shared syntactic representations, and hence that the lemma level is shared between the comprehension and production systems, as Levelt et al. hypothesized. In fact, our findings are much stronger evidence for a shared level of syntactic representation than is Levelt et al.'s own evidence, which depends upon semantic interference – by hypothesis mediated by the lemma level – from visually presented distractors during picture naming. Our results show further how it is possible to integrate the study of comprehension and production, as Cutler and Norris (1999) espoused in their commentary, within Levelt et al.'s framework.

Overall, the syntactic priming results are in keeping with our extension of Levelt et al.'s model. These results demonstrate that this type of framework can account for not only single word production, but also aspects of multiple-word utterance production. Furthermore, they suggest that at least some aspects of Levelt et al.'s model are relevant for comprehension as well as production.

ACKNOWLEDGMENTS

This work was supported by a British Academy Postdoctoral Fellowship, a British Academy grant, and ESRC research grant no. R000237418.

Lexical access as a brain mechanism*

Friedemann Pulvermüller

MRC Cognition and Brain Sciences Unit, Cambridge CB2 2EF, United Kingdom. **friedemann.pulvermuller@mrc-cbu.cam.ac.uk**
http://www.mrc-cbu.cam.ac.uk/People/Friedemann.Pulvermuller.html

*This commentary originally appeared in the Levelt et al. treatment in BBS 22(1) (pp. 52–54).

Abstract: The following questions are addressed concerning how a theory of lexical access can be realized in the brain: (1) Can a brainlike device function without inhibitory mechanisms? (2) Where in the brain can one expect to find processes underlying access to word semantics, syntactic word properties, phonological word forms, and their phonetic gestures? (3) If large neuron ensembles are the basis of such processes, how can one expect these populations to be connected? (4) In particular, how could one-way, reciprocal, and numbered connections be realized? and, (5) How can a neuroscientific approach for multiple access to the same word in the course of the production of a sentence?

A processing model of lexical access such as the one described in detail in the target article is not necessarily a theory about brain mechanisms. Nevertheless, it may be fruitful to ask how the model can be translated into the language of neurons.

Feedback regulation is necessary! The brain is a device with extreme plasticity. Early in ontogenesis, neurons rapidly grow thousands of synapses through which they influence their neighbors and, in turn, receive influence from other neurons. These synaptic links become stronger with repeated use. Therefore, a particular brain-internal data highway that initially consists of a few fibers, may later include thousands or millions of cables with weak synaptic links, and may finally exhibit a comparably large number of high-impact connections. In this case, the same input to the system will lead early on to a minimal wave of activity, but finally lead to a disastrous breaker. A system with such an enormous variation of activity levels requires a regulation mechanism in order to function properly (Braitenberg 1978). The task of this mechanism would be to enhance or depress the global level of activity to keep it within the limits of optimal neuronal functioning.

A simple way to regulate activity in a neuronal system is to monitor activity levels of all neurons, calculate their sum, and provide an additional input to the system that is excitatory if this sum is small (to prevent extinction of excitation), but inhibitory if it is large (to prevent overactivation). Thus, a mechanism of inhibition (or disfacilitation) appears necessary in any brainlike model.

Levelt, Roelofs & Meyer (Levelt et al.) state that their model does not include inhibition (sect. 3.2.2) and the fact that it does not may be interpreted as one of their minimal assumptions – evidencing a research strategy guided by Ockham's razor. Certainly, looking at the theory in abstract space, the assumption of inhibitory links would be an additional postulate that made it less economical and therefore less attractive. However, considering the brain with its well-known intracortical and striatal inhibitory neurons that are likely to be the basis of feedback regulation (Braitenberg & Schüz 1991; Fuster 1994; Wickens 1993), it does not seem desirable to propose that inhibitory mechanisms are absent in a model meant to mirror brain functioning.

