77 primary and, to a lesser degree, secondary areas. The pri- 115  
 78 mary areas most relevant for language processing are located 116  
 79 in the posterior occipital lobes (Brodmann area 17; visual 117  
 80 input), superior temporal lobes (Brodmann area 41; acous- 118  
 81 tic input), anterior parietal lobes (Brodmann areas 1–3; so- 119  
 82 matosensory input) and posterior frontal lobes (Brodmann 120  
 83 area 4; motor output). These sensory and motor fields are 121  
 84 shown in Fig. 1A. The other sensory pathways for olfactory 122  
 85 and gustatory input are not shown, because they are less 123  
 86 important for language. Each of these motor and sensory 124  
 87 systems is characterized by the topographical order of their 125  
 88 projections. This means that adjacent sensory cells project 126  
 89 to adjacent cortical neurons, and adjacent body muscles are 127  
 90 controlled by adjacent neurons in the motor cortex. The so- 128  
 91 matotopy of the primary motor cortex is illustrated in Fig. 1B 129  
 92 (Penfield and Roberts, 1959). 130

93 Research on cortical reorganization has shown great 131  
 94 plasticity of the sensory areas following sensory deprivati- 132  
 95 on (Buonomano and Merzenich, 1998; Merzenich et al., 133  
 96 1983b). Following sensory deprivation, the specific cortical 134  
 135  
 136  
 137

97 areas activated by sensory input can be altered. Some of 98  
 99 the considerations summarized below therefore only apply 100  
 101 to non-deprived individuals. A change of the cortical areas 102  
 103 involved in processing of a particular input can also be a 104  
 105 consequence of learning. For example, string players and 106  
 107 Braille readers show an altered function of somatosensory 108  
 109 areas with enlarged cortical representations of the extremi- 109  
 110 ties involved in complex sensory–motor skills (Elbert et al., 110  
 111 1995; Sterr et al., 1998). This shows that the topographic pro- 112  
 113 jections are not fixed genetically but may vary within certain 114  
 115 boundaries. Nevertheless, even after sensory deprivation, 116  
 117 the principle of topographical connections still holds for the 118  
 119 remaining cortical projections (Merzenich et al., 1983a). 120  
 121  
 122  
 123  
 124  
 125

## 126 2.2. Merging of multimodal information in the cortex

127 What is the function of the cortex? Neuroanatomists 128  
 129 (Braitenberg, 1978b; Braitenberg and Schüz, 1998) and 129  
 130 neurocomputational modelers (Palm, 1982, 1993) have pro- 130  
 131 posed the following answer to this question. The massive 131  
 132 fiber tracts of the cortex connect many of its areas directly, 132  
 133 and calculations show that every arbitrarily selected cortical 133  
 134 neuron is likely to be linked through a small number of 134  
 135 synaptic steps to any other cortical cell (Palm, 1982). It is 135  
 136 therefore likely that the cortex allows for *merging infor-* 136  
 137 *mation from different modalities*. Recent evidence on cells 137  
 138 with multimodal response properties (Fuster et al., 2000; 138  
 139 Rizzolatti et al., 1998; Zhou and Fuster, 2000) strongly 139  
 140 supports the idea that the cortex is an information merging 140  
 141 device allowing single neurons to represent and process 141  
 142 information from various motor and sensory modalities. 142

143 Looking more closely at the structure of the cortical con- 143  
 144 nections, it becomes obvious from animal studies that most 144  
 145 primary cortical areas do not have direct connections to each 145  
 146 other (Pandya and Yeterian, 1985), the primary motor and 146  
 147 sensory cortices (which are next-neighbors) representing the 147  
 148 only exception. Adjacent areas, as a rule, are connected with 148  
 149 very high probability (>70%, Young et al., 1995). For pairs 149  
 150 of distant areas, i.e. areas with more than one other area 150  
 151 between them, this probability is lower in higher mammals 151  
 152 (15–30%). But, still, it is remarkable that, for example in 152  
 153 the macaque monkey where ~70 different areas were dis- 153  
 154 tinguished, most of them would have links to 10 or more 154  
 155  
 156  
 157

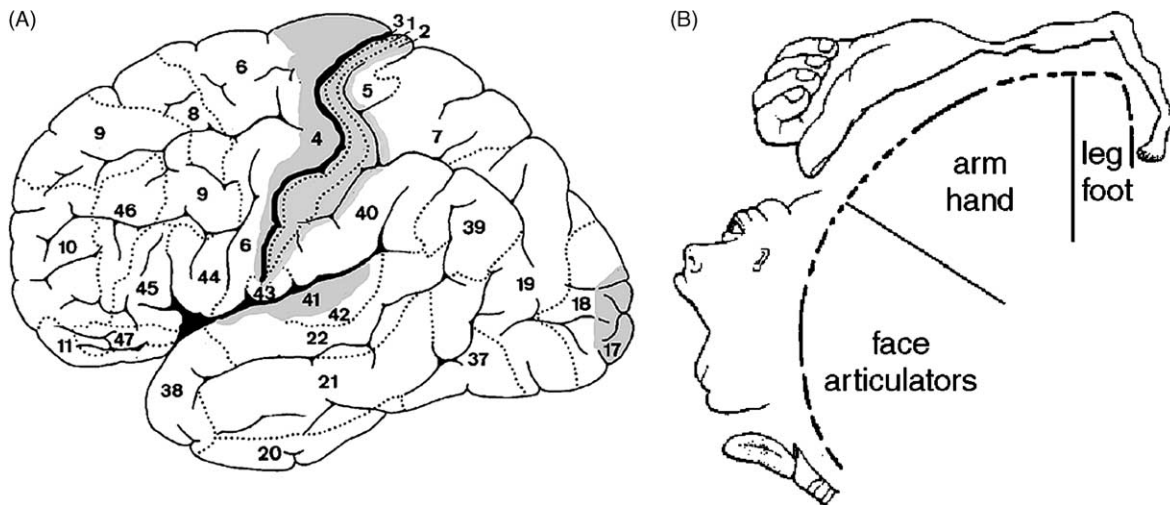


Fig. 1. (A) Lateral view of the cortex with Brodmann's area numbers indicated. Shading indicates primary areas, where most afferent sensory fibers reach the cortex, and from where most efferent motor fibers leave it (from Brodmann, 1909). (B) The somatotopic organization of the motor cortex is illustrated on a schematic frontal section of the pre-central gyrus (Brodmann's area 4; from Penfield and Rasmussen, 1950).

138 distant areas within the same cortical hemisphere. Even in  
 139 the mouse brain, where only 12 local compartments were  
 140 distinguished, each compartment was found to send out  
 141 and receive projections to five other areas in the average  
 142 (Braitenberg and Schüz, 1998). In addition, there are con-  
 143 nections between most homotopic areas of the two hemi-  
 144 spheres. Thus, long-distance links directly connect many,  
 145 though not all, cortical areas.

146 An important feature of cortico-cortical connectivity is  
 147 that the overwhelming majority of *between-area links are re-*  
 148 *ciprocal* (Pandya and Yeterian, 1985; Young et al., 1995).  
 149 This has ready implications for cognitive theories, because  
 150 it implies that, for most information processing highways,  
 151 information flow in one direction implies the possibility of  
 152 such flow also in the reverse direction.

153 Since the neuroanatomical findings discussed here origi-  
 154 nate from studies in animals, it is not certain that all of  
 155 these properties generalize to humans. A detailed picture  
 156 of cortical connectivity can only be obtained using invasive  
 157 techniques, which cannot be applied in humans, although  
 158 important insights come from post-mortem neuroanatomical  
 159 studies (Jacobs et al., 1993; Scheibel et al., 1985). In par-  
 160 ticular, conclusions from animal studies on the pattern of  
 161 long-distance connections of the areas most important for  
 162 language must be handled with care, because these areas  
 163 do not have homologues in the monkey's brain. However,  
 164 a tentative generalization can be proposed in terms of the  
 165 position of the areas relative to the primary area, which are  
 166 present in higher mammals. One such generalization is the  
 167 following: The auditory cortex and the motor cortex con-  
 168 trolling the articulators are not linked directly. Their con-  
 169 nections are indirect, through inferior frontal areas anterior  
 170 to the mouth-motor cortex and superior temporal areas an-  
 171 terior, posterior and inferior to the primary auditory cortex  
 172 (Deacon, 1992).

In summary, it appears that the cortex can serve the func-  
 tion of merging multimodal information. This multimodal  
 merging of information is not done by direct links between  
 primary areas, but necessitates intermediate neuronal steps.  
 The intervening neurons between sensory and motor neu-  
 rons in the cortex allow for complex mappings of informa-  
 tion patterns between modalities.

### 2.3. Correlation learning

Following earlier similar statements by various re-  
 searchers, Hebb (1949) postulated "that any two cells or  
 systems of cells that are repeatedly active at the same time  
 will tend to become 'associated', so that activity in one facil-  
 itates activity in the other" (p. 70). There is now strong evi-  
 dence from single- and multiple-unit recordings proving that  
 this postulate is correct (Ahissar et al., 1992; Fuster, 1997;  
 Tsumoto, 1992). If connected neurons fire together, their  
 mutual influence on each other become stronger. This can  
 be related to biochemical and even structural changes in  
 the neurons, for example to growth and modification of  
 dendritic spines (Braitenberg and Schüz, 1998; Engert and  
 Bonhoeffer, 1999). Whereas neurons become associated  
 when being activated repeatedly at the same time, their  
 anti-phasic activation can result in weakening of their  
 influence on each other (Tsumoto, 1992). Thus, the origi-  
 nal proposal made by Hebb, that coincidence of neuronal  
 firing strengthens connections, appears to represent only  
 half of the truth and had therefore to be modified. Be-  
 cause co-activation of two neurons strengthens their mutual  
 connections and their alternating activity reduces their  
 influence onto each other, it appears to be the positive  
 or negative *correlation* of neuronal firing of connected  
 cells that is, so to speak, translated into their connection  
 strength.

## 205 2.4. Laterality of spoken language

206 Language laterality is a well-known fact since the first sci-  
207 entific investigation of language loss due to stroke (Broca,  
208 1861), but the causes of this laterality have not yet been re-  
209 vealed. The postulate that one hemisphere is dominant for  
210 language is primarily based on lesion studies. Lesions in cer-  
211 tain areas of the left hemisphere cause language deficits, or  
212 *aphasias*, in most individuals. However, this does not allow  
213 one to conclude that only the left hemisphere contributes to  
214 language. It was already pointed out by the English neurolo-  
215 gist, Jackson (1878), that if a lesion of a part of the brain  
216 impairs specific functions, one can by no means conclude  
217 that these functions are *localized* exclusively in the respec-  
218 tive brain part. The lesioned area could have a more general  
219 function, as the brain stem has in regulating arousal, which  
220 is necessary for a specific higher brain function such as lan-  
221 guage. In this case, one would perhaps not want to localize  
222 language in the brain part in question, although language  
223 impairment resulted from its lesion. Likewise, if lesions of  
224 a brain part lead to a clinically apparent deficit regarding  
225 a given function, it is always possible that additional areas  
226 are also relevant for this function, but that their lesion does  
227 not result in clinically apparent dysfunction. Such deficits  
228 may be absent, for example, because the clinical tests ap-  
229 plied were not sensitive enough to reveal a fine-grained  
230 dysfunction (Neininger and Pulvermüller, 2001), or because  
231 other areas had meanwhile taken over the area's function  
232 (Dobel et al., 2001; Price et al., 2001). Lesion data proving  
233 language laterality do, therefore, not argue against the ex-  
234 istence of additional sites in the non-dominant hemisphere  
235 that are also relevant for language processing.

236 Whereas lesions in certain left-hemispheric areas cause  
237 severe language impairments, comparable right-hemispheric  
238 lesions primarily lead to more subtle language-related defi-  
239 cits, such as difficulties affecting prosodic and pragmatic  
240 processing (Joanette et al., 1990) or category-specific defi-  
241 cits in word processing apparent on demanding neuropsy-  
242 chological tests (Neininger and Pulvermüller, 2001). In this  
243 sense, left-hemispheric language dominance is almost al-  
244 ways present in right-handers and also in most left-handed  
245 individuals (~80%, Bryden et al., 1983; Goodglass and  
246 Quadfasel, 1954; Hecaen et al., 1981). The remaining indi-  
247 viduals can be considered to be right-dominant, with a few  
248 showing no language dominance at all. Taking this into ac-  
249 count, it is obvious that, in the large majority of individu-  
250 als, language is lateralized to the left hemisphere. In other  
251 words, left-hemispheric lesions are far more likely to cause  
252 brain lesions than lesions in the right hemisphere.

