

Word Representations in the Cerebral Cortex - Predicting Functional Imaging Data

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Abstract

This paper introduces a theory of words in the cerebral cortex that is in accordance with major empirical data obtained by various methods reported in the literature. The theory specifies how the required cognitive tasks for word learning and naming can be executed in terms of neural computations, where in the brain those computations are executed, and what kind of representations are required to emerge. We demonstrate the computability of the theory by implementing the computations for every brain structure as a connectionist neural model. The model computes the neural activity during task execution to generate hypothesis about observable effects with functional imaging.

Introduction

The increasing number of experimental investigations in the field of brain and language, especially within the last ten years, has led to a prevalence of empirical results over theoretical understanding. Such a situation makes it hard to see where state-of-the-art knowledge about language processing in the brain stands. Contemporary theories of language are either of a structural or of a computational nature. While structural models encapsulate a model of the role of the different brain areas in speech processing and make prediction about the behaviour of patients with specific brain lesions, they do not explain how the hypothesized computation is done in each area. Conversely, contemporary computational models of language [Jordan and Rumelhart, 1992, Plaut and Kello, 1999] usually do not specify the brain structures in which the modelled computations take place.

Scientific progress is based on the possibility of falsification [Popper, 1934]. In order for a theory to be falsified by observations (such as behavioral, physiological, computational etc.), a theory needs to include and integrate those different levels of observation. To qualify as a falsifiable neural theory about language, the theory has to connect the behavioral or computational issues with the measured effects, such as neural activity within certain brain regions. To investigate the effect of *static* brain properties such as the interconnection of brain areas and general learning mechanisms, as well as long term representational changes

during language acquisition, on the short term focal changes in neural activity measurable with functional imaging, neural network simulations offer the required dynamics.

In this paper we introduce a theory that is in accordance with major empirical data obtained by various methods reported in the literature. The theory specifies how the required cognitive tasks for word learning can be executed in terms of neural computations, where in the brain those computations are executed, and what kind of representations are required to emerge. We demonstrate the computability of the theory by implementing the computations for every brain structure as a connectionist neural model. As a first test, the model also computes the neural activity during task execution to see what kind of effect would be observed by functional imaging.

The main questions we were concerned with were (i) what are the representations words are build from, (ii) what exactly is the process of word learning, i.e. how does it change the brain or what kind of representation does it lead to, and (iii) what is the role of the brain regions in production and perception, i.e. which representations and functions are shared and which are specific. We do not address syntactical aspects of words.

For our goal we had to find a task suitable for both, connectionist modelling and functional imaging. For several reasons we chose a learning paradigm. The first reason is that it is a natural task for a connectionist model. The second is that it increases the difficulty for the subjects of functional imaging studies and puts the emphasis one the generation of word representations, which should increase the activity in the areas were words are represented. The task we chose was aimed at giving a simplified (case-study) representation of the auditory-motor information available to children when they learn their first words. In our model, words are sequences of syllables associated with a unique meaning.

First, there is a babbling phase and then another learning phase. During the babbling phase sequences of motor features are produced and by an auditory feedback the motor sequences are associated with sequences of auditory events. The motor representations get a strong bidirectional link with the auditory pattern that occurs, when the produced sound is perceived. The knowledge introduced by this link can be seen as the ability of the child to intentionally produce a certain syllable, such as e.g. in the repetition of words. As meaning we chose simple visual line patterns, represented by *grandmother-cells* in the model. The model creates word representations by associating word-forms (auditory-motor patterns, learned in a babbling phase) with a (visual) meaning component. Of course, in a functional imaging studies we can not examine the babbling phase. Nevertheless, in our model we used an initial babbling phase to create plausible representations of syllables.

Large scale neural models can be used to recast linguistic theory and cognitive approaches in accordance with state-of-the-art knowledge about neural computations, representation, and distributions. In large-scale neural modelling we do not claim to model the behaviour of single neurons, but rather of large neuron groups. However, the claim is that we model cognitive task in terms of the computations of specific brain regions and how they interact to solve the task. These models can be used to connect different kinds of data, e.g. by integrating over the synaptic activity functional imaging data can be simulated. Neural models have already been connected with functional imaging data [Arbib et al., 1995, Tagaments and Horwitz, 1998]. This is the first approach to use a language task.

The model (implemented in C++) generates two kinds of output: (i) the output required by the task (e.g. a word in a naming task) (ii) a value of activation for every defined brain structure and every discrete point in time.

