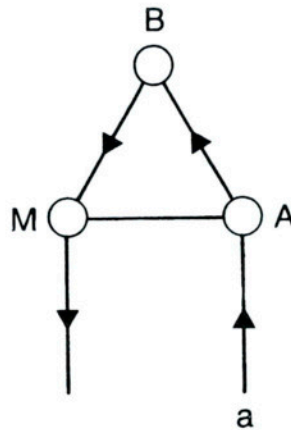**Friedemann Pulvermüller**
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Figure 1: Lichtheim's model of word representation. Separate and autonomous representations of the articulatory form (in motor center M), sound pattern (acoustic center A) and meaning (concept center B - German "Begriff" means "concept") are postulated. Adopted from Ref. 2.

The problem of language and the brain catches the attention of neurologists, psychologists and linguists since the second half of the 19th century, when Broca[1] published his seminal description of language loss due to brain lesion (aphasia). It was in these early years of the language-and-brain sciences when a simple model of cortical language mechanisms was proposed. This model posits that two small centers in the left hemisphere of typical right-handed individuals are the "seat" of word representations (Figure 1)[2,3]. More precisely, a motor language center housed in the left inferior frontal lobe (areas 44 and 45, see Figure 2) was believed to store articulatory plans of words, and a separate acoustic language center in the left superior temporal lobe (area 22) was believed to house the sound patterns of words. Although the exact definition of these "language centers" somewhat varies between different authors[4] they are usually localized close to the sylvian fissure and are, therefore, part of the "perisylvian" areas.
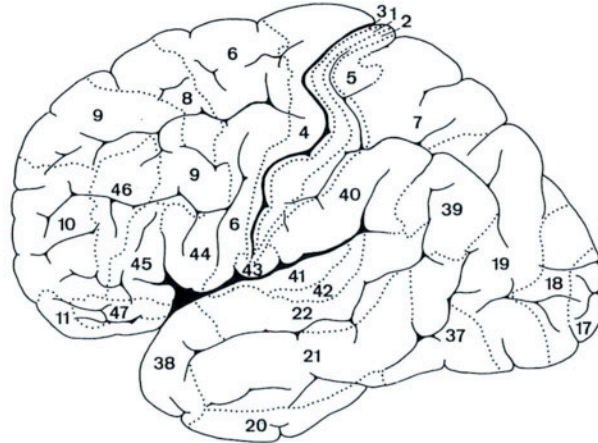
Figure 2: Lateral view of the left cortical hemisphere. Brodmann's areas are indicated. Adopted from Ref. 52.

This narrow localizationist view was subject to some criticism already before the turn of the century, which was formulated, for example, by a famous psychoanalyst who did some brain science in his early career. Based on theoretical considerations, this researcher claimed that processing of individual words should involve not only the two small perisylvian centers in the left hemisphere, but additional widespread cortical areas that are, for example, essential for visual perception. According to this author, there are not two separate brain-internal representations of articulatory plans and sound patterns of words, but, instead, a widely distributed neuron network would represent the articulatory and acoustic word form together with its meaning. Figure 3 presents a sketch of such a network.
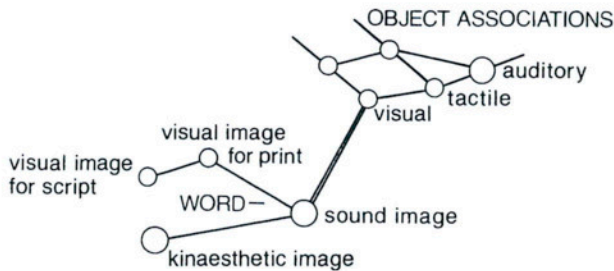

Figure 3: Freud's model of word representation. A widely distributed network is assumed to represent the various aspects of a word (articulatory and acoustic pattern, semantic properties). Lesion anywhere in the network may impair its function. Adopted from Ref. 15.

Are there arguments that would support one or the other view- either the narrow localizationist view of Wernicke and Lichtheim, or the holistic view put forward by Freud? According to what is known from aphasia research, lesions of Broca's area and adjacent areas in the inferior frontal lobe of the language-dominant hemisphere lead to motor aphasia

characterized by severe deficits in producing speech, and lesions in Wernicke's area in the superior temporal gyrus causes sensory aphasia, for which a deficit in understanding language is most characteristic. These facts appear to speak in favor of the localizationist model.

