GAMMA-BAND RESPONSES REFLECT WORD/PSEUDOWORD PROCESSING

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CELL ASSEMBLIES: POSSIBLE BUILDING BLOCKS OF COGNITION

According to one brain-theoretical view, higher brain functions are based on processing units called cell assemblies. Cell assemblies are large groups of cortical pyramidal neurons with strong and reciprocal internal connections. Cell assemblies develop in a randomly connected neuronal network when sets of neurons are frequently active simultaneously so that their connections strengthen (Hebb's law, Hebb, 1949, Gustafsson et al., 1987, Bonhöffer et al., 1989, Ahissar et al., 1992). Neurons making up one assembly do not need to be located in a small cortical area. They may be distributed widely over various cortical regions. Such *transcortical assemblies* are likely to be held together through long axons of pyramidal cells which are well-known to connect distant cortical areas (Pandya and Yeterian, 1985, Braitenberg and Schüz, 1991, Deacon, 1992a, Deacon, 1992b). Due to strong intra-assembly connections, excitation of some neurons of an assembly leads to spreading activation in the network and, finally, to an "ignition" of the whole assembly. Overshooting activity will occur in the cortex when too many assemblies ignite at the same time. Therefore, a regulation mechanism is required which keeps the level of cortical excitation close to a target value (Braitenberg, 1978). This regulation mechanism guarantees that only one or a limited number of assemblies will ignite at a time.

What is the purpose of transcortical assemblies? One obvious answer is the following: transcortical assemblies make it possible to "bind" information represented in different parts of the cortex. Such binding may occur between neurons in the visual system stimulated by features of a perceived object. If assemblies include vari-

ous local clusters of neurons, they may well represent entities composed of numerous features, such as a complex object. Binding in widely distributed cell assemblies may also be relevant for associations between sensory modalities. Such associations are necessary for the representation of objects that can be perceived through various sensory channels. Transcortical assemblies may also be the neurobiological counterpart of sensori-motor associations, a prerequisite of language acquisition. For example, in order to repeat syllables and words the child must associate the auditory pattern perceived with a motor (articulatory) pattern. Binding of information represented in distant parts of the cortex is necessary for solving complex tasks, such as object recognition, gestalt perception, using and understanding language, and reasoning. It appears that these higher or cognitive brain capacities require devices that bridge distances in the cortex and allow for fast inter-area exchange of information. Candidate machines that may serve this function are transcortical assemblies.

If Hebb's rule holds true, formation of cell assemblies takes place during ontogenesis. This can be illustrated using language representation as a paradigm case (Braitenberg, 1980, Braitenberg and Pulvermüller, 1992). During early language development, the infant frequently perceives sounds that lead to an "imprinting" of phonetic perception (Kuhl et al., 1992). Presentation of language sounds causes co-activation of neurons responding to features of these sounds, and neurons co-activated by one phoneme develop into an assembly, the neurobiological correlate of the phoneme. In a later stage of development, the infant repeatedly articulates sound sequences and word forms. These articulations are caused by activity in the motor cortex. Articulations cause acoustic signals which are fed back to the auditory cortex where they lead to additional neuronal activation. Thus, during early articulations specific patterns of activity are present almost simultaneously in three cortical regions, the motor, the somatosensory, and the auditory system. Because there are strong cortico-cortical projections connecting these systems, simultaneously activated neurons will strengthen their connections and develop into an assembly. This argues that early articulations trigger the formation of transcortical assemblies corresponding to specific syllables or word forms. Note that such cell assemblies must be assumed to comprise neurons of *distant* cortical regions located in both hemispheres. However, it is well-known that language is normally lateralized to the left hemisphere in most right-handers, suggesting that the majority of neurons comprised in language assemblies are located in the left hemisphere. If transcortical assemblies are the neurobiological correlates of individual words, it may be assumed that connections between such assemblies are the physical realization of rules determining word sequences. In this case, the hierarchy of linguistic structures (phoneme, morpheme, word, sentence) has its biological equivalent in a hierarchy of cell assemblies corresponding to these cognitive entities (Braitenberg and Pulvermüller, 1992, Pulvermüller, 1993, 1994).

At this point, it must be emphasized that the assumption of transcortical assemblies is still speculative to some degree. However, there is a large body of evidence from various fields which can be accounted for on the basis of the cell assembly approach. For example, the cell assembly theory of language processing accounts for data from aphasia research (Pulvermüller and Preißl, 1991, Pulvermüller, 1992, Pulvermüller and Schönle, 1993, Pulvermüller and Preißl, 1994), from psycholinguistic experiments (Pulvermüller et al., 1993, Mohr et al., 1994), and from electrophysiological investigations of language processes (Lutzenberger et al., 1994, Pulvermüller

et al., 1994a, Pulvermüller et al., 1994b). Therefore, the concept of cell assemblies is speculative but useful.