Brain Regions, Functions, and Connectivity

As a starting point we would like to contrast two widely known models of words in the cortex. The first is Lichtheim's model of single word processing [Lichtheim, 1884]. Lichtheim postulates an auditory speech center projecting to a center of concepts during language understanding. The concept center projects to the motor center of speech during production. The model postulates one concept center used in both production and perception. Word forms, however, are proposed to be represented independently for production and perception and the model postulates independent form-meaning interactions for production and perception. The auditory speech center further project directly to the motor center. The second model is the Wernicke-Geschwind-Model of language [Geschwind, 1965], which is widely accepted and still used in contemporary neurology. Broca's Area is postulated to be the center of motor control of speech (i.e. the transforms phonemes into articulatory programs). Geschwind postulated the phonemes and word forms to be represented in Wernicke's Area (BA 22) and these representations are used in both, speech perception and speech production. The angular gyrus (GA), a major multi-modal association area (BA 39), was not only postulated to be an essential structure in reading (transformation of letters in phonemes), but also to play the fundamental role in all kinds of transformation of visual information to language.

Through post mortem analyses of patients with brain lesions Carl Wernicke revealed that comprehension of speech was impaired when the lesions were located in the posterior BA 22 (superior temporal gyrus) [Wernicke, 1874]. Since Wernicke's early studies, an important amount of information has been gathered on the role of the superior temporal gyrus (STG) in speech perception. However, in general models of language processing the concept of Wernicke's Area has not yet been replaced by a more detailed modelling, which is what we did.

The first cortical area of relevance for speech is the primary auditory cortex (A1). Its tonotopic organisation has been demonstrated in monkeys with single cell recordings [Rauschecker et al., 1995]. Neurons in these areas are responsive to pure tones, and narrow frequency bands. The tonotopic organisation which has been demonstrated in monkeys could be confirmed in humans with fMRI [Wessinger et al., 1997]. A1 projects to the lateral belt areas [Hackett et al., 1998], i.e. the secondary auditory cortex (A2). The responsiveness of the lateral belt areas to more complex sounds has also been demonstrated in monkeys [Rauschecker et al., 1995]. The superior temporal gyrus, which includes the lateral belt areas project to SMA [Deacon, 1992]. The lateral belt also projects to the STS [Hackett et al., 1998]. The responsiveness of the lateral belt areas to more complex sounds has also been demonstrated in humans [Wessinger et al., 2001] with functional imaging. The anterior superior temporal sulcus (STS) projects widely to a-modal association cortices [Jones and Powell, 1970], as well as to lower order visual areas [Maioli et al., 1998]. Deacons major findings are the most extensive projection to prearcuate regions (frontal) from STG and even more dense connection from STS. No connection was found to primary auditory

cortex.

The important production disorders that can be caused by temporal lesions are paraphasias [Damasio, 1992], a problem attributed to errors in the process of phonologically encoding words. Severe Wernicke's Aphasia can lead to severe anomia [Goodglass, 1997], the inability to find high information words. Those two phenomena might both be caused by problems of phonological encoding, i.e. a disorder and a disability. However, the respective words are often preserved in comprehension [Goodglass, 1997] which does not necessarily indicate different representations in perception and production, but can be explained by independent access routes. The counterpart of anomia in perception is *word deafness* (WD) with intact word and speech production and intact perception of complex sounds. Lesions in STG [Tanaka et al., 1987] bilaterally results in pure WD. WD can be caused by several cognitive deficits, such as the inability to recognise word forms or to connect the detected forms with a meaning. Evidence for the involvement of the superior and middle posterior temporal gyrus in prelexical phonological processing, e.g. in perception of an unfamiliar language was found [Mazoyer et al., 1993]. It could also be shown that speech sound are processed more ventrally than non-speech sounds [Zatorre et al., 1992]. Two very recent PET investigation observed activation of the superior temporal gyrus in speech perception. One study showed activation of the left anterior superior temporal sulcus only for intelligible speech [Scott et al., 2000]. While the second found activation in the superior temporal sulcus during performance of a verbal fluency task. The authors, therefore, postulate this region to be involved in the acquisition of phonetic sequences [Wise et al., 2001]. This later PET study further observed the supra-temporal cortical plane responding to both speech and non-speech stimuli and posterior media at the junction to the inferior parietal cortex responded to the speech production.