However, after lesion in Wernicke's area additional deficits in speech production can be observed, and after lesion in Broca's area the patient usually exhibits additional problems in comprehending sentences. Although there are a few cases in the literature for whom it has been claimed that there is a language production deficit without any deficit in language comprehension[5], a test of language comprehension (and short-term verbal memory), the so-called Token Test[6], is usually clinically used for aphasia diagnosis. Thus, it appears that the large majority of aphasics, even those who have one intact language area, exhibit deficits in both language production and comprehension, although one of these deficits may be more pronounced than the other. This fact can only be explained if both language areas are assumed to contribute to both language production and comprehension, a fact which obviously speaks against the narrow localizationist approach and supports the holistic view[7]. However, one may nevertheless object against the holistic approach that probably not all cortical areas are equally involved in word processing, and that the areas involved may not be the same for different parts of speech. In summary, the truth appears to lie in-between the classical localizationistic and holistic views. A brain-theoretical framework is necessary in order to allow for more specific postulates.

One of the most important neuropsychologists of this century, Donald Hebb[8], proposed a brain-theoretical framework that may be of particular relevance for language representation and processing. Hebb assumes that the cortex is an associative memory machine and the strength of connections between cortical neurons depends on how frequently these neurons have been co-activated in the past. Meanwhile, there is strong evidence for this view from both neuroanatomy[9,10] and neurophysiology, although the original Hebbian ideas about learning principles had to be modified based on physiological data[11] and computational considerations[12]. If several neurons are frequently active at the same time, they will acquire strong connections to each other and, therefore, this "cell assembly" will act as a functional unit: If only some of its neurons are being activated by external input, activity will automatically spread throughout the assembly so that all of its members will be active. This explosion-like process has been called ignition of the assembly[9]. Furthermore, if an assembly has ignited, neuronal activity will probably not cease at once, but will reverberate for some time in the various neuronal loops within the assembly[13,14]. Thus, ignition and reverberation appear to be important processes occurring in strongly connected cell assemblies.

Words may be organized in the cortex as strongly connected cell assemblies

If Hebb is correct, simultaneous neuronal activity should be the basic brain principle underlying the formation of cortical representations (cell assemblies). What would this mean for language representation and processing?

If a word is articulated by the infant, neuronal activity controlling articulatory movements is present in the inferior frontal lobe. In addition, neurons in auditory cortices in the superior temporal lobe will be stimulated by the self-produced acoustic signal. If I talk, I also hear myself talking and this necessarily leads to simultaneous neuronal activity in inferior frontal and superior temporal cortices (Broca's and Wernicke's areas). Therefore, in this case Hebb would advocate the Freudian opinion rejecting separate cortical representations of articulatory programs and sound patterns, and emphasizing that cell assemblies distributed over motor and sensory regions should form the neuronal counterpart of word forms[15-17]. Figure 4 presents a sketch of such a perisylvian assembly. Although the existence of such assemblies cannot be proven in humans for ethical reasons, the recent discovery of "mirror neurons" in monkeys' frontal lobes that fire in relation to both hand movements and perceptions of such movements appear to support the view that motor and sensory patterns are not separately stored in cortex but are, instead, bound together in sensory-motor cell assemblies[18].
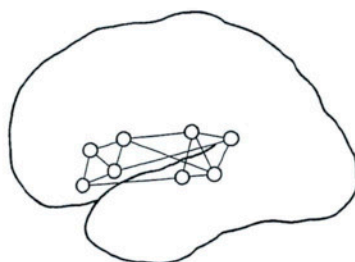
word form representation

Figure 4: The cell assembly representing a phonological word form may be distributed over perisylvian areas. Circles represent local neuron clusters and lines represent bidirectional fiber bundles between such clusters. The connections are assumed to have strengthened because of correlated activity of neurons during articulation of the word form.

How would the meaning of words be stored in cortex? Associative learning is probably one of the important processes that may occur during acquisition of word meanings. A certain word may frequently be heard when a certain object is being visually perceived, or when the language-learning infant performs certain actions, or when it smells a certain smell, hears certain sounds or has some other perceptions. Therefore, when word forms become meaningful neurons in the perisylvian language areas and neurons located outside these areas, probably in various sensory and motor cortices and also in higher association cortices, are activated at the same time. According to Hebb, these neurons will strengthen their mutual connections and will develop into a cell assembly that comprises neurons in the language areas and outside.