The major advantage of a theory bridging neurobiology to cognition is the following: it allows for predictions which cannot be formulated on the basis of biological or cognitive theories alone. In this article, we discuss an implication of the cell assembly theory and some recent data obtained to test this prediction.
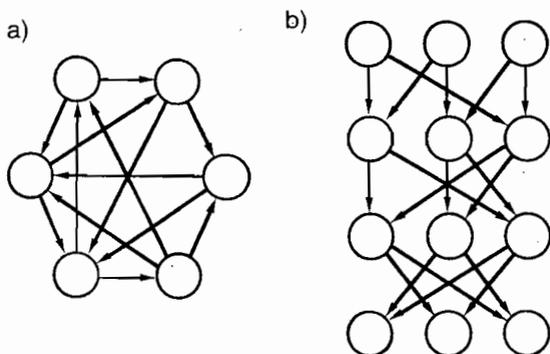

Figure 1. Simple models of strongly connected neuron ensembles. A reciprocally connected cell assembly (a) and a synfire chain (b) are sketched. Circles represent neurons, arrows represent connections between neurons. All neurons have a threshold of two, i.e. they need two simultaneous inputs to become active. For explanation, see text.

SYNCHRONIZATION, SPATIO-TEMPORAL ACTIVITY PATTERNS AND PERIODICITY

If a cell assembly has strong internal connections, its ignition will take place instantaneously so that all or at least many of its neurons become active almost simultaneously. The question of how activity spreads through the assembly has at least two possible answers. First, after activation of a subset of the assembly neurons, almost all remaining assembly neurons will be activated synchronously a few time-steps later. Figure 1a presents a sketch of such an "assembly". If all "neurons" of this network have a threshold of 2 (i.e. they need 2 excitatory inputs to become active), simultaneous activation of four out of the six neurons will lead to synchronous activity of all assembly neurons a few time-steps later. However, as a second possible answer, the internal connections of a neural network may also determine a "stepwise" mode of activation. In the network schematized in Figure 1b, activity spreads from one row to the next after all neurons of the uppermost row have been activated. In this case, the activation process does not lead to synchronous activation of all assembly neurons, but to a well-ordered spatio-temporal pattern of activity within the network. Therefore, only a few assembly neurons become active at exactly the same time. The more likely case is that two neurons become active one after the other with a fixed delay. Although these simple examples are far from providing an adequate picture of cortical mechanisms, they can illustrate an important point. Activation of strongly coupled sets of neurons may take place synchronously or

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stepwise, according to a well-ordered spatio-temporal pattern of activity. The architecture of the network determines the activation process.

If cell assemblies have strong and reciprocal internal connections, these connections warrant that activity is retained for some time within an activated assembly. Using a terminology proposed by Braitenberg (1978), the assembly "holds" after its activation. The processes taking place while activity is retained may vary as a function of assembly architecture. For example, the network depicted in Figure 1a stays active; that is, all of its neurons remain excited after their simultaneous activation. The network illustrated in Figure 2a (which is taken from Palm 1982) shows a simple periodic activity pattern. If only two of the four neurons are active, the other two will become excited at the next time step. (Again, neurons are assumed to have a threshold of 2.) One time-step later, the original pair of neurons become excited and so on. Each neuron of this network repeatedly becomes active and inactive, i.e. it oscillates. A similar process takes place in the assembly illustrated in Figure 2b. Since these neurons form a "circle", activity circulates within the network after one row of neurons has been activated. This results in repeated occurrences of the same spatio-temporal pattern. Again, each assembly neuron will show repetitive or periodic activity.
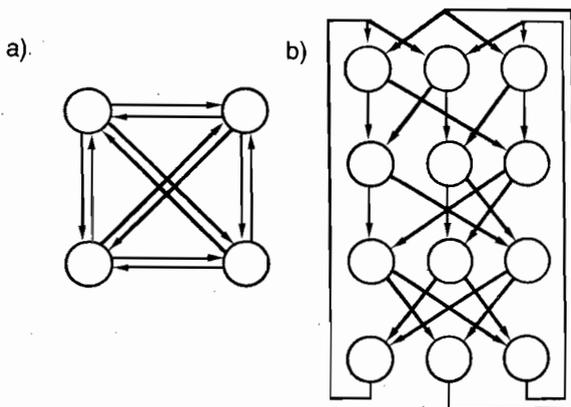

Figure 2. Models of cell assemblies generating periodic neuronal activity. All neurons have a threshold of two. If two neurons of the assembly in (a) are active, the other two neurons will be active at the next time step etc. If three neurons of the reverberating synfire chain in (b) are active simultaneously, a wave of activity will circulate in the network.