253 Language laterality was also reflected in brain physiolo-  
254 gy revealed by modern neuroimaging techniques. Stronger  
255 brain responses on the left side compared with the right were  
256 seen across various language tasks using visual and auditory  
257 stimuli (Näätänen, 2001; Petersen and Fiez, 1993). Since  
258 lateralized activity was elicited already by single language  
259 sounds and syllables (Näätänen et al., 1997; Shtyrov et al.,

260 2000; Zatorre et al., 1992), one may conclude that phono- 260  
261 logical processes, or acoustic processes relevant for the 261  
262 distinction between language sounds, or *phonemes*, are cru- 262  
263 cial for language laterality (Shtyrov et al., 2000). In many 263  
264 of the neuroimaging studies mentioned, in particular in 264  
265 studies using MEG, EEG or fMRI, language laterality was 265  
266 gradual, i.e. there were activity signs in both hemispheres 266  
267 and the left-dominant hemisphere was more active than the 267  
268 right (for review, see Pulvermüller, 1999). This is consis- 268  
269 tent with the view that the neuronal populations involved in 269  
270 language processing are *distributed over both hemispheres*, 270  
271 but that *the majority of the relevant neurons are located in* 271  
272 *the left hemisphere* (Pulvermüller and Mohr, 1996). 272

273 Neuropsychological and neurophysiological studies indi- 273  
274 cate that *laterality of language emerges early in life*. Young 274  
275 children suffering from brain lesions are more likely to 275  
276 develop a temporary language deficit after left- than after 276  
277 right-hemispheric lesion (Woods, 1983). The great plastic- 277  
278 ity of the neural substrate allows for recovery in most cases 278  
279 of early neurological language impairment. EEG recordings 279  
280 in infants demonstrated a physiological correlate of lan- 280  
281 guage laterality within the first year (Dehaene-Lambertz and 281  
282 Dehaene, 1994; Molfese, 1972). These results from neu- 282  
283ropsychological and neuroimaging research indicate that lat- 283  
284 erality of language emerges early in life. 284

285 In which way, if at all, is the lateralization of language 285  
286 functions related to *structural asymmetries*? Numerous 286  
287 anatomical correlates of language laterality have been re- 287  
288 ported, even in cranio-facial asymmetries during early on- 288  
289 togenetic stages (Previc, 1991). Neuroanatomical correlates 289  
290 of language laterality were found to be reflected in the size 290  
291 of language-relevant areas (Geschwind and Levitsky, 1968; 291  
292 Steinmetz et al., 1991), and in the size (Hayes and Lewis, 292  
293 1993), arrangement (Seldon, 1985), local within-area con- 293  
294 nections (Galuske et al., 2000), and dendritic arborization 294  
295 pattern (Jacobs et al., 1993; Scheibel et al., 1985) of corti- 295  
296 cal pyramidal neurons. These anatomical differences may 296  
297 have a causal role in determining which hemisphere be- 297  
298 comes more important for processing spoken language, 298  
299 although the causal chain has, as mentioned, not yet been 299  
300 revealed. On the other hand, one may well argue that some 300  
301 of the structural asymmetries are a consequence of func- 301  
302 tional differences, for example of more strongly correlated 302  
303 neuronal activity (cf. principle (III)), in the relevant areas 303  
304 of the dominant hemisphere. 304

305 Considering the anatomical and functional asymmetries 305  
306 documented, it becomes important to explore possible 306  
307 causal chains explaining laterality of language on the ba- 307  
308 sis of more fundamental neuroanatomical facts. According 308  
309 to one view, specific neuroanatomical differences between 309  
310 the hemispheres cause laterality of neurophysiological pro- 310  
311 cesses important for distinguishing phonemes. Starting 311  
312 from an extensive review of the neuroanatomical literature, 312  
313 Miller (1996) found that the ratio of white to gray matter 313  
314 volume yields a smaller value for the left hemisphere com- 314  
315 pared with the right, in particular for the frontal and tempo- 315

316 ral lobes which are most crucial for spoken language. The  
 317 left frontal and temporal lobes, exhibit a smaller volume of  
 318 white matter than the corresponding structures in the right  
 319 hemisphere. Thus, a *smaller* white matter volume appears  
 320 to be related to language dominance. The white matter  
 321 is primarily made up of axons and their glia sheaths, the  
 322 long-distance cables connecting cortical neurons. A smaller  
 323 white matter volume may indicate that average cortical con-  
 324 nections are thinner, and this implies that these connections  
 325 conduct action potentials more slowly (Lee et al., 1986).  
 326 This line of thought leads Miller to propose that the left  
 327 hemisphere houses a larger number of slowly conducting  
 328 fibers than the right. In local cortical circuits, slow fibers  
 329 may be advantageous for measuring exact temporal delays.  
 330 Measuring exact temporal delays in the order of a few tens  
 331 of milliseconds is necessary for making phonemic distinc-  
 332 tions such as between the phonemes [t] and [d]. According  
 333 to this view, language laterality is a question of phonological  
 334 discrimination and a direct consequence of neuroanatomical  
 335 properties of the human forebrain. However, this theory, as  
 336 all other attempts at further explaining language laterality,  
 337 is in need of further empirical support.

338 In summary, laterality of language is well supported by  
 339 results from neuroanatomical investigations, neuropsycholo-  
 340 gical lesion studies, and neuroimaging experiments. This  
 341 fact can therefore be used as a principle within an explanato-  
 342 ry account of language, in spite of the obvious need for  
 343 further explanation on the basis of more fundamental neu-  
 344 roscientific knowledge. Proposals for such a deeper explana-  
 345 tion have been made, but no single proposal has yet been  
 346 proven to be correct. Until a convincing in-depth explana-  
 347 tion exists, it appears best to treat the laterality of language  
 348 as a principle revealed by empirical research.

### 349 3. Functional webs in the cortex

350 The cortex is a network of neurons characterized by  
 351 ordered input and output connections in modality-specific  
 352 areas, by multimodal merging of information through short-  
 353 and long-distance connections, and by correlation learning.  
 354 Such a device can serve the function of linking neurons re-  
 355 sponding to specific features of input patterns and neurons  
 356 controlling aspects of the motor output. Because different  
 357 primary areas are not linked directly, additional neurons  
 358 in non-primary areas are necessary to bridge between the  
 359 ordered in- and output patterns. The cortical connection  
 360 structure, characterized by a high connection probability  
 361 between adjacent areas and more selective long-distance  
 362 links, enforces the formation of *functionally coupled, but*  
 363 *distributed, webs of neurons* reaching from the primary ar-  
 364 eas into higher-order cortices. Development of these webs  
 365 would be driven by sensory–motor or sensory–sensory  
 366 co-activation, and would be determined by the available  
 367 cortical projections indirectly connecting the co-activated  
 neurons in primary areas to each other.

### 368 3.1. Why should an engram be realized as an ensemble of 369 neurons?

370 It was pointed out by Hebb (1949) and this may be his  
 371 most important contribution to the understanding of the  
 372 brain, that synchronously activated neurons should link into  
 373 *cell assemblies*, and that cell assemblies underlie all higher  
 374 cognitive processes. Hebb's proposal diverged radically  
 375 from earlier neuroscientific approaches to information pro-  
 376 cessing in the brain, because he postulated that *higher brain*  
 377 *processes are realized as functional units above the level of*  
 378 *the neuron*. Earlier proposals had put that either individual  
 379 neurons (Barlow, 1972) or mass activity and interference  
 380 patterns in the entire cortex (Lashley, 1950) are the basis  
 381 of cognition. Hebb's view may appear as a compromise  
 382 between these views (Milner, 1996).

383 While Lashley's proposal can be ruled out by consider-  
 384 ing the specific neuropsychological deficits caused by focal  
 385 brain lesions (Shallice, 1988), one may ask why large neu-  
 386 ron ensembles should become involved in cognitive process-  
 387 ing if single neurons are already capable of performing the  
 388 relevant computations. A tentative answer is that individual  
 389 neurons are too noisy and unreliable computational devices  
 390 so that it is advantageous to use sets of neurons working  
 391 together in functional units to achieve more reliable infor-  
 392 mation processing. If the signal-to-noise ratio of individual  
 393 neurons is low, one can obtain a better signal by simultane-  
 394 ously averaging over a larger number of neurons with simi-  
 395 lar functional characteristics, so that uncorrelated noise is  
 396 cancelled (Zohary, 1992). (Note that this does not rule out  
 397 the possibility that, apart from their shared function, indi-  
 398 vidual neurons in the ensemble can have additional specific  
 399 functions.) It would therefore make good sense if there were  
 400 functional units in the cortex which are larger than the neu-  
 401 ron but much smaller than the neuronal populations in the  
 402 cortex' macroscopic gyri and sulci.

403 A further argument in favor of functional webs composed  
 404 of numerous neurons comes from an estimate of the num-  
 405 ber of neurons necessary for carrying out the tasks the cor-  
 406 tex seems to be primarily engaged in. As mentioned ear-  
 407 lier, the cortex includes >10 billion neurons. The number  
 408 of to-be-stored items can be estimated on the basis of the  
 409 units that need to be stored. To speak a language well, one  
 410 needs a vocabulary of less than 100,000 words or mean-  
 411 ingful language units, called *morphemes*, and a limited set  
 412 of rules governing their serial order (Pinker, 1994). Given  
 413 similar numbers of distinct representations also develop for  
 414 other cognitive domains, the number of to-be-organized en-  
 415 grams may be in the order of a few hundred thousand. If  
 416 this estimate is correct and each engram is represented by  
 417 one neuron, 1 million individual neurons might be sufficient  
 418 for representing the various percepts and motor programs  
 419 cognitive processes operate on. This raises the question why  
 420 there are 100,000–1,000,000 times as many neurons as, as  
 421 these considerations would suggest, would be necessary. A  
 422 possible answer is that the cortex includes so many neurons,

423 because individual engrams are realized as populations of  
424 neurons of  $10^5$ – $10^6$  neurons.

### 425 3.2. Why should neuronal ensembles be widely 426 distributed?

427 Local clusters, or “columns”, of neurons beneath  
428  $\sim 0.1$ – $0.5$  mm<sup>2</sup> of cortical surface which, in various sen-  
429 sory areas, respond to similar stimuli have been proposed  
430 to represent the functional units above the single cell  
431 (Hubel, 1995). However, these local neuron clusters per se  
432 cannot be the substrate of the linkage between different fea-  
433 tures of an object. The features of an object may characterize  
434 input from different modalities, as for example, the shape,  
435 smell, purr and smooth fur of a cat. The binding of these  
436 features into one coherent representation could, in principle,  
437 be instantiated by pathways linking the sensory information  
438 from different modalities to the same “central” neuron(s).  
439 These critical cells should then be housed in areas where  
440 inputs from many sensory fields converge (Damasio, 1989).  
441 It is, however, not necessary to assume a single central  
442 convergence area, or a local (set of) cardinal cell(s). The  
443 neuroanatomical connection pattern of the cortex indicates  
444 that links between primary cortices are provided through  
445 more than one route, involving several non-primary areas.  
446 There is, therefore, no need for assuming single specialized  
447 areas or neurons for binding of the information defining cer-  
448 tain engrams. Together with the neuroscientific knowledge  
449 about cortico-cortical connections, the correlation principle  
450 suggests that it is the entire ensemble of cortical cells fre-  
451 quently activated together when certain objects are being  
452 perceived, or when specific actions are being carried out,  
453 that develops into the functional unit realizing the object or  
454 action at the neuronal level.

455 The proposal would therefore be the following: A web of  
456 neuronal links strongly connecting all neurons involved in  
457 the processes triggered by an object or action becomes the  
458 cortical representation of this object or action. Binding of  
459 object features is established by mutual links within a dis-  
460 tributed neuronal web, i.e. between neurons in widespread  
461 areas including the primary areas. Each neuron member of  
462 the web would, hence, contribute to holding the web to-  
463 gether thereby playing an essential role in its functioning.  
464 The “cat” concept would be realized as a large set of neu-  
465 rons distributed over a small set of cortical areas. Each of  
466 these areas serves as a binding site. A strongly connected set  
467 of neurons capable of working together as a discrete func-  
468 tional unit and distributed over a specific set of cortical areas  
469 will be called a *functional web* below. The term “functional  
470 web” is preferred here to the term “cell assembly” proposed  
471 by Hebb, because the latter has been defined differently by  
472 various researchers and its use therefore bears the danger of  
473 misunderstandings.

474 Which critical predictions are implied by the idea of dis-  
475 tributed functional webs? If all neurons of the functional  
476 web are important for the optimal processing of the entity

477 represented, lesion of a significant portion of the network  
478 neurons must impair the processing of this entity. This is  
479 largely independent of where in the network the lesion oc-  
480 curs. If the functional web is distributed over distant corti-  
481 cal areas, say certain frontal and temporal areas, neurons in  
482 both areas should (a) share some of their specific response  
483 features and (b) show these response features only if the re-  
484 spective other area is intact.

485 These predictions have been examined in macaque mon-  
486 keys using a memory paradigm where the animal has to  
487 keep in mind the shape or color of a stimulus and per-  
488 form a concordant matching response after a delay of sev-  
489 eral seconds (delayed matching to sample task). Through-  
490 out the memory period, where the animal has to keep in  
491 mind, for example, that the stimulus shown was red, neu-  
492 rons fired at an enhance level. Their firing was specific  
493 in the sense that they did not respond, or responded less,  
494 when a stimulus of another color had been shown. Neu-  
495 rons with this stimulus-specific response pattern were found  
496 in the prefrontal cortex (Fuster and Alexander, 1971) and in  
497 the inferior temporal lobe (Fuster and Jervey, 1982). Tem-  
498 porary lesion by cooling of the neurons in one area led  
499 to loss of stimulus-specificity of the neurons in the other  
500 (Fuster, 1997). This is evidence that neurons in both areas,  
501 temporal and frontal, showed (a) shared a rather specific re-  
502 sponse feature and (b) showed this feature only if the other  
503 area was intact (Fuster, 1997).

504 Fuster’s results are reminiscent of facts known from  
505 over 100 years of neurological investigation into language  
506 disorders (Basso et al., 1985; Lichtheim, 1885). Both a pre-  
507 frontal and a temporal area turned out to be most crucial  
508 for language processing, and lesions in either area can lead  
509 to aphasia which, in the majority of cases, includes deficits  
510 in both language production and perception (Pulvermüller,  
511 1995; Rosenbek et al., 1989). Concordant with recent an-  
512 imal studies investigating the consequences of local cool-  
513 ing of prefrontal and temporal areas, this suggests mutual  
514 functional dependence between frontal and temporal areas  
515 (Pulvermüller and Preissl, 1991).

## 516 4. Functional cortical webs and their putative role in 517 processing words

518 The cortex, a neuroanatomically defined associative  
519 memory obeying the correlation learning principle, allows  
520 for the formation of distributed functional webs. During lan-  
521 guage acquisition, the neurobiological principles governing  
522 the cortex give rise to the neuronal machinery underlying  
523 language. Three qualitatively different types of functional  
524 webs are proposed to be relevant for realizing spoken lan-  
525 guage in the cortex: networks linking information about  
526 articulatory movements and acoustic percepts, webs storing  
527 meaning-sound-contingencies characterizing words, and  
528 networks specifically involved in the processing of serial or-  
529 der of language elements. Each type of functional web may

530 be characterized by specific cortical distribution, cognitive  
531 function, and kind of information it processes and stores  
532 (Braitenberg, 1980; Braitenberg and Pulvermüller, 1992;  
533 Braitenberg and Schüz, 1992; Pulvermüller, 1999).

#### 534 4.1. Phonological webs

535 Early babbling and word production are likely caused  
536 by neuronal activity in cortical areas in the inferior frontal  
537 lobe, including the inferior motor cortex and adjacent pre-  
538 frontal areas. The articulations cause sounds and these  
539 activate neurons in the auditory system, including areas  
540 in the superior temporal lobe. The fiber bundles between  
541 inferior frontal and superior temporal areas provide the sub-  
542 strate for associative learning between neurons controlling  
543 specific articulatory motor programs and neurons in the  
544 auditory cortical system stimulated by the self-produced  
545 language sounds. The correlation learning principle im-  
546 plies the formation of such specific associations resulting  
547 in functional webs distributed over the *perisylvian cortex*—  
548 which includes the inferior frontal and superior temporal  
549 core language areas. Fig. 2A schematically indicates the ap-  
550 proximate left-hemispheric distribution of a functional web  
551 envisaged to realize a phonological word form. If neurons  
552 in the left-dominant hemisphere are more likely to specifi-  
553 cally respond to phonological features in the acoustic input  
554 (principle (IV)), the resulting phonological networks must  
555 be lateralized, in the sense of comprising more neurons in  
556 one hemisphere than in the other. These lateralized perisyl-  
557 vian neuron ensembles would later provide the machinery  
558 necessary for activating a word's articulatory program as  
559 a consequence of acoustic stimulation with the same word  
560 form. This is necessary for the ability to repeat words spo-  
561 ken by others. Interestingly, *babbling*, the infant's earliest  
562 language-like articulations, starts around the sixth month  
563 of life (Locke, 1989), and is followed by the develop-  
564 ment of electrophysiological indicators of memory traces  
565 for phonemes (Cheour et al., 1998; Näätänen et al., 1997)  
566 and by the infant's ability to repeat words spoken by  
567 others (Locke, 1993). These observations are consistent  
568 with the idea that babbling is essential for building up  
569 language-specific neuronal representations, in particular  
570 sensory–motor links which may, in turn, be essential for the  
571 ability to repeat spoken words. Articulating words, in the  
572 context of repetition or otherwise, may be essential for the  
573 build-up of specific sensory–motor representations of these  
574 words.