Would this mean that the theory proposed by Levelt et al. is unrealistic from the perspective of brain theory? Certainly not. Although such mechanisms are not explicitly postulated or wired into the network (and therefore do not affect activation spreading), they kick in at the level of node *selection* where Luce ratios are calculated to obtain the probability with which a preactivated representation is selected (fully activated, so to speak). The probability that a particular node is selected depends upon its actual activity value *divided by* the sum of the activation values in a particular layer. Because the calculation performed is very similar to what a regulation device would do, one may want to call this implicit, rather than explicit, inhibition (or regulation). To make it explicit in the network architecture, an addition device in series with numerous intra-layer inhibitory links would have to be introduced. Thus, the model includes inhibition – although on a rather abstract level – and this makes it more realistic from the neurobiological perspective.

Brain loci of lexical access. Where in the brain would one expect the proposed computation of lexical concept, lexical syntax (lemma), word form, and phonetics? Most likely, phonological plans and articulatory gestures are wired in primary motor and premotor cortices in the inferior frontal lobe. The percepts and motor programs to which words can refer probably correspond to activity patterns in various sensory and motor cortices and thus may involve the entire cortex or even the forebrain. More specificity is desirable here; for example, words referring to movements of one's own body are likely to have their lexical concept representations localized in motor cortices and their vicinity, while lexical concepts of words referring to objects that one usually perceives visually should probably be searched for in visual cortices in occipital and inferior temporal lobes (Pulvermüller 1996; Warrington & McCarthy 1987).

Between phonetic-phonological and lexical-semantic representations the model postulates lemmas whose purpose can be considered to be three-fold: (1) not only do they glue together the meaning and form representations of a word, but, in addition, (2) they bind information about the word's articulation pattern and its sound image. Furthermore, (3) lemmas are envisaged to store syntactic knowledge associated with a word.

Intermediary neuronal units mediating between word form and semantics – the possible counterparts of lemmas have been proposed to be housed in the inferior temporal cortex (Damasio et al. 1996). The present theory would predict that lesions in the "lemma area" lead to a deficit in accessing syntactic knowledge about words (in addition to a deficit in naming). However, lesions in inferior temporal areas can lead to a category-specific naming deficit while syntactic knowledge is usually spared. Hence, it appears unlikely that lemmas are housed in the inferior temporal lobe. Is there an alternative to Damasio's suggestion?

One of the jobs of a lemma is to link the production network to the perception network (sect. 3.2.4). On the receptive side, sound waves and features of speech sounds activate neurons in the auditory cortex in the temporal lobe, and in order to store the many-many relation between acoustic phonetic features and articulatory phonetic features, it would have advantages to couple the respective neuron populations in auditory and motor cortices. Such coupling, however, is not trivial, because, for example, direct neuroanatomical connections between the primary motor and auditory cortices are rare, if they exist at all. Therefore, the connection can only be indirect and the detour to take on the articulatory-

https://doi.org/10.1017/S0140525X04260071 Published online by Cambridge University Press

acoustic path would probably lead through more anterior frontal and additional superior temporal areas (Pulvermüller 1992). In contrast to the primary areas, these areas are connected to each other, as can be inferred from neuroanatomical studies in macaca (Deacon 1992; Pandya & Yeterian 1985). The coupling of acoustic and articulatory information will, therefore, involve additional neurons that primarily serve the purpose of binding linguistic information. Thus, the physical basis of lemmas may be distributed neuron populations including at least neurons in inferior prefrontal areas (in Brodmann's terminology, areas 44, 45, and perhaps 46) and in the superior temporal lobe (anterior and posterior parts of area 22 and perhaps area 40). These neurons may not only be the basis of the binding of information about production and perception of language, they may well be the targets of connections linking the word form to its meaning, and, most important, their mutual connections may store syntactic information about a word. This proposal is consistent with the neurological observation that lesions in anterior or posterior perisylvian sites (but not in the inferior temporal lobe) frequently lead to a syntactic deficit called agrammatism (Pulvermüller 1995; Vanier & Caplan 1990).