Another mechanism generating periodic activity requires inhibitory connections (Wilson and Cowan, 1973). Consider the simple networks depicted in Figure 3a, where each neuron has an activation threshold of 1. The uppermost neuron receives constant excitatory input, so that it will be active initially. This leads to activation of the lower, inhibitory neuron, which, in turn, will lead to an inhibition of the upper neuron. When the upper neuron is switched off by the inhibitory input, the inhibitor itself becomes inactive one time-step later. At this point, the constant input can again activate the upper neuron which again inhibits itself through the inhibitory

loop, thus resulting in oscillatory or periodic activity. If the excitatory neuron is interpreted not as a single neuron but as an assembly of neurons, such as the one depicted in Figure 1a, coherent and repetitive activation and deactivation of these neurons can be assumed. Coherent oscillations will occur even if each excitatory neuron of such a network has its own inhibitor (and additional conditions are met; Schuster and Wagner, 1990). If one of the excitatory neurons of Figure 3b is oscillating, it will force its sister neurons into the same oscillations after a short time lag.
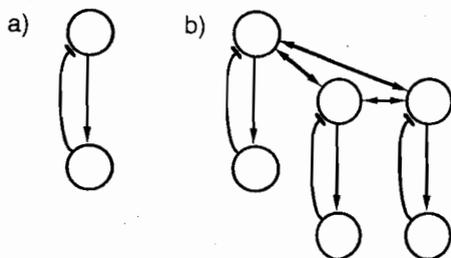

Figure 3. Simple oscillating circuits including inhibitory elements. All neurons have a threshold of 1. If the upper neuron in (a) receives continuous input, the neurons will become active and inactive periodically. If one of the three coupled oscillators in (b) receives constant input, oscillations of all three neuron pairs will occur with a short phase lag.

Activation of strongly connected sets of neurons may lead to synchronous, patterned and/or periodic activity. There is strong electrophysiological evidence indicating that all three phenomena play a role in cortical processing (Abeles, 1982, Gerstein et al., 1989, Abeles, 1991, Engel et al., 1992). If cell assemblies are defined as neuron sets with strong *reciprocal* connections (Braitenberg, 1978), a feed forward net such as the one depicted in Figure 1b is excluded by this definition. Ignition of an assembly with reciprocal connections will, most likely, include periodic activity. If the architecture of the assembly is similar to the networks in Figure 2a and b, periodic activity will occur. If the assembly architecture itself does not determine periodic activity (see Figure 1a), it is plausible that inhibitory regulation processes will generate periodic activity, as illustrated for the simple networks in Figure 3a and b[1]. Thus, it can be assumed that ignition of an assembly includes periodic activity of a large group of neurons. This periodicity may have the form of repetitive spatio-temporal activity patterns in a reverberating assembly and/or of coherent oscillations

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[1] Note that periodicity may be caused by cortical or subcortical mechanisms. The oscillator in Figure 3a could have its analogon in excitatory and inhibitory neurons in the cortex. However, inhibition could also be provided by complex loops involving neurons in the basal ganglia and/or the thalamus.

due to inhibitory regulation processes. In the case of a transcortical assembly, periodic activity should occur in various cortical areas.

A PREDICTION OF THE CELL ASSEMBLY THEORY

If cell assemblies are the basic units of cognition, neuronal populations must become active when cognitive processes take place. This implies correlated activity of numerous neurons. Correlated postsynaptic activity in apical dendrites of numerous pyramidal cells will also affect the local field potential and, if the number of neurons participating in the pattern is large enough, the weighted sum of postsynaptic currents will lead to a surface potential which is visible in the EEG (Speckmann and Elger, 1982, Mitzdorf, 1985, Birbaumer et al., 1990). Magnetic fields caused by the intracellular currents flowing from the dendritic tree towards the soma can also be picked up in the MEG primarily if pyramidal cells are located in Sulci, thus causing currents to flow tangentially to the surface of the head (Cuffin and Cohen, 1979, Hari and Lounasmaa, 1989). Ignition of a cell assembly implies fast activation of a large neuron population. This predicts a sharp rise in EEG and MEG. After activation, an assembly with reciprocal connections will retain its activity and correlated periodic firing of assembly neurons takes place. In this case, EEG and MEG peaks may occur repeatedly, so that the EEG and MEG signal will include enhanced spectral power in at least one frequency band. If, for example, the ignition process implies synchronous 40 Hz oscillations of assembly neurons, the spectral power in the 40 Hz range should specifically be affected. If ignition consists of repetitive spatio-temporal activity patterns, a more complex change results which may affect several frequency bands. Nevertheless, such a more complex change will also be visible in specific frequencies. Equal numbers of neurons may be active at each time-step and their activity may contribute equally to the recorded potential or field. Nevertheless, if numerous neurons are active at each time step, but contribute differently to the surface potential, it is likely that periodic activity will be seen at the recording electrode. On the basis of theoretical considerations it is hardly possible to determine the exact frequency range which will be affected by assembly ignition. However, the spreading of activity and reverberation must take place very quickly, possibly in the range of few to several milliseconds. This suggests that changes in spectral power will occur in the gamma-band (20 Hz and up). In addition, sinchronous periodic activity of large neuron ensembles will possibly cause slow changes of the evoked potential and magnetic field. In this case, a slow wave shift (in addition to changes in the gamma-band) can be expected (Elbert, 1993).