575 It might be considered a shortcoming of this proposal that,  
576 in reality, only a minority of word forms is learned by the  
577 infant by single-word repetition (Pulvermüller, 1999). Most  
578 words are being learned in the context of continuous speech  
579 in which word boundaries are not marked by acoustic cues.  
580 How could infants know which phonemes belong to a partic-  
581 ular word, and where the boundaries are between subsequent  
582 words? The answer is again implied by the correlation learn-  
583 ing principle. The recurring sound sequences constituting

584 words can be distinguished, on statistical grounds, from the  
585 more accidental sound sequences across word boundaries  
586 (Brent and Cartwright, 1996; Harris, 1955; Redlich, 1993).  
587 Recent behavioral evidence suggests that already young  
588 infants distinguish the correlated phoneme and syllable se-  
589 quences making up words from the more accidental sound  
590 sequences in their acoustic input (Saffran et al., 1996).  
591 Therefore, single-word input is not necessary for building  
592 up word representations. Infants can use the correlation  
593 statistics, the transitional probability and/or mutual infor-  
594 mation (Shannon and Weaver, 1949) of phoneme and sylla-  
595 ble sequences, for learning words from continuous speech.  
596 First, an auditory word representation would be established  
597 by correlation learning resulting from continuous speech  
598 input. As a second step, the articulation of the word made  
599 possible by the sensory–motor links set up by babbling  
600 causes co-activation of neurons in inferior frontal and su-  
601 perior temporal areas. This establishes the word-related  
602 functional web distributed over the perisylvian cortex.

603 How would it be possible to prove the existence of func-  
604 tional webs relevant for the processing of words? One view  
605 on the nature of functional webs puts that their massive re-  
606 verberatory circuits produce precisely timed high-frequency  
607 rhythms when active (Milner, 1974; Pulvermüller et al.,  
608 1997; Tallon-Baudry and Bertrand, 1999; von der  
609 Malsburg, 1995). Words in the input would thus activate  
610 the corresponding functional webs thereby eliciting strong  
611 high-frequency rhythms. In contrast, phonologically and or-  
612 thographically regular pseudo-words, which are not part of  
613 the language, would fail to activate a corresponding func-  
614 tional web and the high-frequency activity in the perisylvian  
615 areas should therefore be relatively low.

616 This prediction was put to a test using MEG. A frequency  
617 band around 30 Hz revealed significant differences between  
618 words and pseudo-words presented acoustically. About half  
619 a second after the onset of spoken one-syllabic words,  
620 high-frequency brain responses were significantly stronger  
621 compared with the same interval following pseudo-words.  
622 Fig. 2B shows the results of spectral analyses carried out  
623 on data recorded close to left-anterior perisylvian areas  
624 and the homotopic areas in the right hemisphere of a sub-  
625 ject listening to words and pseudo-words. Word-induced  
626 high-frequency responses were markedly stronger compared  
627 with pseudo-word-related activity, both in the single subject  
628 whose data are displayed (difference of 12%) and in the  
629 group average (8.4%, Pulvermüller et al., 1996a). This can-  
630 not be due to a global enhancement of the signal, because  
631 event-related magnetic fields tended to be weaker for words  
632 than for pseudo-words in the time window analyzed. Recent  
633 EEG and MEG studies confirmed that known words elicit  
634 stronger high-frequency activity in the brain than unknown  
635 word-like material (Eulitz et al., 2000; Krause et al., 1998;  
636 Lutzenberger et al., 1994; Pulvermüller et al., 1996b).

637 The assumption that word presentation activates func-  
638 tional webs with multiple fast reverberatory circuits, which  
639 fail to become fully active if pseudo-words are being  
639

640 perceived, can provide an explanation for this pattern of  
 641 results. The observed reverberations are not necessarily  
 642 generated within functional units, but could also be due, for  
 643 example, to inhibitory connections between the neurons ac-  
 644 tivated by words but not pseudo-words and their inhibitory  
 645 neighbors (cf. Plenz and Kitai, 1996; Traub et al., 1996).  
 646 Nevertheless, the differential high-frequency responses to  
 647 words and pseudo-words provide evidence for the existence  
 648 for distributed neuron populations that are activated by

649 words but not by pseudo-words (for further discussion, see  
 650 Pulvermüller et al., 1997).

651 Physiological differences between words and pseudo-  
 652 words have been found in numerous studies using both elec-  
 653 trophysiological and metabolic neuroimaging techniques  
 654 (Creutzfeldt et al., 1989; Diesch et al., 1998; Hagoort  
 655 et al., 1999; Price et al., 1996; Rugg, 1983). Thus, it is un-  
 656 controversial that the brain response distinguishes between  
 657 words and similar but novel and meaningless patterns. It

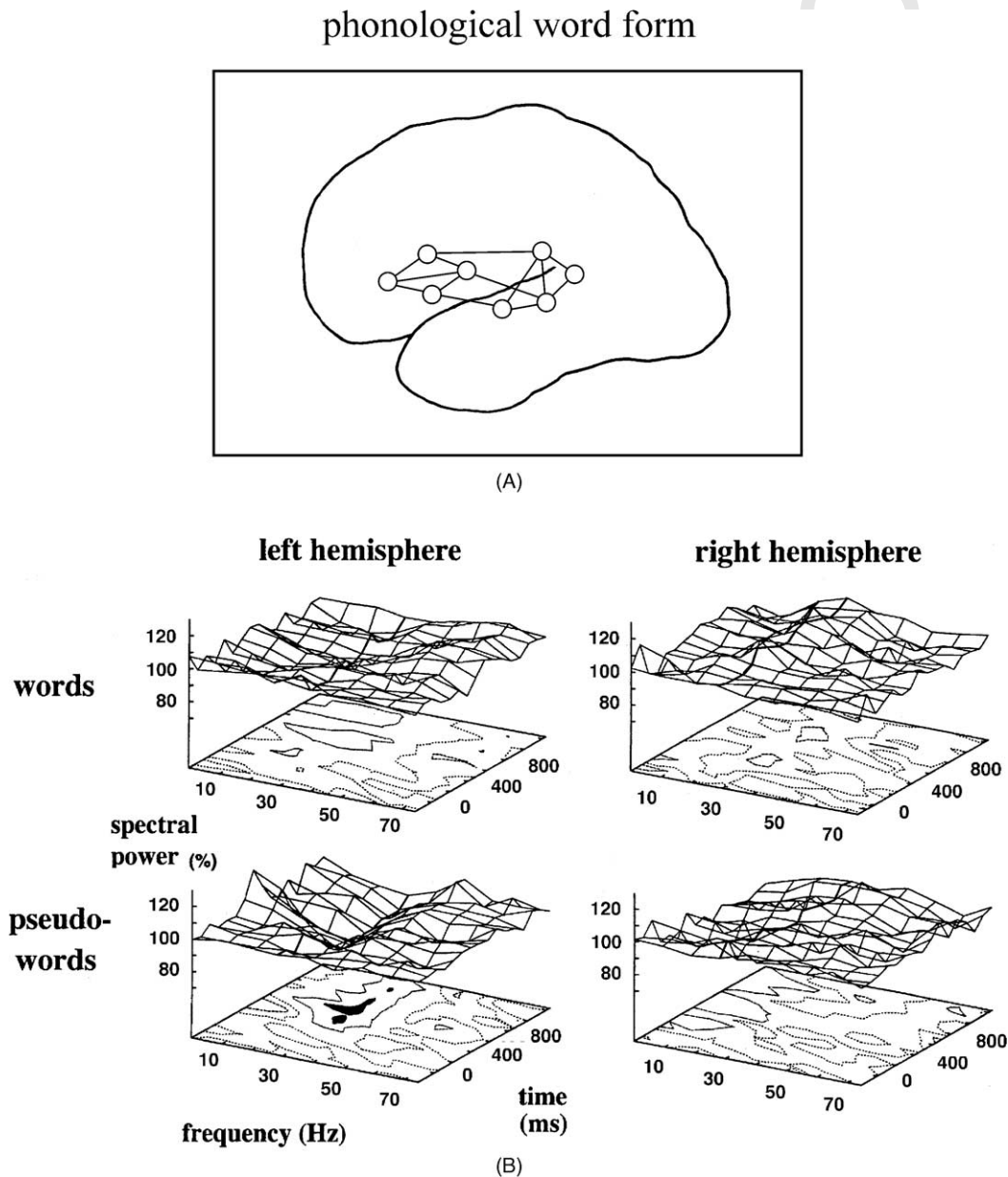
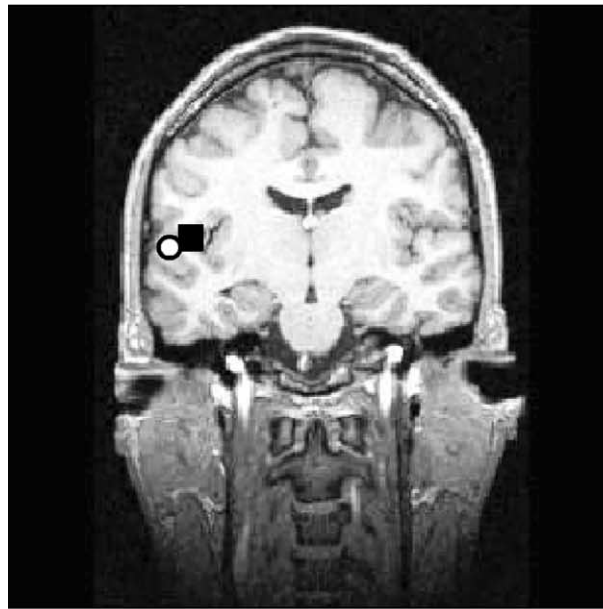
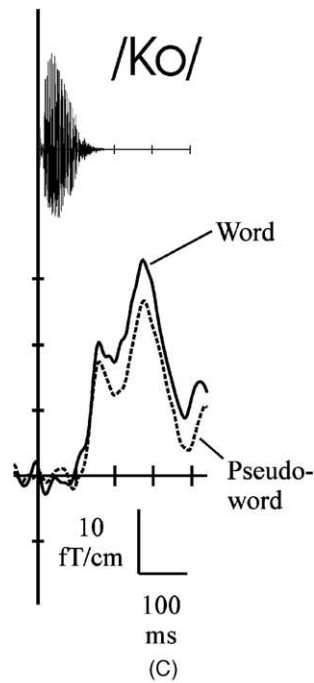


Fig. 2. (A) The functional webs realizing phonological word forms may be distributed over the perisylvian areas of the dominant left hemisphere. Circles represent local neuron clusters and lines represent reciprocal connections between them. (B) Word presentation induced stronger  $\gamma$ -band responses in the 30 Hz range compared with pseudo-word presentation, in particular over the left hemisphere. The reverberatory circuits within word webs may underlie the enhancement of high-frequency responses to words compared with pseudo-words. (C) The magnetic correlate of the MMN, the MMNm, was stronger in response to words compared with pseudo-words. Significant differences appeared already around 150 ms after the word recognition point, suggesting that the activation of word-related functional webs (lexical access) is an early process. (D) The main generator of the word-evoked magnetic mismatch response was localized in the left superior temporal lobe.





■ word  
○ pseudo-word

(D)

Fig. 2. (Continued).

658 has, however, been unclear until recently whether such phys-  
659 iological distinction would only occur if experimental sub-  
660 jects attend to certain features of the stimuli or engage in  
661 language-related tasks.

662 A further important question is at which point in time, af-  
663 ter the information about a spoken or written word is present

664 in the input, the brain makes the word–pseudo-word distinc-  
665 tion. If distributed functional webs underlie word process-  
666 ing, an incoming verbal stimulus should automatically acti-  
667 vate its corresponding representation. If a sufficient number  
668 of input units, specializing in the detection of stimulus fea-  
669 tures, have been activated, the entire strongly connected web

would automatically ignite due to the strong feedforward and feedback connections holding the network together. This process of *ignition* (Braitenberg, 1978a) of the functional web should take place very rapidly, the major factors determining the latency being axonal conduction delays and temporal summation of activity in the neurons involved. Axons can bridge large distances in the cortex within a few milliseconds. The most common cortico-cortical fibers, which have diameters of 0.5–1  $\mu\text{m}$ , can be estimated to propagate action potentials within 10–20 ms over distances of 10 cm (Aboitiz et al., 1992). There is direct physiological evidence for such fast spreading of activity in the intact human brain. For example, the activation of one area by transcranial magnetic stimulation (TMS) is followed by the activation of the homotopic area in the other hemisphere after a delay of  $\sim 20$  ms (Ilmoniemi et al., 1997). A word-related functional web should therefore become active shortly after its initial stimulation, certainly within the first 100–200 ms after the information necessary for identifying a word is present in the input.

Neurophysiological recordings are necessary to determine the point in time when the brain distinguishes words from pseudo-words. Some studies, as for example, the studies of high-frequency cortical responses discussed above, have indicated that word-related brain processes can be detected late, i.e. around 400 ms after presence of the relevant information in the input. However, physiological word–pseudo-word differences in the ERP have also been found substantially earlier, in the so-called N1–P2 complex, 100–200 ms after onset of visually presented stimuli (Rugg, 1983).

In a recent series of EEG and MEG studies, we could confirm this and found that the MMN and its magnetic equivalent (MMNm) were larger in response to spoken words compared with after pseudo-words (Pulvermüller et al., 2001c; Shtyrov and Pulvermüller, in press). The MMN, which can be elicited by rare changes in the acoustic environment, was used because it has been found to reflect the existence of memory traces or engrams in the cortex and because it is largely independent of the subject's attention (Näätänen, 2001; Näätänen and Winkler, 1999). To control for the physical difference, which necessarily distinguishes any word from a pseudo-word, two-syllabic items ending in the same second syllable were chosen. Between their two syllables was the pause characteristic of some Finnish consonants, so-called double stop consonants (for example “kk”). This pause made it possible to record separate non-overlapping brain responses to the two individual syllables of a naturally spoken bi-syllabic word. When the critical second syllable completed a word, its MMN and MMNm were larger compared with when the syllable was placed in a pseudo-word context (Fig. 2C). This difference was most pronounced 100–200 ms after the word recognition point of the lexical items, the earliest point in time when the information about the word is present in the acoustic input (Marslen-Wilson, 1990). This suggests that the functional

web activated by a word in the input becomes active early, a finding consistent with earlier observations based on EEG and MEG recordings (Dale et al., 2000; Pulvermüller et al., 1995, 2001a; Skrandies, 1998). These findings support proposals made on the basis of psycholinguistic reaction time experiments that lexical access is an early process (Marslen-Wilson, 1973; Marslen-Wilson and Tyler, 1980). The main source of the cortical generator of the word-related MMNm, as revealed by the ECD, was localized in the left superior temporal lobe (Fig. 2D). Whereas the dipole moment of the ECD was greater for words than pseudo-words, its anatomical locus did not change with lexical status.