Reciprocal, one-way, and numbered connections. Statistics of cortico-cortical connections suggest that two individual pyramidal neurons located side by side have a moderate (1–2%) probability of exhibiting one direct synaptic link, and only a very low probability of having two or more links (Braitenberg & Schüz 1991). Because synaptic connections are always one-way, a model for interaction of individual neurons may, therefore, favor one-way connections. Language mechanisms, however, are probably related to interactions of large neuronal populations, and if such ensembles include several thousands of neurons, chances are high that two ensembles exhibit numerous connections in both directions (Braitenberg & Schüz 1991). Hence the zero-assumption should probably be reciprocal connections between neuronal representations of cognitive entities such as lemmas, word forms, and their meanings.

The model postulates reciprocal connections between semantic and syntactic representations (Fig. 2) and for some within-layer links (see, e.g., Figs. 4, 6, and 7). Lemmas and word forms are connected through unidirectional links and within the form stratum there are directed and numbered links.

How could two large cortical neuron populations be connected in one direction, but lack the reciprocal link? Here are two possibilities: first, one-way connections could involve directed subcortical links (e.g., through the striatum). As an alternative, connections could in fact (i.e., neuroanatomically) be reciprocal, but activity flow during processing could be primarily in one direction. According to the present theory, the processes of naming include activity spreading from the conceptual to the lemma stratum, and from there to the form stratum whence backward flow of activity to the lemmas is prohibited. This could, for example, be due to early termination of the computation if the appropriate lemma is already selected before upward activity from the form stratum can influence the computation. Conceptualizing the process of selection as the full activation (ignition) of a lemma representation that leads instantaneously to equally strong activation of both conceptual and form representations of the same word, it could be stated that such ultimate activation makes additional activity flow impossible or irrelevant. A regulation mechanism (as detailed above) can be envisaged to suppress all activity in competing nodes as soon as selection has taken place (therefore accounting, for example, for the lack of priming of phonological relatives of words semantically related to the target [Levelt et al. 1991] if lemma selection occurs early). Activity flow primarily in one direction can still be accounted for in a system based on the economical assumption of reciprocal connections between large neuronal populations.

Numbered directed connections are proposed to link morpheme and phoneme nodes. Here, the brain-basis of the numbering needs to be specified. Again, there are (at least) two possibilities: First, different axonal conduction delays could cause sequential activation of phoneme nodes. This option has the disadvantage that differences in the delays would be hardwired in the network making it difficult to account for variations between speaking fast and speaking slow. The second alternative would suggest a slight modification of Levelt et al.'s model: phoneme nodes may receive input from morpheme nodes, but their sequence would be determined by connections between phoneme representations. Here, Abeles's (1991) concept of synfire chains comes to mind. A synfire chain is a collection of neurons consisting of subgroups A, B, C . . . with directed links from A to B, B to C, and so on. Each subgroup includes a small number n of neurons, $7 < n < 100$, and therefore, the assumption of one-way connections appears consistent with the statistics of cortical connectivity (Braitenberg & Schüz 1991).