In the frontal lobe especially the supplementary motor cortex (SMA) and the primary motor cortex (M1) are of interest for speech. SMA is involved in the representation of complex motor programs. It was found that BA 4 (motor cortex) and 6 (premotor cortex) are reciprocally connected, [Pandya and Kuypers, 1969, Jones and Powell, 1970]. SMA projects to M1, which is organised somatotypically [Greyer et al., 2000]. A PET study did showed an activation of what the authors called *posterior Broca*, i.e. BA 44/6 for phonetic encoding of phonological word form into an articulatory plan. Their assumption is that words are stored in form of auditory information. The subtraction was repeating words against listening to words. The authors claim this area to be required for motor plans including speech. An articulation task in the same study activates the sylvian sensorimotor cortex bilateral in tongue, mouth, and respiratory areas, proving further evidence for the involvement of the postcentral gyrus in speech production [Price et al., 1996]. It is further notable that stimulating M1 produces rudimentary vocalisations, while no other area could trigger these responses [Penfield and Roberts, 1959]. The primary motor cortex seems to include representational structure that directly triggers motor output [Ojeman, 1983].

Broca's area [Broca, 1865] was several times redefined and is now relatively well agreed to be Brodmann's Areas 44 *and* 45 [Damasio, 1992]. However, the role of Broca's area to represent motor control of speech came under dispute. The inability to coordinate speech movements with unimpaired perception of speech is known as apraxia. It seems to be caused by lesions in BA 4/6 and not lesions in BA 44/45 [Levine and Sweet, 1982]. The integration of linguistic knowledge in brain research on language brought up the alternative view that the areas 44/45 are housing syntax [Zurif, 1982]. It is now widely agreed that the main symptom of

damage to areas 44 and 45 is agrammatism. As we do not consider the syntactic aspects of words, we do not include Broca's Area as part of the model.

The role of subcortical areas in language tasks, although evident [Doya, 1999], is poorly understood, the main reason being that one cannot easily specify its computational role in interaction with the cortex. For this reason, we excluded subcortical areas from this model.

There are connections from the cingulate cortex, in particular from the anterior cingulate cortex to the prearcuate area (possibly corresponding to SMA within BA 6 in humans) [Deacon, 1992]. Connection from the anterior cingulate to SMA have also been found by other researchers [Greyer et al., 2000]. The cingulate cortex also plays a major role in primate vocalisations [Arbib, 1998]. In humans the anterior cingulate is associated with autism when damaged [Deacon, 1992]. The involvement of the cingulate cortex in speech production is a stable observation. It was recently shown that this activation can not be attributed to attentional mechanisms [Murtha et al., 1999]. It is therefore likely that the cingulum has a motivational role in speech production.

A Theory of Words in the Cerebral Cortex

Our neural theory of words includes a model of learning, perception, and production of words. The theory specifies the computation and the localisation within the brain of each stage of processing.

Figure 1 shows a schematic representation of the theory. During the babbling phase the cingulate cortex (Cing) triggers articulatory motor events in M1. The produced sequences are detected, encoded and represented in SMA. The role of SMA is also to reactivate these sequences of motor events in M1. The sequences of articulatory movements lead to sound, which can be perceived and analysed in A1. A2 detects auditory features. Sequences of auditory features are detected in STS. The motor sequences in SMA are then associated to the auditory sequences in STS. The resulting structure is the auditory-motor representation of syllables on which we base word learning. The motor sequences can be reactivated by associated complex auditory events in STS.

Word learning starts with processing of the sound input of the word. Sequences of syllables are detected and represented in STS. They are then associated with a semantic representation, such as a visual representation formed in IT. STS detects and stores sequences of auditory features in A2, as well as detects sequences within STS itself.

In our theory, a word is perceived if a familiar speech sound sequence is re-detected. This is the case, once a learned representation of a sequence of auditory features is activated. If this sequence representation is meaningful, i.e. it was associated with meaning in the past, then it will activate this meaning representation. To prevent a detected motor pattern in SMA to trigger articulation, a functional device is needed to inhibit motor output. The cingulate cortex is postulated to fulfill this task.

During naming, the visual representation activate the word representation in STS, which in turn activates the auditory part of the syllable representations. The auditory representation

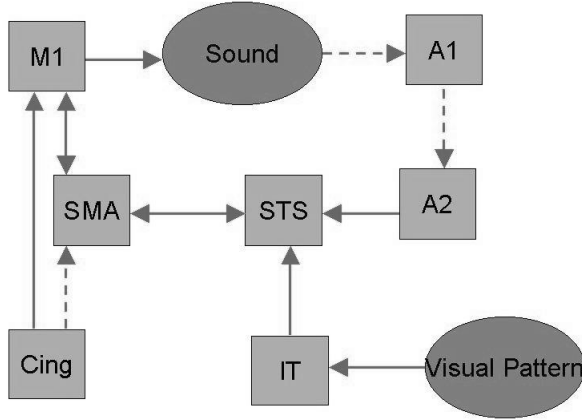


Figure 1: Schema of the word network in the cerebral cortex

of syllables can activate the motor representations of syllables, which in turn trigger the execution of motor events by M1.