It is noteworthy that, in the studies of the MMN and MMNm elicited by words (Korpilahti et al., 2001; Pulvermüller et al., 2001c; Shtyrov and Pulvermüller, 2002, in press), the enhancement of these responses to words was seen although the experimental subjects were instructed to ignore the acoustic input and watch a silent movie. Together with results from metabolic imaging studies (Price et al., 1996), the physiological distinction of words and pseudo-words in these experiments proves that focussing attention on words is not necessary for activating the words' cortical memory traces.

In summary, physiological studies provide support for the existence of word representations in the brain. The enhanced high-frequency responses in the  $\gamma$ -band to words are consistent with coordinated fast reverberatory neuronal activity generated by functional webs. The word-related enhancement of the MMN may lead one to an estimate of the point in time when language representations in the brain are being accessed.

#### 4.2. Word webs

Word-use in the context of objects and actions may lead to stronger links between neurons in the cortical core language areas and neurons in areas processing information about the words' referents. This is implied by the correlation learning principle and the cortex' long-range connections between motor and sensory systems. Functional webs would therefore provide the basis for the association (in the psychological sense) between an animal name and the visual image it relates to, or between an action verb and the action it normally expresses. Strong links within the web set up by such correlation learning can account for one's impression that the image is automatically aroused by the word form presented alone and that, vice versa, the image almost automatically calls the name into active memory. The neuron ensembles linking phonological information and information about the actions and perceptions to which a word refers will be called *word webs* here. They would include the phonological webs in perisylvian areas and, in addition, neurons in more widespread cortical areas critically involved in processing perceptions and actions. The type of entity a word usually refers to should be reflected in the cortical topography of the functional web that realizes it.

780 The meaning of an animal name such as “whale” or  
781 “shark” is usually known from visual experiences, pictures,  
782 or films, whereas the meaning of a tool name such as “nail”  
783 or “fork” refers to objects one uses for certain actions. This  
784 is not to say that one could not know a whale from interact-  
785 ing with it, or nails from looking at them, but it may appear  
786 plausible that, in general, more relevant information char-  
787 acterizing whales and nails is related to vision in one case  
788 and to actions in the other. In principle, in order to draw  
789 firm conclusions on perceptual and functional attributes of  
790 word and conceptual categories, the perceptual and action  
791 associations of the stimuli need to be determined empiri-  
792 cally. The lack of such stimulus evaluation is a caveat of  
793 many studies of category-specific brain processes. Behav-  
794 ioral investigations carried out with healthy volunteers re-  
795 vealed that many animal and tool names show the expected  
796 differential elicitation of visual or action associations, re-  
797 spectively. However, the most striking double dissociation  
798 in perceptual and action attributes was seen between action  
799 verbs on the one hand and selected nouns referring to ani-  
800 mals or large man-made objects on the other (cf. Fig. 3D;  
801 Pulvermüller et al., 1999a). Also, categories such as “ani-  
802 mal names” were not well defined with regard to the modal-  
803 ity for which most striking associations are being reported.  
804 For example, whereas words such as “whale” or “shark”  
805 are reported to elicit primarily visual associations, however  
806 the results for “cat” are less clear cut, for obvious reasons.  
807 Thus, the differential associations cut across the categories  
808 suggested by a philosophical approach (e.g. living versus  
809 non-living), as was earlier found for category-specific neu-  
810 ropsychological deficits (Warrington and McCarthy, 1987).  
811 The sensory/action modalities through which the referent of  
812 a word is known appear to be relevant (Fuster, 1999).

813 It is a limitation of the considerations made so far that they  
814 only cover communication where words are being learned  
815 in the context of their referent objects or actions. However,  
816 word meanings can also be picked up from contexts in  
817 which the actual referents are absent. The meaning of newly  
818 introduced words can be revealed by known words used in  
819 the same sentence or piece of discourse. It has been pro-  
820 posed that a word’s meaning can be defined in terms of the  
821 other words that frequently co-occur with it (Landauer and  
822 Dumais, 1997). This would translate into a different neuro-  
823 biological scenario for the learning of word meaning. Given  
824 there is a stock of words whose meaning has been acquired  
825 on the basis of word-object or word-action contingencies, a  
826 new word occurring in good correlation with such known  
827 words would only activate its phonological perisylvian rep-  
828 resentation. However, neurons in extra-perisylvian space  
829 related to the meaning of the context words would fre-  
830 quently be active together with the phonological web of the  
831 new word. The correlated activity of semantically-related  
832 neurons included in the neuronal representations of known  
833 words and the phonological web of the new word may  
834 allow for “parasitic” learning of word meaning. This im-  
835 plies that the semantically-related neurons will finally

836 be shared between known and new words, so that their  
837 neuronal representations would overlap in their semantic  
838 parts. This line of thought shows that the learning of word  
839 meaning on the basis of correlated neuronal activity is not  
840 restricted to the word-object-contingency scenario. Given  
841 enough words have already been learned, additional dis-  
842 crete webs of neurons linking information about a new  
843 word’s form and meaning can be set up by exposure to  
844 texts.

845 Fig. 3A sketches the postulated neuronal architectures  
846 of functional webs representing words with strong visual  
847 or action associations, respectively. The circles in the dia-  
848 grams symbolize local clusters of neurons strongly linked  
849 by cortico-cortical fibers. The diagrams illustrate the idea of  
850 word webs that include neurons related to semantic aspects.  
851 More precisely, the proposal is that aspects of the words’  
852 referents, the entities they refer to, are woven into the net-  
853 works. If the referent is an object usually perceived through  
854 the visual modality, neurons in temporo-occipital areas  
855 should be included in the web. If a word refers to actions or  
856 to objects that are being manipulated frequently, neurons in  
857 fronto-central action-related areas are assumed to be wired  
858 into the cortical representations. This can easily be extended  
859 to other sensory modalities as well (Pulvermüller, 1999).

860 A shortcoming of the diagrams in Fig. 3A (see also  
861 Fig. 4A) is that only one type of association is shown for  
862 each word web. Usually, a word that is primarily visu-  
863 ally related is reported to elicit some action associations  
864 too, and vice versa, an action-related word also yields  
865 some visual associations (cf. Fig. 3D). The all-or-nothing  
866 aspect one may infer from the diagrams is therefore un-  
867 realistic. To make the diagrams more realistic, each web  
868 should include some additional neurons in the respec-  
869 tive other field, although the ensembles’ *neuron density*  
870 in these additional areas would be lower than in the  
871 areas processing the words’ primary referential aspect  
872 (Kiefer and Spitzer, 2001). Further, action associations im-  
873 ply that there are associations with self-perceived aspects  
874 of the action in the somatosensory and/or visual modality.  
875 The visual perception of one’s own hand during knocking  
876 likely arouses neurons in movement-related areas of the vi-  
877 sual system not activated if, for example, a stationary visual  
878 stimulus is perceived (Rizzolatti and Arbib, 1998). There-  
879 fore, there would be good reason to add detail to the  
880 diagrams—at the cost of making them more complex.  
881 Nevertheless, the topographies of the functional webs of  
882 semantic word types can be postulated to be different, and  
883 the diagrams convey the gist of this idea.

884 The postulated differential topographies of word webs  
885 imply meaning-related processing differences between word  
886 categories. A major source of evidence for such differences  
887 are neuropsychological patient studies where, for example,  
888 the production or comprehension of nouns and verbs, or ani-  
889 mal and tool names was found to be differentially affected  
890 by disease of the brain (Bak et al., 2001; Cappa et al.,  
891 1998; Damasio and Tranel, 1993; Daniele et al., 1994; Miceli

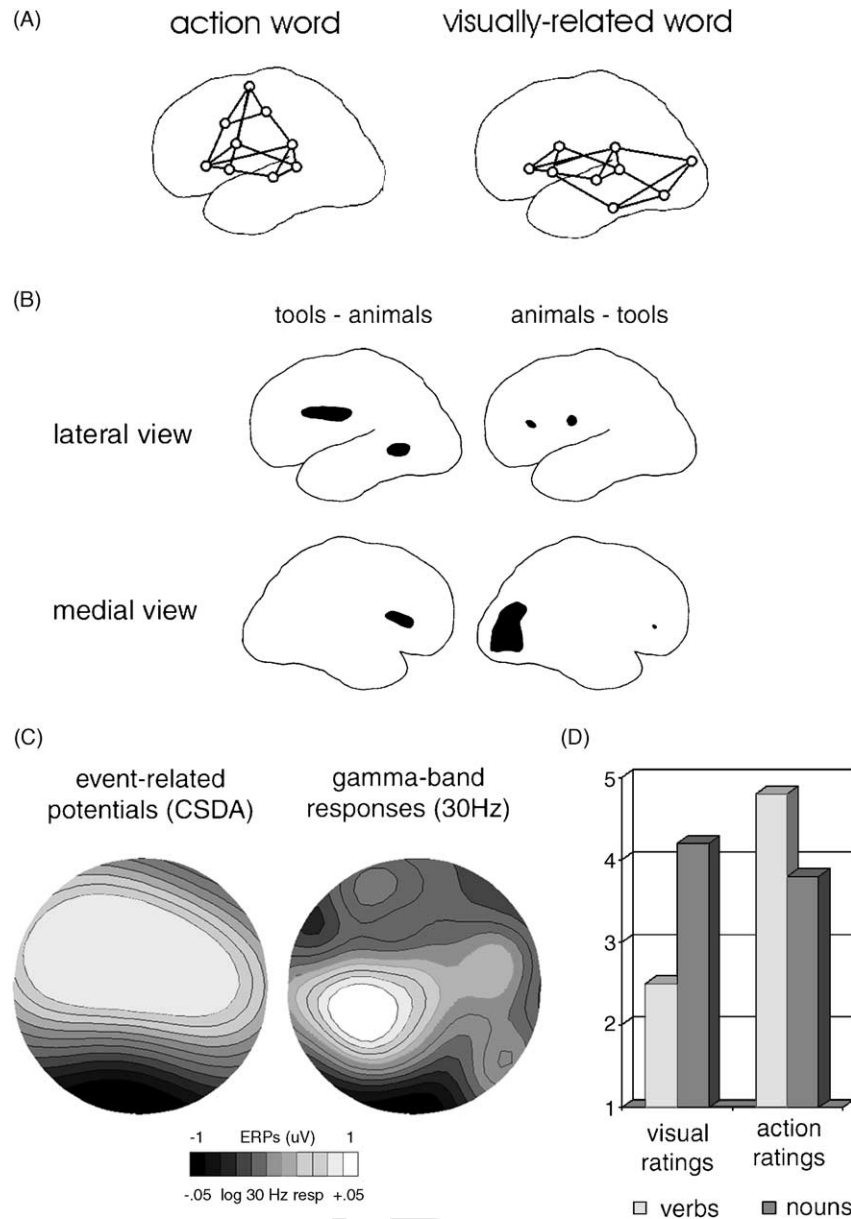
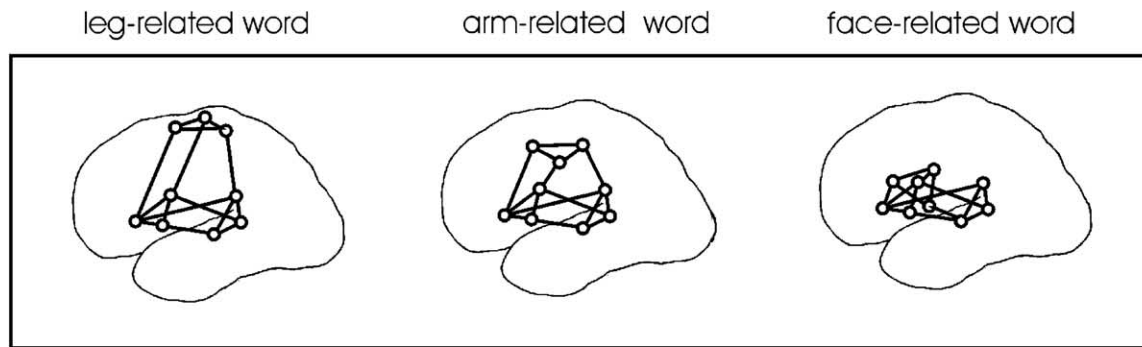


Fig. 3. (A) Visual and action associations of words may be mapped by functional webs extending over perisylvian language areas and additional visually- and action-related areas in the temporo-occipital and fronto-central areas. The cortical topography of word-related functional webs of words primarily characterized by visual associations may therefore differ from those of words with strong action associations. (B) Differences in metabolic brain activation related to the processing of nouns referring to animals and tools in a naming task. Whereas the tool words more strongly activated a pre-motor region and an area in the middle temporal gyrus, animal names most strongly aroused occipital areas. (C) Electrophysiological differences between nouns and verbs in a lexical decision task recorded at central (close to motor cortex) and posterior (above visual cortex) recording sites.  $\gamma$ -Band responses in the 30 Hz range were stronger close to the motor cortex for action verbs, and stronger above visual areas for nouns with strong visual associations. A similar difference was revealed by ERPs submitted to Current Source Density Analysis (CSDA). (D) Behavioral experiments showed that the stimulus nouns elicited strong visual associations whereas the verbs were primarily action-related.