So far, it appears that, from a modern perspective, Freud's approach to language representation was correct. However, not all words are the same, and for certain word classes

the Freudian assumptions are most likely incorrect[7]. There are, for example, words with highly abstract meaning that primarily serve a grammatical function. For these grammatical function words (including pronouns, articles, auxiliary verbs, conjunctions etc.) a representation in widely distributed cell assemblies appears unlikely, because for these words there is no strong correlation between the occurrences of the word form and non-linguistic stimuli or actions. Therefore, grammatical function words should be cortically represented by cell assemblies restricted to the perisylvian areas.

It is well-known that language is localized to the left hemisphere. However, the Hebbian approach suggests that laterality of language is not complete but gradual. If I hear myself say a word, neurons in both hemispheres are necessarily activated at the same time and, according to the associative learning principle, the co-activated neurons in both hemispheres should become part of the assembly representing the word form[19]. Laterality of language may therefore mean that more neurons in the left hemisphere are included in the assemblies than neurons in the right hemisphere. If word meanings are being associated with word forms, the lateralized assembly representing the word form is probably activated together with neurons in both hemispheres, because the perception of a visual stimulus (or the execution of motor programs) will most likely lead to activation of similar numbers of neurons in both hemispheres. Therefore, meaning association should reduce the laterality of word representations. Cell assemblies representing nouns or verbs and other so-called "content words" should be less strongly lateralized to the left than assemblies representing grammatical function words[7,20].

More fine-grained word class-distinctions are desirable based on the Hebbian approach. Some words refer to objects that can be visually perceived, others refer to actions that are usually performed by the own body, and even other words refer to sounds, tastes, somatosensory perceptions etc. According to the modality through which meaning-related information is being transmitted, these word categories can be called "visual words", "motor words", and so on. If Hebb is correct, the cortical distribution of the assembly is a consequence of simultaneous activity occurring in different areas. This implies that a word frequently perceived together with certain visual stimuli (a likely event during learning of words referring to objects) has a cortical assembly quite different from the assembly representing a motor word (which may frequently co-occur with certain movements of the own body). Most nouns with well-imaginable meaning probably are visual words whose assemblies include additional neurons in visual cortices, whereas many action verbs are motor words whose assemblies may include additional neurons in motor cortices, and some nouns, such as tool names, may be considered a mixed category (motor and visual) from this point of view[21]. These modality-distinctions are, however, not the only ones suggested by the Hebbian approach. Because of the somatotopic organization of the motor cortex, words referring to foot movements (to kick) should include neurons in more dorsal motor cortices than words referring to hand movements (to write), and "semantic neurons" of words related to movements involving only a few muscles

(to knock) may have a more narrow localization compared to those of words related to complex body movements (to caress). Similar more fine-grained distinctions are, of course, possible for visual words [21,22] and for words whose semantics are anchored in other modalities.

To make these ideas more plastic, Figure 5 presents sketches of possible cortical counterpart of function words, motor words and visual words, respectively. In addition to differences in the language-dominant left hemisphere, a strong degree of laterality can be assumed for function word assemblies and a reduced laterality degree for the other assembly types.

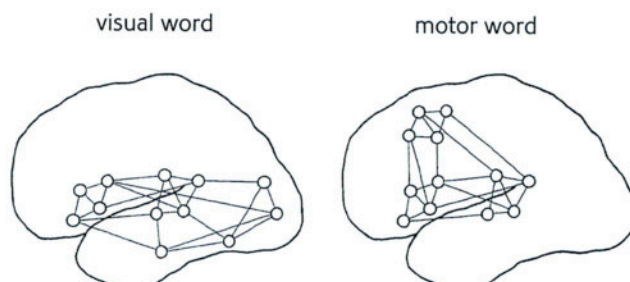visual word   motor word

Figure 5: Grammatical function words (pronouns, articles etc.), and words referring to objects and actions may have different neuronal counterparts. A function word may be cortically represented by a perisylvian assembly (see Fig. 4). Words referring to objects usually perceived visually ("visual words") may be organized in assemblies distributed over perisylvian and additional visual cortices (A), and words that usually refer to movements of the own body ("motor words") may be organized in assemblies distributed over perisylvian and additional motor cortices (B). Many (but not all) concrete nouns are visual words and many action verbs are motor words.