Simulation

The model need to use the Dynamical Recurrent Associative Memory Architecture (DRAMA) [Billard and Hayes, 1999] and general Hebbian Learning. Similarly to time delay networks [Lin et al., 1993], each connection is associated with two parameters, a weight w_{ij} and a time parameter τ_{ij} . Weights correspond to the synaptic strength, while the time parameter specifies a synaptic delay, that is a delay on the time required to propagate the activity from one neuron to the other. Both parameters are modulated by learning in order to represent the spatial (w) and temporal (τ) regularity of the input to a node. The parameters are updated following Hebbian rules, given by Equations 1 and 2. Learning starts with all weights and time parameters set to zero, unless specified differently to represent predefined connection.

$$\delta w_{ji}(t) = a \cdot y_i(t) \cdot y_j(t) \quad (1)$$

$$\tau_{ji}(t) = \left(\frac{\tau_{ji}(t-1) \cdot \frac{w_{ji}}{a} + \frac{y_i(t)}{y_i(t)}}{\frac{w_{ji}}{a} + 1} \right) \cdot y_i(t) \cdot y_j(t) \quad (2)$$

where a is a constant factor by which the weights are incremented.

In DRAMA, the neuron activation function follows a linear first order differential equation

given by Equation 3, below.

$$y_i(t) = F(x_i(t) + \tau_{ii} \cdot y_i(t-1) + \sum_{j \neq i} G(\tau_{ji}, w_{ji}, y_j(t-1))) \quad (3)$$

F is the identity function for input values less than 1 and saturates to 1 for input values greater than 1 ($F(x) = x$ if $x \leq 1$ and $F(x) = 1$ otherwise) and G is the retrieving function whose equation is given in 4.

$$G(\tau_{ji}, w_{ji}, y_j(t-1)) = A(\tau_{ji}) \cdot B(w_{ji}) \quad (4)$$

$$A(\tau_{ji}) = 1 - \Theta(|y_j(t-1) - \tau_{ji}|, \epsilon(\tau_{ij}))$$

$$B(w_{ji}) = \theta(w_{ji}, \delta(w_{ij}))$$

The function $\Theta(x, H)$ is a threshold function that outputs 1 when $x \geq H$ and 0 otherwise. The factor ϵ is a error margin on the time parameter. It is equal to $0.1 \cdot \tau_{ij}$ in the simulations, allowing a 10% imprecision in the record of the time delay of units co-activation. The term $\delta(w_{ij})$ is a threshold on the weight. It is equal to $\frac{\max_{y_j > 0}(w_{ji})}{\theta(w_{ij})}$. $\theta(w_{ij}) = 2$ in the experiments. $\max_{y_j > 0}(w_{ji})$ is the maximum value of the weight of all the connections between activated units j and unit i , which satisfy the temporal condition encoded in $A(\tau_{ji})$.

Each unit in the network has a self-connection, associated with a time parameters τ_{ii} . This provides a short-term memory of unit activation, whose rate is specified by the value of $\tau_{ii} < 1$. This decay is represented by the term $dy_i/dt = (\tau_{ii} - 1) \cdot y_i$, obtained from Equation 3, when putting to zero

Equation 3 can be paraphrased as follows: the output y_i of a unit i in the network takes values between 0 and 1: $y_i(t) = 1$, when (i) an input unit x_i has just been activated or (ii) when the sum of activation provided by the other network units is sufficient to pass the two thresholds of time and weight, represented by the function G (see Equation 4). A value less than 1 represents the memory of a past full activation (value 1).

DRAMA is used to implement SMA and STS. STS is composed of two layers of neural units. The first layer receives input from the secondary auditory cortex (A2) and, thus detects and represents sequences of auditory features (syllables). The second layer receives input from the first layer of STS and from IT. The units in this layer connect sequences of syllables and visual semantic representations, thus each unit represents the information that makes up a word in its connections. Note that the two-layer structure of STS in our model bears no direct relationship with two structurally distinguishable anatomical regions in STS. These have been created for the purpose of the modelling.

Once the representation of the syllables has been constructed (during the *babbling phase*), the model is then capable of encoding words, through association of sequences of syllables with a visual input (the meaning).