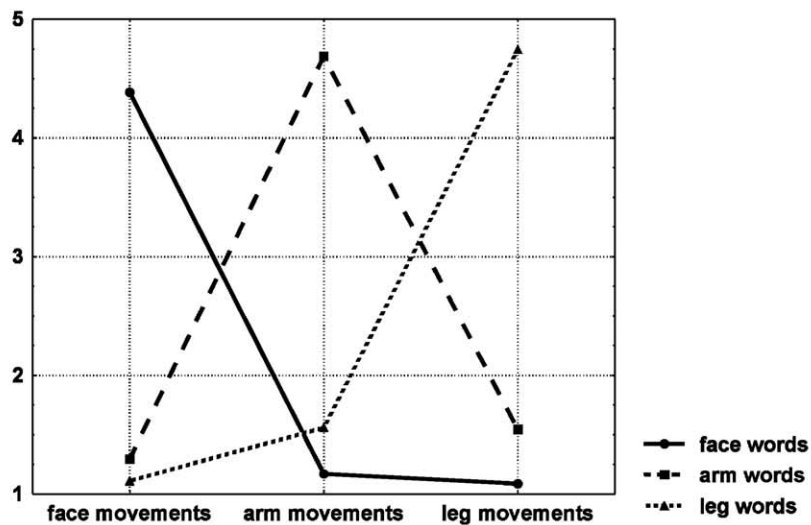
892 et al., 1984, 1988; Patterson and Hodges, in press;  
 893 Warrington and McCarthy, 1983; Warrington and Shallice,  
 894 1984). These dissociations between kinds of words and con-  
 895 ceptual categories can be understood based on the assump-  
 896 tion of distributed neuron ensembles reflecting *perceptual*  
 897 *and structural attributes*, including visual features and the  
 898 degree of overlap between exemplars, and the *functional at-*

899 *tributes*, the actions to which the words and concepts relate  
 900 (Humphreys and Forde, 2001).

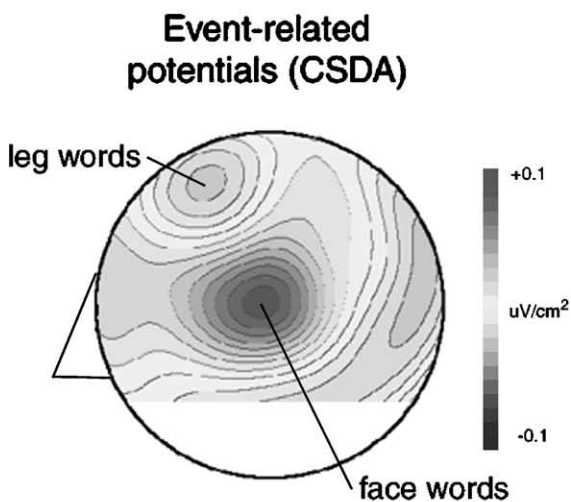
901 It can also be asked whether the intact brain demon-  
 902 strates differential activation of brain areas when action- or  
 903 perceptually-related words are being processed. A critical  
 904 prediction appears to be the following. If words of one kind  
 905 are characterized by stronger action (visual) associations



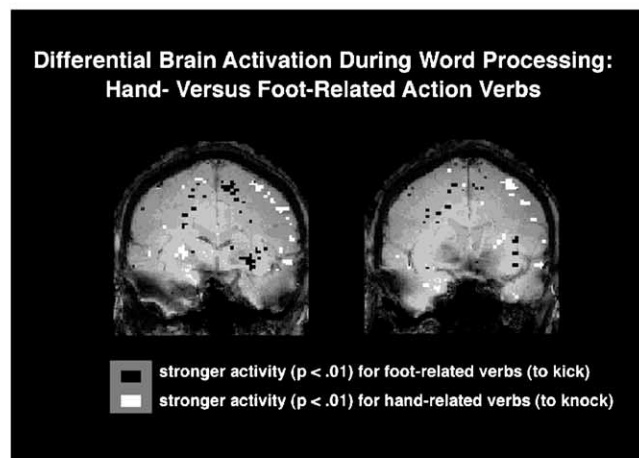
(A)



(B)



(C)



(D)

Fig. 4. (A) Cortical topographies of functional webs representing different types of action verbs may differ. Action words can refer to actions executed by contracting face, arm or leg muscles (*to lick, to pick, to kick*). Different neuron ensembles in the primary motor cortex may therefore be woven into the word-related neuron ensembles (cf. Fig. 1 B). (B) Ratings of face-, arm-, and leg-associations confirming differential referential semantics of three action verb groups. (C) Results from an EEG study. Topographical differences between brain responses to face- and leg-related verbs. Stronger in-going currents were seen close to the vertex for leg-related items (red spot at the top) and at left-lateral sites, close to the face representation, for face-related words (blue spot on the left). (D) Result from an fMRI study comparing arm- and leg-related verbs (single subject data). Differences were seen in the pre-central gyrus of the left hemisphere. Blue pixels indicate stronger activation for arm-words and red pixels indicate stronger activation for leg-words.

906 than those of another kind, their processing should be ac-  
907 companied by stronger brain activity in the relevant action-  
908 (sensory-) related areas. Relevant action-related areas are in  
909 the frontal lobe and the areas necessary for visual perception  
910 of objects are in the occipital and inferior temporal lobes.

911 When pictures of animals and tools were presented  
912 in a naming experiment, several areas, including occip-  
913 ital and temporal sites and the classical language areas,  
914 were found to increase their activity (Martin et al., 1996).  
915 Category-specific activation was found in the pre-motor  
916 cortex and the middle temporal gyrus when tools had to  
917 be silently named, and in the occipital and inferior tem-  
918 poral lobe when animals had to be named (Fig. 3B). The  
919 pre-motor activation may be related to the action associa-  
920 tions of tool names, as the activation in inferior temporal  
921 and occipital areas may be related to visual attributes of ani-  
922 mal names. The additional activation in the middle temporal  
923 gyrus in tool naming may be related to movement associa-  
924 tions elicited by the words involved. Differential cortical ac-  
925 tivation by action- and visually-related concepts and words  
926 were confirmed, in part, by more recent metabolic imaging  
927 studies of category-specific processes using PET and fMRI  
928 (Damasio et al., 1996; Grabowski et al., 1998; Martin and  
929 Chao, 2001; Moore and Price, 1999; Mummery et al.,  
930 1998; Perani et al., 1999; Spitzer et al., 1998; Warburton  
931 et al., 1996), although not all researcher could confirm such  
932 differences (e.g. Devlin et al., 2002).

933 Neurophysiological imaging investigation of noun and  
934 verb processing provided further evidence for category-spe-  
935 cific brain processes relevant for language (Brown and  
936 Lehmann, 1979; Dehaene, 1995; Koenig and Lehmann,  
937 1996; Molfese et al., 1996; Preissl et al., 1995; Pulvermüller  
938 et al., 1996b, 1999a). In one of these studies, differential vi-  
939 sual and action associations of the nouns and verbs selected  
940 were demonstrated by a rating study performed by all exper-  
941 iment participants (Pulvermüller et al., 1999a). ERPs and  
942 high-frequency cortical responses revealed a physiological  
943 double dissociation consistent with differential activation  
944 of fronto-central areas and occipital areas (Fig. 3C). The  
945 ERP difference was apparent ~200 ms after onset of visual  
946 word stimuli, consistent with early activation of the word  
947 webs involved. Topographically specific high-frequency re-  
948 sponses, which were stronger over central areas for verbs  
949 and over occipital areas for nouns, started later (400 ms).

950 In a recent publication, Rösler and colleagues could not  
951 replicate differential pattern of neurophysiological responses  
952 to nouns and verbs (Haan et al., 2000). In an even more  
953 recent publication (Rösler et al., 2001), however, these au-  
954 thors reported a noun verb difference reminiscent of that  
955 in earlier studies (e.g. Dehaene, 1995; Preissl et al., 1995).  
956 Nevertheless, these authors still argue that their data, con-  
957 sidered separately, give no convincing support to the hy-  
958 pothesis that the two word categories activate distinct neu-  
959 ronal populations. They prefer to attribute the differential  
960 topographies to differences in response latencies, because,  
961 in their study, in which subjects had to respond to words

962 by button presses, the response latencies differed between  
963 nouns and verbs. Their interpretation is, however, incon-  
964 sistent with earlier findings in studies of noun and verb  
965 processing where no such latency differences were present  
966 (e.g. Pulvermüller et al., 1999a). Clearly, the data reported  
967 by Rösler and colleagues are consistent with the hypothe-  
968 sis that there are word-category-specific differences in the  
969 topographies of cortical activation.

970 Kutas' group recently replicated noun verb differences  
971 in ERPs when words were presented in sentence context  
972 (Federmeier et al., 2000). In addition to these differences,  
973 these authors found an enhancement of the brain response  
974 for syntactically ambiguous words that can function as either  
975 verbs or nouns. However, because these authors did not in-  
976 vestigate the semantic properties of their word material, their  
977 data are open to the possibility that aspects of word meaning  
978 were relevant for eliciting differential brain responses.

979 Further investigations of physiological manifestations of  
980 word processing were performed to address the question of  
981 whether grammatical or semantic aspects of words are cru-  
982 cial for determining word-category-specific brain responses.  
983 In a study using spoken words, the physiological distinction  
984 between visually-related nouns and action verbs could be  
985 replicated and similar differential activation was found be-  
986 tween visually- and action-related nouns. In contrast, there  
987 was no difference in the topography of brain responses be-  
988 tween action verbs and nouns for which strong action as-  
989 sociations were reported (Pulvermüller et al., 1999b). These  
990 topographical differences in the activation patterns elicited  
991 by action- and visually-related words resembled those ob-  
992 served between written tool and animal names (Pulvermüller  
993 et al., 1999a) and between pictures of animals and tools  
994 (Kiefer, 2001). All of these results indicate that the differen-  
995 tial activity patterns are not grammatically-related, but rather  
996 reflect semantic properties of the stimulus words and their  
997 related concepts. Pulvermüller et al. (2001a) found a global  
998 enhancement of the evoked brain response for a certain  
999 sub-category of nouns, which, according to the behavioral  
1000 data reported by these authors, had particularly strong se-  
1001 mantic associations to both objects and actions (multimodal  
1002 semantics). Control nouns without multimodal semantics  
1003 failed to elicit the result, again arguing against an inter-  
1004 pretation in terms of grammatical word categories. Further-  
1005 more, lexical ambiguity (cf. Federmeier et al., 2000) cannot  
1006 account for the difference, because the stimuli used in this  
1007 study were members of one lexical category only (they were  
1008 either nouns, verbs, or members of a different grammat-  
1009 ical class). Finally, there was a linear increase of an early  
1010 component of the event-related magnetic field with a mea-  
1011 sure of the strength of semantic associations of a word ( $r =$   
1012 0.8). Therefore, these data enforce an account in terms of  
1013 word semantics. It may be that the strong associations, in  
1014 the psychological sense, of words with multimodal seman-  
1015 tics are realized as strong connections within particularly  
1016 widespread and large cortical neuronal assemblies. Activa-  
1017 tion of these particularly widespread and strongly connected

1018 networks may underlie the enhancement of brain responses  
1019 seen in the neuromagnetic response.

1020 More fine-grained predictions are possible on the basis of  
1021 the postulate that topographies of word webs reflect word  
1022 meaning, in particular aspects of the words' referents. Action  
1023 verbs can refer to actions performed with the legs (walking),  
1024 arms (waving), or mouth (talking). It is well known that  
1025 the motor cortex is organized somatotopically, i.e. adjacent  
1026 body muscles are represented in neighboring areas within  
1027 the motor cortex (Penfield and Rasmussen, 1950). Neu-  
1028 rons controlling face movements are located in the inferior  
1029 pre-central gyrus, those involved in hand and arm move-  
1030 ments accumulate in its middle part, and leg movements  
1031 are controlled by neurons in its dorsal and medial portion  
1032 (cf. Fig. 1B). On the basis of the correlation learning prin-  
1033 ciple, one can therefore postulate differential topographies  
1034 for cell assemblies organizing leg-, arm- and face-related  
1035 words (Fig. 4A). Differential action-related associations of  
1036 sub-categories of verbs could be demonstrated by behav-  
1037 ioral studies (Fig. 4B, Pulvermüller et al., 2001b).

1038 In an EEG study, we compared face- and leg-related action  
1039 verbs ("talking" versus "walking"). Current source density  
1040 maps revealed early differential activation along the motor  
1041 strip. Words of the "walking" type evoked stronger in-going  
1042 currents at dorsal sites, over the cortical leg-area, whereas  
1043 those of the "talking" type elicited the stronger currents at  
1044 inferior sites, next to the motor representation of the face and  
1045 articulators (Fig. 4C, Pulvermüller et al., 2000). The early  
1046 differential activation of fronto-central cortical areas by  
1047 sub-types of action words about 200 ms after onset of visual  
1048 word stimuli was recently confirmed by an ERP study using  
1049 localization of multiple current sources in the brain based on  
1050 MNE (Hauk and Pulvermüller, submitted for publication).  
1051 A similar study comparing arm- and leg-related words was  
1052 performed with fMRI (Pulvermüller et al., in preparation).  
1053 The preliminary data shown in Fig. 4D are consistent with  
1054 the view that the body parts involved in the actions referred  
1055 to by the words are reflected in the cortical neuron webs  
1056 these words activate. Further, the earliness at which the  
1057 word category differences were present in the neurophysi-  
1058 ological response indicates that there was no substantial  
1059 delay between word form access and the processing of  
1060 action attributes. This supports the view that information  
1061 about the word form and the body parts, with which the  
1062 word-related actions are being carried out, are woven into  
1063 the same word-related cortical networks.

#### 1064 4.3. The time course of lexical and semantic activation

1065 The lexical status of a written or spoken word, whether  
1066 it is a word or not, and aspects of word semantics appear  
1067 to crucially determine the brain response. The differences  
1068 between semantic word categories can appear early in the  
1069 neurophysiological brain response, i.e. ~100–200 ms after  
1070 stimulus onset (e.g. Pulvermüller et al., 2001a; Skrandies,  
1071 1998). This latency range corresponds to the time range

1072 where the earliest neurophysiological differences between  
1073 words and pseudo-words were found (e.g. Pulvermüller  
1074 et al., 2001c; Rugg, 1983). Thus, the earliest latencies  
1075 at which the lexical status and the semantic category  
1076 of word stimuli were reflected in the neurophysiological  
1077 response coincided with each other. These neurophysio-  
1078 logical data support psycholinguistic models postulating  
1079 that information about a word's meaning can be accessed  
1080 near-simultaneously with information about its form, a pro-  
1081 posal motivated by behavioral studies (Marslen-Wilson and  
1082 Tyler, 1975, 1980). Likewise, they are consistent with  
1083 the view that a word is cortically processed by a discrete  
1084 functional unit storing information about the word's form  
1085 together with that about its semantics.

1086 While the semantically- and form-related parts of dis-  
1087 tributed word webs may be activated near-simultaneously,  
1088 there is evidence that different physiological processes  
1089 appear in sequence in the same cognitive brain representa-  
1090 tions. A stage of access to the representation (ignition of  
1091 the cell assembly, see Braitenberg, 1978a) may be followed  
1092 by sustained reverberatory activity (active memory, see  
1093 Fuster, 1995) of the word web. Whereas the early access  
1094 stage may occur within one quarter of a second after the  
1095 information in the input allows for recognizing a stimulus  
1096 word, the reverberatory activity related to active memory  
1097 would follow after more than 250 ms. The early access  
1098 process may be reflected in early ERPs, and the late re-  
1099 verberations may lead to high-frequency responses in the  
1100  $\gamma$ -band. These hypotheses can tentatively explain recent  
1101 findings about the time course of neurophysiological re-  
1102 sponses to words (for further discussion, see Kiefer, 2001;  
1103 Pulvermüller, 1999).