Processing of different word categories involves different cortical areas

Starting with the considerations offered by Freud [15], there were numerous studies investigating language deficits arising from lesions outside the perisylvian language areas, some of which proved that word categories were selectively affected by lesions in areas outside the perisylvian regions [21-26]. This lesion evidence can, in part, be interpreted as empirical support for the Hebbian perspective outlined above [7,27]. However, the Hebbian ideas can also be tested in psychophysiological investigations of word processing in the intact human brain. Physiological studies can use various imaging techniques based either on direct measures of activity signs caused by electrophysiological activity in neurons (electroencephalography (EEG), magnetoencephalography (MEG), event-related potentials (ERP)), or on indirect measures of metabolic changes probably related to neuronal activity (positron emission tomography (PET), functional magnetic resonance imaging (fMRI)).

Electrocortical differences between content and function words have been found by several ERP studies [28-31]. A finding which was present in all studies - or at least in those using large electrode arrays (> 20, sometimes 64 and more electrodes) - was the following: Function words

led to lateralized event-related potentials, whereas the potentials caused by presentation of content words were more symmetrical over the hemispheres. This is consistent with the idea of lateralized assemblies representing function words and less lateralized assemblies underlying processing of content words [27].

Numerous metabolic imaging studies have looked at processing of nouns and verbs. In most of these studies, the so-called "verb generation task" was used, that is, subjects were required to say aloud (or think of silently) a verb semantically related to a noun presented acoustically or visually. The brain activity pattern obtained during verb generation was usually compared to the activity pattern while reading or repeating (silently or aloud) the same nouns. Results of these experiments are highly heterogeneous. However, taken together, enhanced metabolism during verb generation was found not only in Broca's and Wernicke's areas, but, in addition, in adjacent prefrontal and temporal areas and sometimes in both hemispheres [32-35]. This may be taken as evidence that verb processing involves perisylvian language areas and cortices outside. However, it has been argued that verb generation and repeating nouns are tasks that vary not only with regard to the words being relevant. Therefore, other psychological processes (arousal, attention, search and judgement processes etc.) may be related to the observed metabolic differences.

In studies of electrocortical noun/verb differences in the intact brain, both word types were presented in the same tasks, for example lexical decision, where subjects have to decide whether letter strings are meaningful words or meaningless pseudowords. Such studies revealed word category differences in event-related potentials (ERPs) [36,37]. After submitting data to current source density analysis, a method for enhancing the contribution of local cortical generators to the electrocortical signal, event-related potentials revealed stronger signs of cortical activity at central recording sites - over motor and premotor cortices - when motor words (action verbs) were being processes, whereas activity signs were enhanced at posterior recording sites - over visual cortices - when visual words (nouns with well-imaginable meaning) were processed. This pattern of results provides support for the Hebbian view that visual and motor words are represented and processed differently in the cortex [27].

One may argue, however, that nouns and verbs do not only differ with regard to their semantic properties, they also belong to different lexical categories. The physiological differences observed may, therefore, be related to lexical rather than semantic properties. This is certainly an important point, however, the assumption of the semantic difference being relevant can explain why differences in electrocortical activity between action verbs and imaginable nouns were present over visual and motor cortices, and this speaks in favor of the present interpretation. Furthermore, more recent imaging work investigated differences in brain metabolism between animal names and tool names which led to somewhat similar results. Most animal names belong to the category of visual words because their meaning is learned (by most individuals in the western culture) based on input through the visual modality, whereas tool names probably elicit not only visual associations but, in addition, remind

subjects of the body movements involved when using the tools. Processing of tool names in a naming task led to activation of premotor cortices in frontal lobe, whereas processing of animal names in the same task enhanced metabolism in visual cortices in the occipital lobe [38]. (In the case of tool naming, an additional focus of activity enhancement was present more posteriorly in the middle temporal gyrus which may be related to associations of visually perceived movements related to tool usage or to imagination of their shapes [24,38].) These data provide additional evidence for the view that words with motor and visual associations are represented differently in the intact brain, and that they involve areas outside the classical language areas that reflect semantic word properties.