The cell assembly theory predicts ignition when cognitive processing takes place. In this case, large numbers of neurons become active simultaneously and possibly join a periodic pattern thereafter. This may be visible in the gamma-band response of the cortex. If cognitive processing does not take place, cell assemblies do not become active. More precisely, cell assemblies may be stimulated and, therefore, become slightly active, but no full activation or ignition takes place. Therefore, gamma-band responses should be reduced. In summary, gamma-band spectral power should be strong when cognitive processing takes place, but reduced when such processing does not occur.

IS GAMMA-BAND ACTIVITY AN INDICATOR OF COGNITIVE PROCESSING?

Gamma-band responses have been observed in various mammals (including humans) using different methods, such as single and multiple unit recordings, local field potentials, and EEG and MEG recordings. Gamma-band activity can be elicited by visually perceived moving bars (Eckhorn et al., 1988, Engel et al., 1992), by simple auditory stimuli such as tones (Pantev et al., 1991), by somatosensory stimuli (Ahissar and Vaadia, 1990) and by odors (Bressler and Freeman, 1980, Freeman, 1991). They also accompany manipulative movements (Murthy and Fetz, 1992). However, this does not imply a specifically cognitive function of gamma-band responses. Very simple stimuli, such as bars or tones, are unlikely to elicit cognitive processing. Such stimulations trigger perception processes, but it is unclear whether additional processes follow.

To decide whether synchronized and/or repetitive activity of neurons serves a specifically cognitive function, it is necessary to compare brain responses between two paradigms only one of which invokes cognitive processing of a certain kind. In recent experiments it was found, that two bars moving in the same direction lead to synchronous and fast oscillatory activity of neurons activated by the stimuli (Eckhorn et al., 1988, Gray and Singer, 1989). These neurons may be located in distant cortical areas. In contrast, if two bars move in different directions, two neurons responding to one of the stimuli, respectively, do not respond synchronously (Gray et al., 1989, Engel et al., 1990). While this indicates that cortical spatio-temporal responses change with *Gestalt features* (Engel et al., 1992, Singer, 1994), such as continuity, it is still unclear how these responses relate to perception of complex *Gestalts*. A complex moving stimulus may well lead to the perception of lines moving in different directions. If cortical synchrony was an indicator of Gestalt integration, it could rather be expected that two moving stimuli invoke more complex Gestalt integration processes and, therefore, more pronounced synchronized activity (von der Malsburg, p.c.). However, it may be argued that the two lines will not be integrated into a gestalt. For this experiment, it appears difficult to decide which cognitive processes are triggered by the differing stimuli.

More or less complex manipulative movements are also correlated with different patterns of synchronized oscillatory brain activity in the gamma range. When a monkey performs a complex motor movement, such as retrieving raisins from slots of a Klüver board, synchronized gamma-band activity can be recorded from motor and somatosensory cortices (Murthy and Fetz, 1992). Coherent gamma-band activity was reduced when monkeys performed simple movements, such as alternating flexion and extension of the wrist. These results were confirmed, in part, by an MEG investigation of human brain responses during complex movements (Kristeva-Feige et al., 1993). During performance of a complex manual task, enhanced gamma-band activity around 30 Hz was found. The enhancement of gamma-band responses around 30 Hz can possibly be attributed to the level of attention or the amount of sensorimotor integration required by complex movements. However, the complexity of the muscle movements could also be critical for the gamma-band response to occur. While these results are consistent with the assumption that cognitive processes, i.e. selective attention to sensorimotor integration, underlie stronger gamma-band re-

sponses, they can also be considered a consequence of the complexity of the motor movement to be performed.