#### 1104 4.4. Summary and conclusions

1105 The brain response to words and word-like materi-  
1106 als appears to reflect lexical status and word semantics.  
1107 Word-pseudo-word and word category differences were re-  
1108 ported in metabolic and neurophysiological imaging studies.  
1109 Both types of differences were found already at 100–200 ms  
1110 after the information in the input allowed for recognizing  
1111 the words, whereas some differences, e.g. in high-frequency  
1112 responses, appeared only with longer delays. These results  
1113 can be explained on the basis of the idea that words are rep-  
1114 resented and processed by distributed but discrete neuron  
1115 webs with distinct cortical topographies. They are some-  
1116 what less easily explained by alternative approaches. If  
1117 words were represented by single neurons, for example, the  
1118 corresponding brain activity states could probably not be  
1119 measured with large-scale neuroimaging techniques, such  
1120 as MEG or fMRI. Also, it is in question how the specific  
1121 changes observed between words and pseudo-words could  
1122 be explained if both stimulus types were processed alike by  
1123 a distributed network of neurons in which no discrete rep-  
1124 resentations exist, or by interference patterns over the entire  
1125 cortex. Furthermore, an explanation of word-category dif-

ferences may turn out to be even more difficult on the basis of such approaches. Thus, while competing approaches are challenged by the data discussed, the postulate of discrete functional webs representing words explains them well.

The results on category differences indicate that aspects of the meaning of words are reflected in the topography of brain activation. They are also consistent with the view that the referents of particular word kinds are relevant for determining the brain areas involved in their processing. The data do not explain the entire spectrum of areas found to be active during category-specific word processing. There are findings about different semantically-related activity patterns that are not readily explained by elementary neuroscientific principles, such as the principles (I)–(IV) discussed above. For example, the differential activation of right- versus left-parietal areas by names of body parts and numerals (Le Clec'H et al., 2000), cannot be explained by the four principles alone. It is likely that additional as yet not fully understood principles of cortical functioning are necessary to account for these data. Furthermore, it needs to be added that the semantic category of the stimulus words is by far not the only variable determining the topography of brain activation. Clearly, the modality of stimulation (visual or auditory) and the task context in which words have to be processed (lexical decision, naming, memory, etc.) play an additional important role in determining the set of active brain areas (Angrilli et al., 2000; Mummery et al., 1998). Further, other features of the stimulus material, for example the length and frequency of words, play an important role (Assadollahi and Pulvermüller, 2001; Rugg, 1990). The present approach suggests, and the summarized data indicate, that, if possibly confounding variables are appropriately controlled for, category-specific differences are present between word categories and conceptual kinds across tasks and stimulus modalities.

## 5. Serial order in the brain

In language use, words usually occur in sequences. They are part of sentences of several words; although early in infancy, single-word utterances play an important role, and also later in life, communication using single-word utterances is common. The majority of utterances, however, are composed of several words that follow each other according to rules. How may the rules governing serial order of language elements be realized in the brain?

This question can be asked with regard to the level of meaningful language units, words and *morphemes*, and a similar question can also be asked at the level of *phonemes*, language sounds distinguishing between words with different meanings. How may phoneme and morpheme sequences stored and processed neuronally? The following sections will summarize a few brain mechanisms that could, at different levels, be relevant for establishing serial order of language units. Three different mechanisms will be dis-

cussed that may relate to different types of serial order in language.

### 5.1. Synfire chains

A sequence AB of events can be represented by two neuronal units directly connected to each other, one corresponding to A and the other to B. If the respective neuronal units were referred to by Greek letters,  $\alpha$  and  $\beta$ , the sequence of events would be realized as  $\alpha$ ,  $\beta$ , and, in addition, a direct connection from  $\alpha$  to  $\beta$ . A single neuron  $\alpha$  could, therefore, by way of its direct projection to a neuron  $\beta$ , arouse it whenever active. However, it is unlikely that single cortical neurons connected in this way play a role in language processing. The connections of most neurons in the cortex are known to be weak so that input from one single neuron would usually not be sufficient to strongly enhance the firing probability of a second neuron on which the first one projects (Abeles, 1991). Therefore, it appears more likely that sets of neurons project onto each other thereby making up broad neuron chains, which determine spatio-temporal patterns of activity.

Physiological evidence for complex spatio-temporal patterns of activity comes from correlation studies performed on multiple unit recordings (Abeles et al., 1993; Vaadia et al., 1995). The firing probability of a single neuron could best be determined when more than one preceding neuronal event, and in addition, behavioral context, were taken into account. This context-dependence cannot be modeled by a chain of single neurons, each projecting onto the next in the chain. However, the context-dependence of firing probabilities follows from a model in which *groups of neurons* are connected in chains. In this case, the synchronous activity of one of the groups, which are connected in sequence, is necessary to arouse the next set. This type of neuronal circuit has been labeled a *synfire chain* (Abeles, 1991). The synfire model implies that a cortical neuron can be part of different spatio-temporal firing patterns and can therefore become active in different well-defined behavioral and neuronal contexts.

To illustrate the synfire mechanism, a schematic representation of two intersecting synfire chains is shown in Fig. 5. In this illustration, each neuron will be assumed to require two simultaneous inputs to become active, and each of the sequentially connected sets of the chains will include three neurons. These are simplifications made for ease of exhibition; the number of neurons of each neuron set connected in sequence is probably higher, between 50 and 100 neurons (Diesmann et al., 1999), and their firing threshold is probably in the order of 5–10 simultaneous inputs (Abeles, 1991). Whenever the neuron group at the upper left is active, an excitation wave will spread downward terminating at the lower right. Although the neurons in the very center are also heavily connected to the neuron groups at the lower left, activity on the lower left will die out in this case. In the same way, a wave from the upper right will spread to the lower left only.



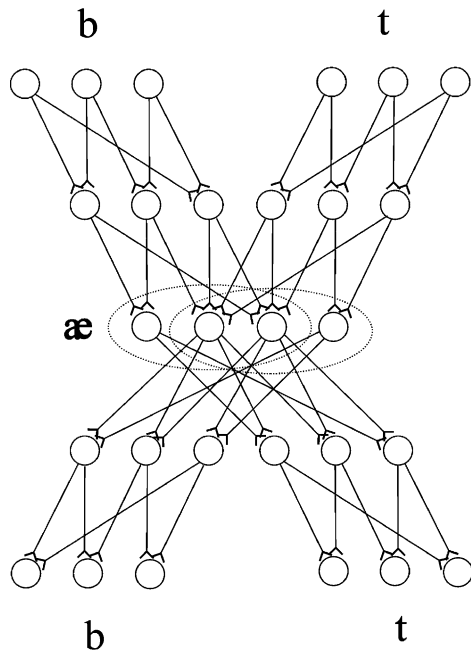


Fig. 5. Synfire chains that cross. Each circle represents a neuron and arrows represent connections between neurons. Each neuron is assumed to have a threshold of 2. Possible phonemic correlates of subsets of the synfire chains are indicated by ovals.

1233 There are two distinct spatio-temporal patterns of activity  
 1234 that are prevented from getting mixed up by the very nature  
 1235 of their connections, although the structural bases of these  
 1236 patterns strongly overlap. The majority of the neurons in the  
 1237 central layer where the two synfire chains cross are activated  
 1238 whenever an excitation wave is initiated at the top. Each of  
 1239 the neurons included in a synfire chain may actually be part  
 1240 of several other chains as well.

1241 The essential feature of the synfire model is that informa-  
 1242 tion highways share sub-components and that the effect of  
 1243 each neuron's firing strongly depends on its firing context.  
 1244 This can be further illustrated by Fig. 5. The two neurons  
 1245 in the middle of the central neuron group (where the two  
 1246 ovals intersect) would be part of both synfire chains. They  
 1247 will become active as part of an activity wave starting at the  
 1248 upper left, but will as well be activated if an activity wave  
 1249 started at the upper right. The firing of these middle neurons  
 1250 in the central layer alone does not determine the path of the  
 1251 excitation wave. However, the path can be determined if the  
 1252 context of their firing is taken into account. The left- and  
 1253 right-most neurons in the central group have the role of such  
 1254 context-indicators channeling the wave of activity either to  
 1255 the left or right. If one of these lateral neurons is active to-  
 1256 gether with the central ones, the activity wave is channeled  
 1257 either to the left or right.

1258 Synfire chains have been proposed as a neuronal basis of  
 1259 articulatory programs (Braitenberg and Pulvermüller, 1992).  
 1260 The exact timing of nerve cell firings determined by the  
 1261 circuitry would be exactly what is required for realizing pre-

cisely timed articulations. From a cognitive perspective, the  
 beauty of the synfire chain mechanism lies in its potential to  
 provide a straightforward solution of what Lashley (1951)  
 described as one of the main aspects of the problem of  
 serial order in behavior. If each letter was represented as a  
 separate entity, the possible words of a language could not  
 be modeled simply by direct connections between the 50 or  
 so phoneme or letter representations. Too many sequences  
 would be allowed whenever for any given set of phoneme or  
 letter representations. If a set of representations is activated,  
 for example those of the phonemes [t], [æ] and [b], there  
 would be no information about serial order, so that different  
 sequences would be possible, for example "tab" and "bat".  
 However, if not phonemes but, instead, *phonemes variants*  
 that are determined by their phonotactic context and show  
 complementary distributions, so-called *allophones*, were  
 represented by sets of neurons, each possible sequence  
 could be realized by direct links between individual neuron  
 sets. The representations of context-sensitive phoneme vari-  
 ants could be described, for example, as [b] at word onset  
 and followed by [æ]—which can be abbreviated as #Bæ,  
 as [æ] following [b] and followed by [t], bÆt, and by [t]  
 terminating a word and preceded by [æ], æT#. The three  
 context-sensitive phonemes, here described as #Bæ, bÆt  
 and æT#, respectively, would determine the elements of the  
 phoneme sequence and their serial order. A similar solution  
 to one facet of the serial order problem has earlier been  
 suggested by Wickelgren (1969). The synfire model now  
 allows for specifying the putative underlying mechanisms.

Fig. 5 can be used to further illustrate putative articulatory-  
 phonological mechanisms. If the synfire chain starting at the  
 upper left and running to the lower right is considered the  
 correlate of the syllable [bæt], its component neuron groups  
 can be taken as the putative neurobiological correlate of the  
 relevant linguistic elements, phonemes, or more precisely,  
 allophones. Each phonological representation would be  
 composed of two different kinds of neuronal elements, one  
 related to invariant properties of the articulation of a partic-  
 ular phoneme, the other related to systematic phonetic, i.e.  
 physical, variations determined by the context. For example,  
 the neurons shared between the two context-sensitive rep-  
 resentations of the phoneme [æ]—the two middle neurons  
 in the central layer of Fig. 5—could relate to articulatory  
 features of the phoneme, e.g. lips open but not rounded,  
 tongue at the bottom of the mouth. In contrast, the neurons  
 deciding between the possible successor sounds and distin-  
 guishing between the alternative synfire chains—the left-  
 and right-most neurons of the middle layer—would process  
 information about how to realize co-articulation effects  
 related to the respective phoneme contexts—for example,  
 information that the tongue is being moved towards the  
 teeth, in preparation of the [t] articulation. The neurobi-  
 ological equivalent of a phoneme-in-context would therefore  
 consist of neurons related to articulatory distinctive features  
 and others realizing context-dependent phonetic features  
 of a language sound defining allophones. Since it offers a

1318 mechanism for precisely timed articulations, a solution for  
1319 one aspect of the serial order problem, and a mechanism  
1320 for co-articulation effects, the synfire model may provide a  
1321 brain perspective on articulatory-phonological programs.

1322 One of the features this proposal shares with psycholin-  
1323 guistic approaches (Marslen-Wilson and Warren, 1994) is  
1324 that it does not require separate representations of phonemes.  
1325 Overlapping sets of neurons related to distinctive features  
1326 and context features are proposed to be represented. Sets  
1327 of feature representations are considered the cortical basis  
1328 of context-sensitive phoneme variants, allophones. If one  
1329 wishes to specify the putative neurobiological correlate of a  
1330 phoneme within this model, one is free to choose between the  
1331 intersection, or as an alternative, the union of the overlapping  
1332 neuron sets. However, these putative “phoneme correlates”  
1333 would not represent discrete functional units within a syn-  
1334 fire model. Discrete functional units would be postulated for  
1335 allophones only.