Reverberation of neuronal activity in cell assemblies representing words may be reflected in high-frequency cortical responses

The cell assembly concept is a tool for theorizing about cortical representations. It is difficult to actually prove that cell assemblies exist in cortex, and it is even more difficult to provide a proof that they are the basis of cognitive processing, as suggested by Hebb. However, recent evidence from neurophysiology demonstrates that multiple neurons in various cortical areas can exhibit synchronous rhythmic activity patterns in a rather high frequency range, that is around 30 Hz and above [39]. High-frequency activity is stimulus-specific, that is, particular neuron sets may synchronize their rhythmic responses when a particular visual stimulus is being presented, whereas other neurons become synchronized when a different stimulus is shown. This kind of synchrony in cortex is only possible if cortico-cortical fibers are intact, although subcortical connections may play an additional role in synchronizing cortical responses [40]. Stimulus-specific synchronous high-frequency activity in cortex is difficult to explain without using the cell assembly concept, and may, therefore, be considered as evidence for this notion. If reveberation of neuronal activity in cortical cell assemblies causes enhancement of well-timed high-frequency responses in these neurons, some of the ideas formulated above can be experimentally tested. For non-invasive recordings of such responses, EEG- and MEG-mapping are necessary, because only these recording techniques have the fine-grained temporal resolution in the millisecond range necessary for recording high-frequency activity in cortex.

Assuming that reverberation of neuronal activity in cell assemblies is visible in high-frequency responses one would predict that these responses are stronger when a cognitive representation is being activated compared to a state in which no such representation is being accessed. According to the Hebbian view, words are represented in cortical assemblies while meaningless pseudowords, such as "noom", lack a cortical representation because they have never been learned. This predicts stronger high-frequency cortical responses to words compared to pseudowords ("moon" vs. "noom"). In a series of experiments, we obtained

empirical support for this prediction [41-44]. EEG and MEG responses to words and pseudowords presented acoustically or visually consistently revealed differences in spectral responses in the 30 Hz-range. Importantly, no similar differences were present in lower parts of the spectrum (alpha-band around 10 Hz) or in the higher spectrum, where muscle activity would be most strongly visible. Differences in high-frequency responses were most pronounced and significant at recording sites above the language cortices in the left hemisphere of right-handed experiment participants. These results are consistent with the view that cell assemblies exhibiting well-timed reverberation of neuronal activity with a predominant frequency around 30 Hz become active when words are being processed but fail to ignite after presentation of meaningless pseudowords. Similar dynamics of 30 Hz-responses have recently been reported from a comparison of meaningful visual gestalts vs. physically similar but meaningless visual stimuli that are not perceived as a coherent gestalt [45]. All of these findings support the view that meaningful elements (words, gestalts) - but not similar meaningless stimuli - activate cell assemblies generating 30 Hz-activity.
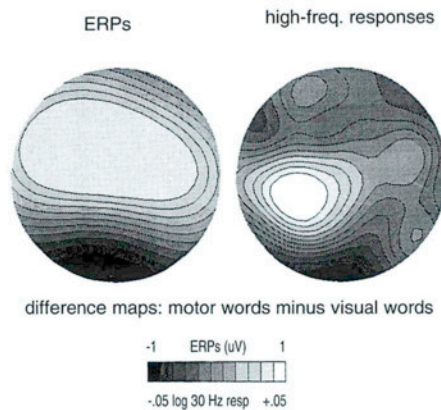

Figure 6: Processing of motor words (verbs) and visual words (nouns) is accompanied by significantly different electrocortical responses. Difference maps (nouns minus verbs) are shown. Large circles represent the head seen from above (anterior is up). Verbs elicit stronger signs of activity over motor cortices of both hemispheres, whereas nouns elicit stronger signs of activity over visual cortices. Differential topographies of event-related potentials are compared to evoked spectral responses in the frequency range 25-35 Hz. Adopted from Ref. 27.

The Hebbian cell assembly perspective would, however, allow for even more specific predictions. For example, processing of words with different meanings, such as motor and visual words, should not only induce different global activity in motor and visual cortices, but, in additon, there should be a specific change of high-frequency activity in the same cortical areas. This prediction was tested in a recent experiment again using action verbs and nouns with well-imaginable visual meaning [44]. Significant differences in 30 Hz EEG responses were present over motor cortices, and additional differences were seen over occipital visual areas (recording sites C3/C4 vs. O1/O2 of the international 10/20-system). High-frequency

responses to motor words were stronger over motor cortices, whereas they were stronger over visual cortices for visual words. This provides another piece of evidence for the Hebbian perspective on language representation in the brain.