Another investigation of MEG responses of the human brain indicates that gamma-band responses reflect cognitive processing. Llinas and Ribary (1993) found reduced 40 Hz activity during delta sleep, while oscillatory activity was stronger during both wakefulness and REM sleep. Because vivid dreaming (which usually occurs during REM sleep) and wakefulness imply cognitive processing, the authors propose that enhanced gamma-band responses are a correlate of cognition. However, it may be argued that various other variables (arousal level, brain activity level etc.) distinguish delta sleep from REM sleep or wakefulness.

In earlier studies, EEG recordings were used for investigating changes of gamma-band activity associated with tasks, such as verbal and visual-spatial problem solving. Sheer and coworkers (Spydel et al., 1979, Sheer, 1984) reported increased spectral power around 40 Hz when subjects engaged in cognitive tasks requiring focusing of attention. However, a possible methodological problem of these studies are EEG artifacts caused by muscle activity. While these authors report no correlation between EEG and EMG spectral responses recorded from temporal and splenius muscles, one may argue that changes in 40 Hz power can be caused by muscles not monitored in these experiments. However, this problem can be solved by investigating spectral responses of even higher frequencies. Spectral power of EMG responses increases with frequency until at least 80 Hz (Cacioppo et al., 1990). Thus, if muscle activity causes differences, for example in the 40 Hz range, the same effects must be present (and they must be even more pronounced) in higher frequency intervals, for example around 60 or 80 Hz. If no differences occur in these bands, muscle activity cannot be the cause of an effect observed in lower frequencies.

In order to decide whether cognitive processing implies specific changes in high frequency brain responses, two conditions must be compared that only differ with regard to the cognitive processes they invoke. Comparing responses to bars and "meaningful" pictures of objects would be one option. However, bars and pictures have very different perceptual complexity and a difference in evoked spectral responses could be a consequence of this physical difference. Two stimulus classes that are of equal perceptual complexity but nevertheless trigger distinct cognitive processes are words and meaningless pseudowords made up of the same letters. A word, such as *moon*, will immediately be comprehended, while a matched pseudoword, such as *noom*, will fail to elicit immediate comprehension. On the cortical level, word presentation should lead to cell assembly ignition, while presentation of pseudowords should fail to ignite specific assemblies. This leads to an obvious prediction: Gamma-band responses to words should be stronger than responses to pseudowords.

DIFFERENT GAMMA-BAND RESPONSES TO WORDS AND PSEUDO-WORDS

The following experiment was carried out in order to investigate EEG responses to words and pseudowords. 15 right-handed German native speakers performed lexical decisions on visually presented words and matched pseudowords (64 stimuli of each category). Each word was presented for 100 ms in the center of a video screen. The inter-stimulus interval varied between 3.5-4.5 s. Words subtended

0.5 degrees of vertical visual angel and a maximum of 2.3 degrees of horizontal visual angel. They were written in black letters on a gray background. The lexical decision was expressed by moving the index finger of the left hand. The EEG was recorded through 17 tin electrodes against linked mastoids. Six of the electrodes were placed close to the perisylvian regions of each hemisphere, respectively. The EEG was recorded for 1.28 s per trial, starting 0.1 s before stimulus presentation (0.1 s baseline). Event-related potentials (ERPs) were calculated for each electrode, condition and subject (artifact rejection and correction as described in Elbert et al., 1985). In order to obtain reference-free data, artifact-free signals obtained from single trials were also submitted to current source density (CSD) analyses. CSD data were filtered in three frequency bands: 25-35 Hz, 35-45 Hz, and 55-65 Hz. These data were normalized by dividing them by the average value obtained in the respective baseline. Finally, mean normalized evoked spectral power was calculated for both conditions (words/pseudowords), for each subject, and for each electrode. For statistical evaluation, data from the 2 x 6 electrodes monitoring the perisylvian cortices were chosen. Average values in three time windows were evaluated: 120-320 ms, 320-520 ms and 520-720 ms post stimulus onset. Three-way analyses of variance were carried out (design: Wordness (word/pseudoword) x Hemisphere (left/right) x Site (six electrodes from anterior to posterior)). Greenhouse-Geisser correction of degrees of freedom was applied when adequate. (For a more detailed description of the methods, see Lutzenberger, Pulvermüller and Birbaumer, 1994.)
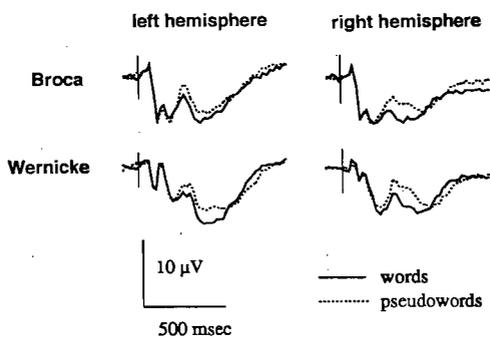