### 1336 5.2. Sequence detectors

1337 It may be tempting to apply the synfire model to  
1338 higher-order sequences of meaningful units, morphemes  
1339 and words. It is possible to define and to neurally im-  
1340 plement a word’s syntactic role in relation to its context  
1341 words, the items that frequently occur before and after it  
1342 in continuous speech, and to postulate a representation of  
1343 these various contexts by multiple crossing and intersecting  
1344 synfire chains. There are, however, at least five reasons why  
1345 this strategy is prone to fail:

- 1346 (i) Word sequences span one to several seconds. Synfire  
1347 chains provide precise adjustment of neuronal events  
1348 that follow each other at short delays, usually in the  
1349 millisecond range. The synfire model therefore oper-  
1350 ates at a time scale different from that relevant for  
1351 word chain processing. Whereas synfire chains provide  
1352 a plausible model of articulatory programs within syl-  
1353 lables and words, different mechanisms must be rele-  
1354 vant for word sequencing, because these mechanisms  
1355 need to operate at a *larger time scale*.
- 1356 (ii) The occurrence of a word does usually not allow for  
1357 good predictions on the particular word(s) that fol-  
1358 low(s) it. Cases in which the occurrence of one particu-  
1359 lar word predicts, with high probability, the occurrence  
1360 of a particular complement word, as is the case for  
1361 “neither . . . nor”, represent rare exceptions. Whereas  
1362 within a word, a phoneme is followed by one out of  
1363 5–20 other phonemes (Harris, 1955), the number of  
1364 possible successors of a word can reach the order of  
1365  $10^4$ . While a synfire model for phoneme sequences ap-  
1366 pears feasible, such a model for word sequences would  
1367 require an astronomical number of chains, due to the  
1368 very *large number of possible word sequences*.
- 1369 (iii) The regularities determining word sequences likely op-  
1370 erate on more abstract word groups called *lexical cat-*

egories. Examples of lexical categories are noun (N), 1371  
personal pronoun (Ppr) or verb (V). The occurrence of 1372  
a word from one particular category, for example the 1373  
category noun or personal pronoun, predicts with high 1374  
probability the later occurrence of a member of a com- 1375  
plement category, for example verb. However, there is 1376  
freedom as to which verb to select. It is unclear how a 1377  
synfire model could realize *lexical categorization*. 1378

- (iv) When competent speakers are being confronted with 1379  
sentences they have never encountered before, they 1380  
may nevertheless judge them as correct. This requires 1381  
generalization from a limited sample to new sequences 1382  
that have not been learned. The synfire model leaves 1383  
open the question how to neurally implement such 1384  
*generalization*. 1385
- (v) The occurrence of a word of a particular type predicts 1386  
the occurrence of complement words, but there is free- 1387  
dom as to *at which position* the complement will follow 1388  
its antecedent. For example, the occurrence of a noun 1389  
or personal pronoun predicts the later occurrence of a 1390  
complement verb, but material may intervene between 1391  
the two, as, for example, in “*Peter comes to town*”, 1392  
“*Peter the singer comes . . .*”, “*Peter the greatest singer* 1393  
in the world *comes . . .*”. A synfire model would not 1394  
allow for such *variable delays*. 1395

Which alternative mechanisms for establishing serial or- 1396  
der do exist in the nervous system? As emphasized above 1397  
the synfire model realizes a sequence of elementary events 1398  
“A then B” by direct connections between their neuronal 1399  
representations,  $\alpha$  and  $\beta$ . As an alternative, it is possible to 1400  
connect a third element to both representations of elemen- 1401  
tary events. The third element,  $\gamma$ , would become active if 1402  
the sequence AB occurs. The basic idea for such a mech- 1403  
anism has been formulated by McCulloch and Pitts (1943) 1404  
(Kleene, 1956). Meanwhile, several lines of research have 1405  
proven its existence in the nervous system of animals. 1406

Most animals can specifically respond to stimuli that 1407  
move. Therefore, they must be equipped with a mechanism 1408  
for *movement detection*. The problem of movement detec- 1409  
tion shares properties with the serial order problem, and 1410  
this becomes obvious in the following formulation. If there 1411  
are two sensory cells  $\alpha$  and  $\beta$  looking at adjacent areas A 1412  
and B of visual space, a moving stimulus first appearing in 1413  
A and later appearing in B will sequentially stimulate the 1414  
neurons  $\alpha$  and  $\beta$ . A third neuron,  $\gamma$ , receiving input from 1415  
both  $\alpha$  and  $\beta$  may function as a detector of a movement 1416  
in the AB direction. It should respond to the sequential 1417  
stimulation of  $\alpha$  and  $\beta$ , but not to the reverse sequence. 1418  
The mechanism yielding sequence sensitivity may involve 1419  
low-pass filtering of the signal from  $\alpha$ , thereby delaying 1420  
and stretching it over time. Simple addition of the delayed 1421  
and stretched signal from  $\alpha$  and the actual signal from  $\beta$  1422  
will yield a value which is large when the activation of  $\alpha$  1423  
precedes that of  $\beta$ , but small values instead when the acti- 1424  
vations of  $\alpha$  and  $\beta$  occur simultaneously or in the reverse 1425

1426 order. This mechanism of directional selectivity has first  
1427 been described in the visual system of insects (Reichardt  
1428 and Varju, 1959; Varju and Reichardt, 1967). Analogous  
1429 mechanisms of movement detection by sequence detec-  
1430 tion have been uncovered in higher mammals as well  
1431 (Barlow and Levick, 1965; Hubel, 1995) and a similar  
1432 mechanism of mediated sequence processing exists in the  
1433 cerebellum (Braitenberg et al., 1997). What all of these  
1434 mechanisms have in common is that a sequence of element-  
1435 ary events is detected by a separate higher-order element  
1436 (labeled  $\gamma$  here), which receives input from the neuronal  
1437 correlates of the elementary events (labeled  $\alpha$  and  $\beta$ ). Since  
1438 this type of mechanism is characterized by the existence of  
1439 neuronal elements that specialize in computing serial order  
1440 information by mediating between more elementary units,  
1441 it will be called *mediated serial order processing* (in con-  
1442 trast to unmediated or *direct serial order mechanisms* as,  
1443 for example, synfire chains).

1444 Mediated sequence processing may be relevant for pro-  
1445 cessing serial order of words and morphemes in sentences.  
1446 This is probably not achieved by *exactly* one of the mech-  
1447 anisms found in the visual system of arthropods and ver-  
1448 tebrates, because of the time domain differences. As it is  
1449 the case for the synfire chain mechanism, the mechanisms  
1450 for direction-sensitive movement detection apply for delays  
1451 smaller than a second, whereas much longer delays occur be-  
1452 tween sequentially aligned words and morphemes (cf. point  
1453 (i) above). For example, Reichardt's model is designed for  
1454 delays in the millisecond range (Reichardt and Varju, 1959).  
1455 Barlow et al. (1964) report that some neurons in the visual  
1456 system of vertebrates exhibit rather long decay times that  
1457 could be compatible with the detection of sequences span-  
1458 ning tens of seconds.

1459 A model of sequence detectors fed by word webs can be  
1460 subject to all of the points raised above against a synfire  
1461 model of word sequencing. Points (i)–(v) will therefore be  
1462 addressed again below. The strategy here is to explore what  
1463 the mediated sequence processing mechanism already well  
1464 established by neuroscientific research can achieve, and how  
1465 it would operate at the level of functional webs to yield serial  
1466 order of words in sentences.

1467 (i) *Time scale*: Sequence detectors for words must allow  
1468 for delays of several seconds. The elementary units  
1469 that may contribute to syntactic sequence detection  
1470 are cell assemblies representing words and additional  
1471 neuronal units mediating between word-related neu-  
1472 ron populations. Activation–deactivation cycles of dis-  
1473 tributed functional webs can span several seconds (at  
1474 least up to 20 s, Fuster, 1995), which is the appropri-  
1475 ate time scale for syntactic processes. Therefore, word  
1476 webs can store the information about a word occur-  
1477 rence for several seconds, so that a sequence detector  
1478 fed by word webs can process this information at the  
1479 time scale relevant for the processing of serial order of  
1480 words.

- (ii) *Number of represented sequences*: One may argue that  
a sequence detection model for word strings requires  
a very large number of such detectors, each respond-  
ing to a particular sentence. However, this is not nec-  
essarily so. In the same way as movement detectors,  
word-sensitive sequence detectors can be assumed to  
operate on *pairs* of elementary units. If there is a se-  
quence detector for each frequently occurring sequence  
of two words, the number of necessary sequence de-  
tectors can be reduced substantially. Still, the number  
would be large (but see (iii)).
- (iii) *Categorization*: If a sequence detector  $\gamma$  responds to  
a sequence “first  $\alpha_1$  then  $\beta_1$ ” of neuronal events, it is  
possible that it responds to a sequence “first  $\alpha_2$  then  
 $\beta_2$ ” as well (where  $\alpha_1, \alpha_2, \beta_1$  and  $\beta_2$  symbolize word  
webs). By connections to  $\alpha_1, \alpha_2, \dots, \alpha_m$  on the one  
hand side, and to  $\beta_1, \beta_2, \dots, \beta_n$  on the other,  $\gamma$  can be  
sensitive to activation sequences of elements of *groups*  
of word webs, i.e. to a sequence of any member of the  
 $\alpha$ -group followed by any member of the  $\beta$ -group. The  
 $\alpha$ -group could, for example, be the lexical category  
of nouns or personal pronouns and the  $\beta$ -group could  
be the verbs. The sequence detectors could operate on  
webs representing words and morphemes from given  
*lexical categories*.
- (iv) *Generalization*: Suppose a sequence detector  $\gamma$  be-  
comes frequently active together with the activation se-  
quence of word webs  $\alpha_1$  and  $\beta_1$ , and develops, by as-  
sociative learning, strong connections to both of them  
so that it will finally respond reliably to the sequence  
“first  $\alpha_1$  then  $\beta_1$ ”. Additional confrontation with the  
sequences “first  $\alpha_1$  then  $\beta_2$ ” may also strengthen the  
sequence detector's connections to  $\beta_2$ , and finally, if  
the activation of  $\alpha_2$  is frequently followed by that of  
 $\beta_1$ , the  $\alpha_2$  web may furthermore be chained to  $\gamma$ . The  
“generalization”, that the sequence detector is also sen-  
sitive to the event “first  $\alpha_2$  then  $\beta_2$ ”, although this par-  
ticular sequence may never have been present in the  
input, follows from the earlier learning steps. This type  
of substitution-based associative learning can account  
for at least one type of *generalization of syntactic rules*  
to novel word strings.
- (v) *Variable delays*: A sequence detector does not re-  
quire fixed temporal delays between the activations  
of the units feeding into it in order to become active.  
Reichardt-type motion detectors can respond to stim-  
uli moving with variable speed, and in the very same  
way, a functional web fed into by two word webs  
may respond to their serial activation independently of  
the exact delay in-between activations. A noun–verb  
sequence detector may therefore become active when-  
ever confronted with one of the strings “*Peter comes*  
to town”, “*Peter the singer comes ...*”, or “*Peter the*  
greatest disc jockey of the world *comes ...*”. Clearly,  
there must be an upper limit for the delays possible,  
which, in a Reichardt-like model, would depend on

1537 the decay times of the word webs (several seconds)  
 1538 and the characteristics of the low-pass filter. However,  
 1539 delays of several seconds do not appear to constitute  
 1540 a problem for this type of model.

1541 In summary, the proposal is that mediated sequence pro-  
 1542 cessing known from other neuroscientific domains is an im-  
 1543 portant mechanism for syntactic processing. In contrast to  
 1544 the already known mechanisms operating at the single neu-  
 1545 ron level—i.e. single neurons representing the input and  
 1546 mediating the sequence—the present proposal puts that the  
 1547 same type of mechanism exists at the level of functional  
 1548 webs. Thus, the relevant *sequence detectors* would be func-  
 1549 tional webs responding to sequences of neuron populations  
 1550 related to the processing of single words. A sequence de-  
 1551 tector would become active if the word  $A_i$  from a word  
 1552 category A is followed by a word  $B_j$  from category B,  
 1553 thereby sequentially activating the corresponding functional  
 1554 webs  $\alpha_i$  and  $\beta_j$ . Frequent co-occurrence of words in lin-  
 1555 ear sequences may be an important factor for establish-  
 1556 ing neuron ensembles specializing in the detection of word  
 1557 sequences. This allows for an economic representation of  
 1558 word pair sequences, largely independent of the actual de-  
 1559 lay between the words within a sentence. The same type of  
 1560 wiring may underlie the perception of a word string and its  
 1561 production.

1562 The postulate that word sequences are assessed by se-  
 1563 quence detectors leads to a novel view on syntactic pro-  
 1564 cesses. The dominating view in linguistics has been that a  
 1565 hierarchical tree of syntactic category representations is built  
 1566 up in the process of parsing a sentence, and that the indi-  
 1567 vidual words of the sentence are attached to the tree as its  
 1568 leaves. The tree would have the sentence symbol S as its  
 1569 root, and branches would lead to phrase nodes (labeled, for  
 1570 example Np for noun phrase and Vp for verb phrase). From  
 1571 there, further branches can connect to the lexical category  
 1572 nodes labeled N for noun, Ppr for personal pronoun, V for  
 1573 verb stem, or Vs for verb suffix which can index person,  
 1574 number and time. An example of a syntactic tree is presented  
 1575 in Fig. 6A.

1576 The tree representation has the disadvantage of not  
 1577 capturing what has been called *agreement*. The rela-  
 1578 tionship between the sentence-initial pronoun and the  
 1579 sentence-final suffix—which agree in number (singular)  
 1580 and person (third)—requires an extension of the concept  
 1581 of a two-dimensional tree structure. Linguists have pro-  
 1582 posed supplementary mechanisms operating within trees to  
 1583 model the inter-dependence of these elements. The most  
 1584 popular approach proposes that features of the words and  
 1585 morphemes are transported through the branches of the tree  
 1586 to mediate between its leaves. Such feature transport may  
 1587 guarantee that, in the example in Fig. 6A, the subject agrees  
 1588 in number with the verb (“He ... s”). A disadvantage of  
 1589 this strategy is that it postulates a separate mechanism—  
 1590 within-tree transport of features—where there is no need  
 1591 for it.

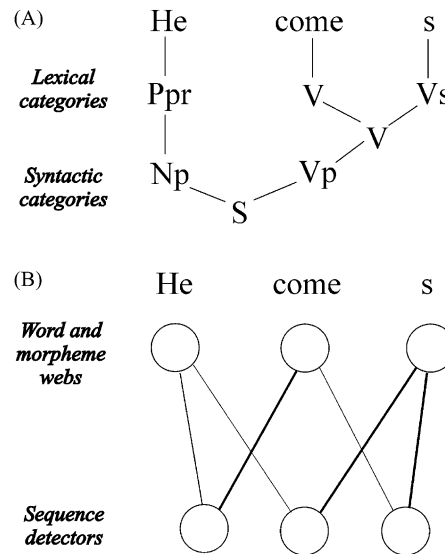


Fig. 6. (A) A phrase structure representation of the sentence “He comes”. Lines represent structural relationships. Abbreviations: Ppr, personal pronoun; V, verb; Vs, verb suffix; Np, noun phrase; Vp, verb phrase; S, sentence. (B) Putative neuronal circuit processing the same word string by word webs and mediated sequence detectors. Circles represent functional webs. Labels close to circles indicate the morphemes represented by word webs (lower line of circles) and the sequences of lexical category members sequence detectors are assumed to be sensitive to (upper line). Thin and thick lines represent qualitatively different types of reciprocal neuronal connections between sequence detectors and word/morpheme webs.

A syntactic model built on sequence detectors replaces 1592  
 the tree construct by a set of neuronal elements mediating 1593  
 between word webs (Fig. 6). Separate sequence detectors 1594  
 responding to word pairs, in the present example (a) to 1595  
 the pronoun–verb sequence, (b) to the verb–verb suffix se- 1596  
 quence, and, in the very same way, (c) to the pronoun–verb 1597  
 suffix sequence, are envisaged to be activated by the word 1598  
 string. The activation of these three sequence detectors 1599  
 would represent and process structural information of the 1600  
 word string. This approach arising from neuroscientific ob- 1601  
 servations seems more economical than the syntactic-tree 1602  
 approach, because it postulates one unified mechanism, 1603  
 mediated sequence processing, which may replace subor- 1604  
 dination and agreement by feature transport in syntactic 1605  
 trees. Furthermore, the neurobiological approach may pro- 1606  
 vide a brain-based explanation of neurophysiological and 1607  
 metabolic changes in brain activity related to the processing 1608  
 of syntactic information (Friederici et al., 1993; Hagoort 1609  
 et al., 1993; Indefrey et al., 2001; Moro et al., 2001; Neville 1610  
 et al., 1991; Osterhout et al., 1992). 1611

Another phenomenon may receive a simple and straight- 1612  
 forward explanation by the mechanism of mediated se- 1613  
 quence detection. The observation is that previously per- 1614  
 ceived syntactic structures are being imitated in subsequent 1615  
 verbal actions. This occurs with above chance probability in 1616  
 both conversations and controlled experiments (Bock, 1986; 1617  
 Bock et al., 1992; Pickering and Branigan, 1999). The phe- 1618

1619 nomenon is independent of whether or not the two sentences  
 1620 share words. A double object sentence as a prime (“...  
 1621 showed the children the pictures”) will yield later produc-  
 1622 tion of double object sentences (“... gave the butcher the  
 1623 knife”), and a similar priming effect can be observed for  
 1624 the prepositional object paraphrase (“... showed the pic-  
 1625 tures to the children”). Imitation of sequences of different  
 1626 words from the same lexical category can be explained by  
 1627 sequence detectors operating on categories of word repre-  
 1628 sentations. Priming of these neuronal webs by an incoming  
 1629 sentence will enhance the activity level of the neuronal  
 1630 units, thus later enhancing the probability that similar word  
 1631 sequences are being produced.