It may, however, be claimed that differential high-frequency responses are not necessarily a sign of cell assembly ignition and reverberation of neuronal activity therein. More global neuron loops may also generate high-frequency activity, as has been made evident by recordings in arthropods [46] and in the retina of vertebrates [47]. One may, therefore, claim that differential high-frequency cortical responses can be a consequence of various cortical activation processes. However, it is important to note that there is at all any difference between high-frequency responses to physically similar meaningful and meaningless elements, to words and pseudowords, to gestalts and pseudogestalts, to nouns and verbs. This can only be explained if high-frequency responses are interpreted as a consequence of the activation of cortical representations that depend on the meaning (or gestalt properties) of stimuli. Furthermore, if dynamics in 30 Hz responses were a sign of global changes of cortical activity in cortical areas, their spatio-temporal properties should be the same as for other global activity indicators such as event-related potentials. This, however, is clearly not the case [27]. At this point, more experimental work is necessary in order to decide whether 30 Hz-responses actually reflect fast reverberation of neuronal activity within cell assemblies or reverberation processes caused by activation of cognitive cortical representations (ignition of cell assemblies) but involving additional neurons outside the representation (assembly).

The Hebbian approach to language representation in the brain may provide biological answers to additional questions from language science

These results provide support for the claim that words of different semantic classes are represented in cell assemblies with different cortical distributions. All of these assemblies appear to have some of their neurons located in the perisylvian language areas of Broca and Wernicke, and some words may be represented by assemblies including additional neurons outside the language areas, and possibly in both hemispheres. Semantic word properties appear to be reflected in the additional areas becoming relevant. Evidence for different distributions of cell assemblies can be obtained from global activity measures such as provided by metabolic or neurophysiological imaging techniques, and, in addition, important clues about reverberating neuronal activity in cell assemblies (or related to cell assembly activation) may come from investigations of high-frequency cortical responses recorded in the EEG and MEG.

It should be emphasized that the Hebbian model put forward here is related to large-scale neuronal theories of language that are based on Hebbian associationist learning principles [16,22,48,49]. All these models have in common that 1) widely distributed neuron sets in

cortex (and additional subcortical structures) are assumed to be the substrate of language processing, and that 2) such assemblies are assumed to form as a consequence of associative learning. Distinctive features of the approach discussed above include the assumptions (i) that processing of an individual word (and of any meaningful stimulus) does not only lead to the activation of cortical areas, but rather to the activation of a distinct neuron set, a cell assembly representing the individual meaningful element, (ii) that phonological, semantic and other features of a word are bound together in its neuronal representation so that stimulation of the assembly leads to almost simultaneous activation of the word representation implying simultaneous access to all of its features on the cognitive level, (iii) that two distinct processes, ignition and reverberation of neuronal activity, follow stimulation of an assembly, and (iv) that right-hemispheric processes are involved in word processing and that right-hemispheric processes are different for words of different classes. Claim (i) is primarily motivated by theoretical considerations, but the finding that there are cortical neurons specifically activated by low-frequency words provides support for this assumption [50]. Claim (ii) is supported by early electrocortical differences between vocabulary types which were present as early as around 200 ms after stimulus onset not only over perisylvian areas, but, in addition, over motor and visual areas probably involved in processing of word meanings. Assumption (iii) is consistent with the finding that word-class differences in event-related potentials (possibly indicating differences in ignition) occurred shortly after stimulus onset (around 200 ms) whereas dynamics in high-frequency responses (possibly related to reverberation) usually occurred only later. Finally, assumption (iv) is supported by studies evidencing a) different degrees of laterality of electrocortical activity elicited by words of different classes and b) word class-specific activity differences in the right hemisphere.

From a linguistic point of view, however, the question addressed above - the question of the cortical organization of words of different classes - is only a very basic one, and it is absolutely clear that neurobiological models cannot, at this point, answer complex questions about the brain mechanisms that govern the sequencing of words in sentences and the sequencing of speech acts in complex dialogues. Whereas some sequencing rules may be biologically realized as connections between cell assemblies that form based on associative learning principles, genetically programmed information may be necessary for other syntactic mechanisms [51]. Specification of these mechanisms in terms of neurons and cell assemblies appears to be one of the most exciting goals in cognitive neuroscience.

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