Figure 4. Results from EEG experiment. Event-related potentials (ERPs) after word and pseudoword presentation recorded over the perisylvian cortices of both hemispheres (Broca's and Wernicke's area and homologous areas on the right). Data are averaged over 15 subjects. The late negative-going component around 400 ms after stimulus onset is larger after pseudowords (redrawn from Pulvermüller et al. 1994b)

Figure 4 displays ERPs recorded from two lateral electrodes after word and pseudoword presentation. Around 400 ms post stimulus onset pseudowords elicited more negative ERPs compared to words. There was a significant main effect of Wordness in the 320-520 ms time window, $F (1,14) = 12.6$, $p < 0.003$. A larger late negativity after pseudowords compared to words has been reported in an earlier study (Holcomb and Neville, 1990). This larger negativity can be taken as evidence that pseudoword presentation elicited more activity, i.e., a larger number of excita-

tory post-synaptic potentials, in apical dendrites of numerous neurons (Speckmann and Elger, 1982, Birbaumer et al., 1990).

Figure 5a presents normalized evoked spectral responses in the 30 Hz (25-35 Hz) band recorded from scalp over the left and right perisylvian cortices. Because statistical analysis did not reveal any reliable effect of the factor Site, averaged data from all six electrodes are displayed in this diagram. Spectral responses to words and pseudowords differed around 400 ms past stimulus onset. Statistical analysis revealed a significant Wordness by Hemisphere interaction for the time interval between 320 and 520 ms, $F(1,14) = 8.4$, $p < 0.01$. This interaction is displayed in Figure 5b. Word presentation did not change 30 Hz power compared to the baseline. In contrast, pseudowords elicited reduction of 30 Hz cortical responses over the left hemisphere. This deflection was small (1-2 percent of the baseline values). However, it could consistently be observed in most subjects tested. In contrast, analysis of all other frequency bands did not reveal a similar interaction in any of the time windows.
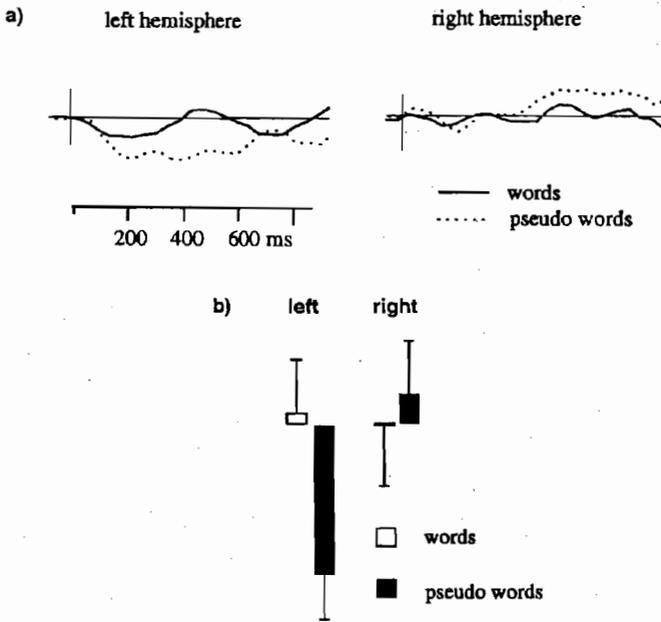

Figure 5. Results from EEG experiment. (a) Normalized evoked spectral responses (arbitrary units) between 25 and 35 Hz elicited by words and pseudowords as a function of time after stimulus presentation. Responses are averaged over 15 subjects. Around 400 ms post stimulus onset, 30 Hz activity is reduced over the left hemisphere after pseudowords ("pseudoword depression"). (b) The significant hemisphere by wordness interaction is displayed. Averaged normalized 30 Hz power recorded from the left and right hemisphere are shown. Redrawn from Lutzenberger et al. 1994.

This difference cannot be the result of an artifact caused by muscle activity. As noted earlier, the power spectrum of potential changes caused by muscle contractions increases with frequencies until around 80 Hz (Cacioppo et al., 1990). The fact

that no significant interactions or main effects were observed in the highest frequency band provides (60 Hz band) evidence that muscle potentials did not cause the result.