1632 There cannot be any doubt that networks made up of  
 1633 neurons can realize important aspects of the serial order  
 1634 of events. It is, nevertheless, important to point to some  
 1635 of the neurocomputational research that investigated in  
 1636 detail mechanisms discussed here. There is a long his-  
 1637 tory of work exploring the capabilities of associative  
 1638 networks, which has been sparked by theoretical propos-  
 1639 als (e.g. McCulloch and Pitts, 1943) and empirical results  
 1640 (e.g. Reichardt and Varju, 1959). Willwacher (1976, 1982),  
 1641 for example, presented an early implementation of a  
 1642 single-layer network capable of learning and retrieving let-  
 1643 ter sequences, and Buonomano (2000) recently showed that  
 1644 a variety of precise delays between events can be learned  
 1645 and represented in an associative network consisting of  
 1646 excitatory and inhibitory neurons that are organized in one  
 1647 neuronal layer. Some researchers have included much detail  
 1648 into their simulations, about the specific features of the se-  
 1649 quences under study, such as complex grasping or walking  
 1650 movements (Cruse et al., 1995; Cruse and Bruwer, 1987),  
 1651 and about neuronal responses as revealed by neurophysi-  
 1652 ological investigation (Kleinfeld and Sompolinsky, 1988).  
 1653 Apart from single-layer associative networks, more com-  
 1654 plex networks have been used with some success. Elman  
 1655 used an architecture that includes hierarchically organized  
 1656 layers one of which is reciprocally connected to an addi-  
 1657 tional so-called memory layer where information about past  
 1658 events can accumulate. This architecture proved particu-  
 1659 larly fruitful for modeling serial order of language elements  
 1660 (Elman, 1990; Elman et al., 1996). Dehaene et al. (1987)  
 1661 used a three-layer model including one layer where  
 1662 sequence detectors were very similar to the ones dis-  
 1663 cussed here in the context of syntactic processes could  
 1664 develop.

1665 Despite these successes in modeling serial order relation-  
 1666 ships in neural models, it should be kept in mind that the  
 1667 successful application of a network to a problem of serial or-  
 1668 der does not always imply that the relevant mechanisms on  
 1669 which sequence production or detection is based have been  
 1670 uncovered. For some simulation approaches, for example, it  
 1671 remains to be shown whether the crucial mechanism is di-  
 1672 rect sequence detection by delay lines or, as an alternative,  
 1673 mediated sequence detection relying on separate neuronal  
 1674 units devoted to the processing of serial order information.

This can be decided by looking closely at the behavior of  
 individual neurons included in the network.

The model of sequence detection discussed here makes  
 specific predictions on the outcome of neurophysiological  
 experiments, which have, as to the author’s knowledge, not  
 been carried out yet. The considerations on syntax offered  
 in this section would suggest that it might be advantageous  
 to have neuronal units available that respond specifically to  
 a sequence of events A and B, but that their *response is*  
*largely independent of the delay*. A further prediction might  
 be that the relevant delays range between 0.2 s and tens of  
 seconds. The model discussed here would suggest that such  
 sequence detectors responding to specific word sequences  
 would be particularly common in the left perisylvian cortex.

### 5.3. Activity dynamics

Still, a neuronal network including delay lines and se-  
 quence detectors may miss important aspects of the serial  
 order of words in sentences. Early neural network mod-  
 els (McCulloch and Pitts, 1943) were found to be insuffi-  
 cient by linguists (Chomsky, 1963), because the types of  
 sequences they can process, the so-called *regular events*  
 (Kleene, 1956), are only a subset of the string types linguistics  
 is concerned with. Although it remains to be shown that  
 a network containing synfire chains and sequence detectors  
 can only process regular events, one may ask for perspec-  
 tives for extending this neurobiological framework of serial  
 order.

Certainly, it is possible to supply a neuronal network  
 with additional mechanisms whose relationship to the brain  
 may be in question, so that the network is finally be ca-  
 pable of processing the more complex linguistic strings  
 also (e.g. Kaplan, 1972; Petri, 1970). However, it would,  
 no doubt, be nicer if the extension were motivated neuro-  
 scientifically. The proposal discussed in this section will  
 be that activity dynamics in the cortex may be the key for  
 solving additional problems of serial order. This general  
 idea has been explored in earlier theoretical work in neuro-  
 biology (e.g. Milner, 2001; Pulvermüller, 1993), linguistics  
 (Schnelle, 1996), and cognitive science (Page and Norris,  
 1998).

One string type linguists have used to reject a neurobio-  
 logically-related approach (McCulloch and Pitts, 1943) is  
 center-embedded sentences. If a speaker intends to say that  
 three different persons have performed three different ac-  
 tions, he could first talk about the three actors and specify  
 the three actions later. However, the sequence with which  
 the actors (here called A, B and C) are being referred to  
 determines the sequence in which their actions (labeled A\*,  
 B\* and C\* below) have to be named. In many languages,  
 a sequence of actor names ABC only allows the reverse  
 sequence of the action words C\*B\*A\*. This results in  
*center-embedded* strings, such as, “The man {whom the girl  
 {whom the dog bit} met} came home”—where the embed-  
 ded sentences are placed between brackets. Chomsky (1963)

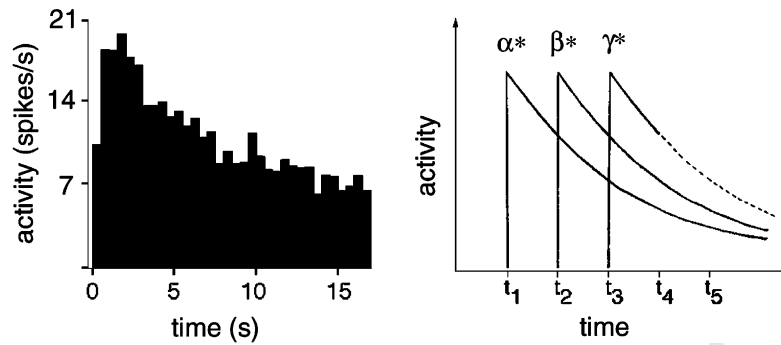


Fig. 7. Left: Activity of a memory cell possibly reflecting activity dynamics in a large cell assembly it belongs to. Note the almost exponential decrease of activity with time (adopted from Fuster, 1995). Right: If several assemblies of this kind are activated one after the other, the activation sequence is stored in the *hierarchy of activity levels* of assemblies. This mechanism could be used as a neuronal pushdown store (adopted from Pulvermüller, 1993).

1729 has argued that a storage device of a certain type, a so-called  
1730 pushdown store, is helpful for processing sentences of this  
1731 type. One may, therefore, ask whether there is reason to  
1732 postulate that such a memory device is realized in the  
1733 brain.

1734 The finding that cells activated by specific stimulus prop-  
1735 erties can stay active for a period of several seconds af-  
1736 ter stimulus presentation (Fuster, 1995) may again be of  
1737 utmost importance here. It is possible that these memory  
1738 cells retain their activity because they are part of neuronal  
1739 ensembles in which neuronal activity reverberates (Fuster,  
1740 1997; Zipser et al., 1993). If so, these cells reveal important  
1741 information about activity dynamics of the neuronal popu-  
1742 lations they are part of (Fuster, 1997).

1743 Many memory cells exhibit well-defined activity dynam-  
1744 ics. They do not show constantly enhanced activity after  
1745 presentation of the stimulus they are specialized for, but in-  
1746 stead, they are first strongly activated and then lose activ-  
1747 ity almost exponentially (Fig. 7, left). If several functional  
1748 webs exhibit this property, their stimulation in a particular  
1749 order implies that *the hierarchy of their activity levels stores*  
1750 *the information about the sequence*. Due to the exponential  
1751 decline of activity, the assembly activated first will later be  
1752 at the lowest activity level, whereas the last unit activated  
1753 will still maintain the highest level of activity. The webs  $\alpha$ ,  
1754  $\beta$  and  $\gamma$  activated in the order  $\alpha\beta\gamma$  may, therefore, exhibit  
1755 the hierarchy of activity levels  $\alpha < \beta < \gamma$  (Fig. 7, right).  
1756 If each of the units  $\alpha$ ,  $\beta$  and  $\gamma$  primes its respective action  
1757 word representations  $\alpha^*$ ,  $\beta^*$  and  $\gamma^*$ , the latter will adopt the  
1758 activity hierarchy of the former, resulting in  $\alpha^* < \beta^* < \gamma^*$ .  
1759 A readout mechanism fully activating, and then deactivat-  
1760 ing, the most strongly primed unit will lead to the generation  
1761 of the action words in the reverse order of their correspond-  
1762 ing actor expressions. Thereby a center-embedded sequence  
1763  $\alpha\beta\gamma\gamma^*\beta^*\alpha^*$  of neuronal activation and the corresponding  
1764 linguistic sequence  $ABCC^*B^*A^*$  can be produced. A senten-  
1765 ce such as “The man {whom the girl {whom the dog  
1766 bit} met} came home” could be generated. The mechanism  
1767 would determine that a series of words or word groups would  
1768 be followed by the inverse sequence of their complements.

Given an appropriate readout mechanism is available, a  
set of functional webs that lose activity exponentially after  
their activation and, in doing so, follow the same deacti-  
vation slope, can be considered a *neuronal pushdown store*  
(Pulvermüller, 1993, 1994). The proposed neuronal mecha-  
nism is but one possibility how a pushdown device could be  
realized in a neurobiologically plausible network consisting  
of discrete distributed neuronal units. For it to operate prop-  
erly, it must be postulated that all functional webs involved  
lose activity according to the same deactivation slope. Gen-  
eral principles of activity dynamics—that either hold true  
for a large class of brains or cortices, or for the human  
brain, or a part thereof—may therefore underlie the push-  
down mechanism. As mentioned, the proposal that more  
general principles of activity dynamics may underlie the  
processing of sequential information has been made ear-  
lier (e.g. Milner, 2001; Page and Norris, 1998), but the pre-  
cise mechanism and the type of temporally ordered strings  
it processes are still under discussion. Despite the obvious  
methodological difficulties, it may be possible to address  
these issues in future neurophysiological research on lan-  
guage.

#### 5.4. Summary and conclusions

To sum up, a neurobiological approach to serial order  
in language suggests that different mechanisms underlie  
the processing of phoneme sequences within syllables and  
words on the one hand side and the processing of word  
and morpheme sequences in sentences on the other. The se-  
rial order of phonemes may be organized by synfire chains,  
and that of meaningful units, words and morphemes, may  
be established by separate discrete functional webs specifi-  
cally responding their temporal succession, similar to those  
known from animal research. Furthermore, activity dynam-  
ics in large neuronal populations may be relevant for ade-  
quately processing complex sentences. While the remarks  
on serial order mechanisms still leave many questions unan-  
swered, they may nevertheless open a perspective for future  
fruitful research into the neurobiology of syntax.

1806 **6. An overview of putative language mechanisms**

1807 The main proposals about language processing in the brain  
1808 discussed in this review were the following:

- 1809 (1) Phonological word forms are represented and processed  
1810 by strongly connected discrete neuron ensembles dis-  
1811 tributed over the perisylvian cortical areas and strongly  
1812 lateralized to the language-dominant hemisphere. The  
1813 activation of word-related functional webs may under-  
1814 lie the neurophysiological and metabolic differences be-  
1815 tween words and pseudo-words, in particular the early  
1816 word-related enhancement of the MMN and the ob-  
1817 served modulation of high-frequency responses by lex-  
1818 ical status (cf. Section 4.1).
- 1819 (2) Words from different semantic categories are repre-  
1820 sented and processed by discrete neuron webs with  
1821 different cortical topographies. Information about the  
1822 meaning of the words, for example, the actions and  
1823 perceptions the words refer to, and the locus of the  
1824 primary cortical areas processing this information may  
1825 be relevant for determining the topographies of their  
1826 neuronal representations. This explains distinct cortical  
1827 topographies of word-evoked neurophysiological and  
1828 metabolic brain responses (cf. Section 4.2).
- 1829 (3) Words are represented and processed by discrete func-  
1830 tional webs in which information about a word's  
1831 form and that about its semantics are interwoven.  
1832 This postulate explains why the early neurophysio-  
1833 logical distinction of words and pseudo-words, and  
1834 that between semantic categories of words, can arise  
1835 near-simultaneously and immediately (within 200 ms)  
1836 after the information necessary for recognizing a word  
1837 is present in the input (cf. Section 4.3).
- 1838 (4) Phonological-phonetic sequences are cortically repre-  
1839 sented and processed by synfire chains, i.e. serially  
1840 connected sets of local neuron clusters. Each seri-  
1841 ally connected subset of neurons would correspond to  
1842 context-variants of phonemes, so-called allophones (cf.  
1843 Section 5.1).
- 1844 (5) Serial order of words in sentences is organized by me-  
1845 diated sequence processing; separate discrete sequence  
1846 detectors connected with pairs of word webs, or with  
1847 pairs of larger sets of word webs, represent syntactic  
1848 rules and process syntactic information within a simple  
1849 sentence (cf. Section 5.2).
- 1850 (6) Complex syntactic phenomena, such as center-embedding,  
1851 may depend on the activity dynamics of large neuronal  
1852 populations (cf. Section 5.3).

1853 Although more experimental work is clearly needed to  
1854 further support these proposals, they are consistent with  
1855 much of the data piled up so far. Importantly, the proposals  
1856 may motivate future studies. Great progress in understanding  
1857 brain–language relationships has been made in the last few  
1858 years. This demonstrates that the neuroscience of language  
1859 is a fruitful and prosperous new research field. In this en-

deavor, concrete proposals about neuronal mechanisms are 1860  
necessary. 1861

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