While performing the task, the neural activity in each modelled brain region is computed for every discrete time step. Figure 2 shows the neural activity over time during encoding (straight line) and retrieval (dotted line) of words. It can be seen how the auditory information is processed from LB to STS during word encoding, while in retrieval the visual input immediately triggers the representations in STS which in turn triggers motor output in the frontal areas. Integration of neural activity over the relevant time intervals of the simulation showed that STS has a higher activity in both tasks were words are involved compared with

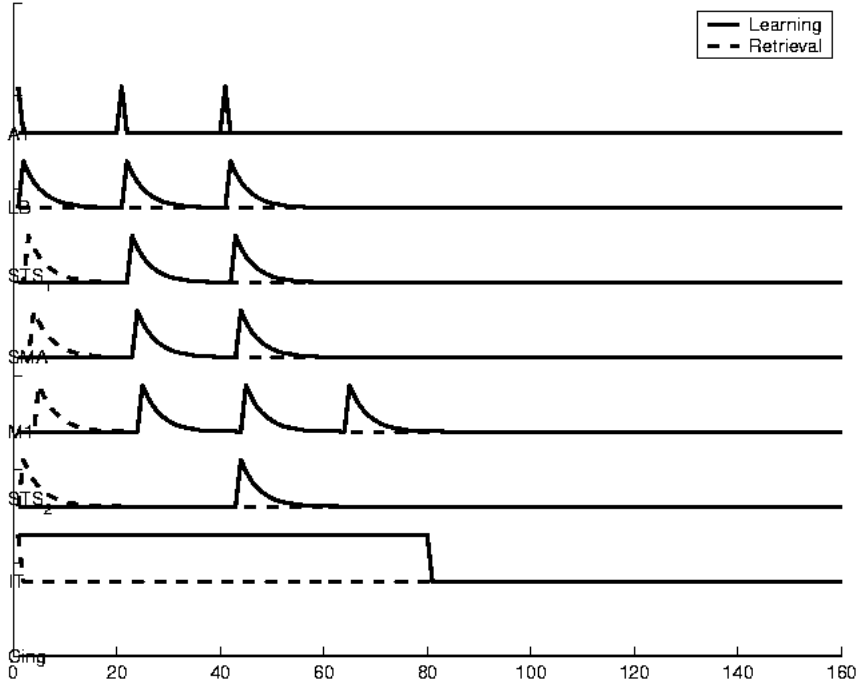


Figure 2: Neural activity over time during encoding and retrieval of one word

the syllable tasks. The activation of both, STS and SMA, is identical during the encoding and the retrieval task.

Discussion

The theory is precise about the impossibility to produce words without accessing the sequence representation in the temporal area and is, in this point, in accordance with the Wernicke-Geschwind model. We are specific about the requirement of representations in STS, while STG is not required for production. In contrast to Geschwind we do not regard GA as required for the transformation of visual images to high level auditory representations. Our theory is also not in accordance with the motor theory of speech perception [Liberman and Mattingly, 1985], which states that the object of speech perception are the intended phonetic gestures of the speaker represented in the brain as invariant motor commands. No case of word deafness caused by frontal lesions is known to us. It is also hardly reported that any lesions in frontal areas result in disturbance of speech perception. Nevertheless we would predict, that a perceived unit of speech is detected as producible if it activates a motor representation in SMA.

To transform the obtained simulation results into a functional imaging experiment several points have to be noted. As mentioned before, in a functional imaging study we can not examine the babbling phase. We used the babbling phase in the model only to establish plausible representations of syllables. However, in a functional imaging experiment we would

have to use words consisting of syllables which are definitely very common to the subjects. As it is also likely that the neural activity reflecting semantic processing is dependent on the task and nature of the meaning (modality, abstractness), in functional imaging tasks using semantic representations in one focal area are likely to lead to a better activation than arbitrary and widely distributed representations. To test out theory simple artificial uni-model visual patterns should be used as meanings.

We specified a theory of words including learning, representations, perception and naming. By implementing the theory as a neural model and simulating the tasks we gain precise hypothesis about the results of a functional imaging experiment. However, it might turn out to be a problem if the hypothesis is: *no change* in neural activity. Contemporary statistical analysis approaches try to reject the null-hypothesis of no difference. Neural models predicting more precisely the changes in neural activity would call for a new approach of analysing imaging data.

Let us end with some final remarks about language acquisition. It has been a boiling discussion since decades what aspects of language are *genetically* specified and which are learned. Connectionism has been postulated to be a good paradigm to study what is required in terms of structure and mechanisms to enable language learning [Elman et al., 1996]. In our model very specific connections between and functional capability of brain areas (such as STS or SMA) were required for word acquisition.

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