It may be argued that the reduction of gamma-band power after pseudowords was the consequence of some other recording or evaluation artifact. In addition, we cannot exclude the possibility that this reduction was related to the language used in the experiment (German), to visual stimulus presentation, or to the motor response the participants had to perform. Therefore, we carried out another experiment in which all these features of experimental setting and evaluation procedure were changed. Biomagnetic signals were recorded simultaneously from both hemispheres of five right-handed native speakers of English who heard English words and pseudowords spoken by a professional speaker. In this case, 30 items of each stimulus category (words/pseudowords) were repeated four times, resulting in 120 tokens of each category. The inter-stimulus-interval varied between 2.5 - 3.5 s. Subjects did not have to respond to the stimuli. However, they were asked to memorize all stimuli in order to answer questionnaires which were presented during breaks. In this case, no CSD analysis was necessary, since MEG provides reference-free data. For evaluating spectral responses a method described by Makeig (1993) was used. For a variety of frequency bands (width: 9.6 Hz), spectral power was calculated in overlapping time windows of 200 ms. Two adjacent time windows overlapped by 50 percent. Spectral power values were, again, normalized (0.6 s baseline), and averaged. (For further details, see Pulvermüller, Eulitz, Pantev et al.,1994.)
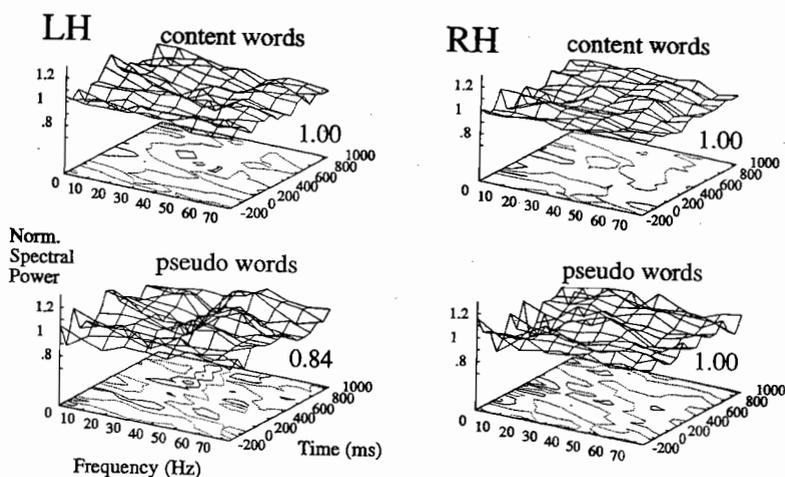

Figure 6. Results from MEG experiment. Normalized evoked spectral responses to words (upper diagrams) and pseudowords (lower diagrams) recorded from one channel over the left hemisphere (diagrams on the left) and the right hemisphere (diagrams on the right) of one individual. Note the "valley" around 30 Hz in the diagram on the lower left.

Figure 6 presents normalized spectral responses of one subject to words and pseudowords obtained from one channel over the left and right hemisphere, respec-

tively. While no pronounced change was elicited by presentation of words, a pronounced deflection of spectral power around 30 Hz followed pseudoword presentation. Reduction of 30 Hz spectral power after pseudowords was observed over the left hemisphere of all five subjects tested. No consistent change of spectral power was present in any of the other frequency bands, or over the right hemisphere. These changes were only seen at anterior channels located above the left inferior frontal lobe. At these channels, magnetic fields evoked by words and pseudowords were larger compared to all other channels, so that a maximal signal-to-noise-ratio can be assumed.

The consistency of results of the EEG and the MEG experiments makes it unlikely that pseudoword-specific gamma-depression is an artifact caused by recording or quantification procedures or that it is affected by parameters such as experimental language, stimulus modality, or response mode.

DIFFERENTIAL GAMMA-BAND RESPONSES: EVIDENCE FOR "COGNITIVE" ASSEMBLIES?

Based on these data, the original prediction of stronger gamma-band responses to words compared to pseudowords, can obviously be verified. A preliminary explanation of this difference is the following: Cell assembly ignition takes place after word presentation. This leads to correlated and periodic activation of large neuron sets which can be observed in EEG and MEG responses. In contrast, pseudoword presentation does not lead to an ignition and, therefore, it causes reduction of 30 Hz power. Activity differences in the gamma-band are primarily seen over the left hemisphere, because most neurons of language assemblies are located in the left hemisphere.

This preliminary hypothesis can be questioned for several reasons: First, the cell assembly theory would predict enhanced gamma-band activity after words compared to the baseline, rather than a reduction after pseudowords. However, it can be assumed that word processing takes place not only immediately after stimulus presentation. Word processing and thinking about these words may last for a few seconds, i.e. throughout the entire inter stimulus interval (which was 2.5-3.5 s in the MEG experiment and 3.5-4.5 s in the EEG experiment). This is consistent with the cell assembly theory. It was postulated that each activated assembly would "hold" for some time. Therefore, word evoked spectral responses may have contaminated the baseline and pseudoword-specific gamma-depression can be interpreted as a power decrease relative to word processing.

A second objection to the reported results concerns the size of the difference between responses to words and pseudowords. These differences are rather small in the EEG experiment (about 1-2 percent of the baseline power) and even the most pronounced differences seen in MEG recordings only amount to some 20 percent of the baseline. This indicates that the differences induced by stimulus presentation was small compared to cortical background activity. However, this is not surprising. Most likely, not all cortical neurons participate in processing information contained in a stimulus word. Perhaps only one cell assembly is activated after a word has been presented. Assemblies are usually assumed to comprise less than 10^6 neurons (Palm, 1993), only a small portion of the 10^{10} to 10^{11} neurons of the cortex. From this per-

spective, it is rather surprising that a small percentage of neurons generates a change in global activity of one to several percent.

A third possible objection addresses the relationship between spectral responses and event-related potentials (ERPs). Pseudowords lead to larger late negativities around 400 ms post stimulus onset, while 30 Hz power is reduced in this interval compared to words. If both event-related potentials and spectral responses were an indicator of arousal, attention, and/or neuronal mobilization processes, there would be an obvious incompatibility. It appears that ERPs and gamma-band responses reflect different processes. A cognitive and neurobiological model has to account for both 30 Hz depression and larger late negativities evoked by pseudowords.

On the psychological level, 30 Hz activity and late negativities in these experiments may be indicators of lexical access, lexical processing or lexical search. When a word is perceived, comprehended or stored, relatively strong 30 Hz activity is observed. The possible psychological processes underlying gamma depression may be comprehension failure or an unsuccessful lexical search. If no equivalent of a stimulus word is found in the "cortical lexicon", 30 Hz activity decreases. However, there may be an intense lexical search when pseudowords are perceived, whereas for word presentation the search processes terminate much faster, since the stimulus can be matched to a mental representation. In earlier studies it has been found that more intense memory search processes induce larger negativities in the event-related potential (Rockstroh et al., 1989, Rösler et al., 1993). Thus, it may be speculated that 30-Hz power and late event-related potentials indeed mirror distinct cognitive processes. While 30 Hz power indicates whether lexical access and processing take place, late negativities indicate the intensity of lexical search processes. Another view relates the reported data to attention and arousal processes. Pseudowords have never been perceived and are therefore highly unexpected. Thus, their presentation leads to enhanced arousal while word presentation fails to evoke such enhancement. In contrast, word presentation leads to the processing of only one word and to focusing on this stimulus, while pseudoword presentation may activate various associations. According to this latter view, stronger gamma-band responses to words would correspond to the process of selectively attending to words and late negative evoked potentials would covary with general arousal processes. However, such postulates stating correspondence between cognitive processes and psychophysiological measures can be considered unsatisfactory. They have even been called "psychophysioanalytic" by some researchers. It would be highly desirable to specify the neurobiological mechanisms underlying such cognitive processes that also cause the physiological responses. To explain the reported data, brain processes must be referred to.

The following neurobiological model can account for both ERP and 30 Hz differences. After word presentation, *ignition of exactly one assembly* takes place (while competing assemblies are inhibited). This ignition causes a small negative shift in the ERP. Because assembly ignition implies fast periodic and correlated activity of a large number of assembly neurons, strong 30 Hz responses are present. Processes taking place after pseudoword presentation are the following. Not only one, but *several assemblies are preactivated* to some degree. However, no ignition takes place in any of the preactivated assemblies. These assemblies are the neuronal equivalents of words phonologically similar to the pseudoword stimulus (the stimulus *noom* may activate assemblies corresponding to words such as *noon, moon, room* etc.). Because several assemblies are activated, the sum of cortical excitation is larger compared to

full ignition of only one assembly. This results in relatively large late negativities in the event-related potential. However, neuronal activity in several assemblies is not correlated, i.e. activation-deactivation cycles differ between assemblies[2]. At a device recording global cortical activity, the effects of fast uncorrelated and periodic activity tend to cancel each other. Therefore, reduced high-frequency responses are observed at recording electrodes and channels. In psychological terms, ignition of a word-specific assembly corresponds to lexical access and processing (which implies focused attention to one particular word), and preactivation of several assemblies without ignition can be considered the correlate of an unsuccessful search process (which may be linked to enhanced global arousal).

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[2]Strictly speaking, this implies the following. If periodic activation is caused by inhibitory elements, these inhibitors must be assembly-specific. Otherwise, inhibitors could synchronize activity in distinct assemblies. However, because inhibitory neurons are small and, therefore, do not reach distant pyramidal cells, it can be assumed that each local cluster of assembly neurons activates only its own inhibitors.

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