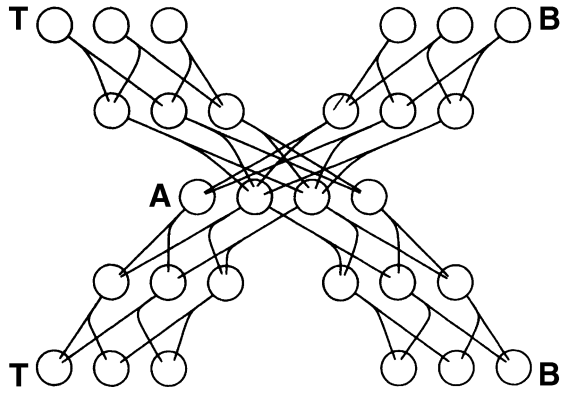


Figure 1 (Pulvermüller). Synfire chains possibly underlying the serial order of phonemes in the words "tab" and "bat." Circles represent neurons, and lines, their connections (the penetrated neurons being the ones that receive activation). The A (or /æ/-sound) is shared by the two words, but its neuronal counterparts are not identical – they have overlapping representations, the non-overlapping neurons (leftmost and rightmost neurons in middle row) processing information about the sequence in which the phoneme occurs ("context-sensitive neurons"). Also the syllable-initial and syllable-final phonemes have distinct representations. If all neurons have a threshold of 3 and receive 1 input from their respective lemma node, selection of one of the word-initial phoneme representations (uppermost triplets) leads to a well-defined activation sequence spreading through the respective chain (but not through the competitor chain). (Modified from Braitenberg & Pulvermüller 1992.)

Because phonemes can occur in variable contexts, it is not sufficient to assume that phoneme representations are the elements corresponding to the neuronal subgroups of the synfire chains in the phonological machinery (Lashley 1951). In order to distinguish the phonemes in "bat" and "tab," it is necessary to postulate that not phonemes, but phonemes-in-context are the elements of representation. Thus, the representation of a /æ/ following a /b/ and followed by a /t/ would be distinct from that of an /æ/ followed by a /b/ and preceded by a /t/ (cf. Wickelgren 1969). In addition, it has advantages to distinguish syllable-initial, central, and syllable-final phonemes, as suggested in the target article. The two /æ/s occurring in the words /tæb/ and /bæt/ could be neuronally organized as sketched in Figure 1. The selection of one of the chains would be determined (1) by activating input to all to-be-selected context-sensitive phonemes and (2) by strong input to the first neuronal element that initializes the chain. This proposal opens the possibility of determining the speed with which activity runs through the synfire chain by the amount of activation from the lemma and morpheme representations to context-sensitive phoneme representations.

https://doi.org/10.1017/S0140525X04260071 Published online by Cambridge University Press

Predictions about neurobiological mechanisms of language may be helpful for planning experiments in cognitive neuroscience and for interpreting their results. However, these considerations are at present necessarily preliminary, as pointed out in the target article, not only because the proposals may be falsified by future research, but also because they leave so many questions unanswered. For example, how is it possible to model multiple occurrences of a particular word (same form, same syntax, same meaning) in a given sentence? A not so attractive possibility would be that there are multiple representations for every word type in the processing model or its neurobiological counterpart. Other solutions may make the models much more complicated. Although it is clear that we can, at present, only scratch the surface of lexical processes in the brain, Levelt et al.'s target article clearly evidences that the insights obtained so far are worth the scientific enterprise.

ACKNOWLEDGMENTS

This work is supported by grants from the Deutsche Forschungsgemeinschaft. I am grateful to Valentino Braitenberg and to Bettina Mohr for comments on an earlier version of the text.

Authors' Response

BBS Note: **The original manuscript of this Response article was received on January 14, 2000.**

Relations of lexical access to neural implementation and syntactic encoding

Willem J. M. Levelt,[a] Antje S. Meyer,[b] and Ardi Roelofs[a]

[a]*Max Planck Institute for Psycholinguistics, 6500 AH Nijmegen, The Netherlands;* [b]*School of Psychology, University of Birmingham, Birmingham, B15 2TT, United Kingdom.* **pim@mpi.nl A.S.Meyer@bham.ac.uk ardi@mpi.nl http://www.mpi.nl http://www.bham.ac.uk/psychology/research_03/lang_cog.htm**

Abstract: How can one conceive of the neuronal implementation of the processing model we proposed in our target article? In his commentary (Pulvermüller 1999, reprinted here in this issue), **Pulvermüller** makes various proposals concerning the underlying neural mechanisms and their potential localizations in the brain. These proposals demonstrate the compatibility of our processing model and current neuroscience. We add further evidence on details of localization based on a recent meta-analysis of neuroimaging studies of word production (Indefrey & Levelt 2000). We also express some minor disagreements with respect to Pulvermüller's interpretation of the "lemma" notion, and concerning his neural modeling of phonological code retrieval. **Branigan & Pickering** discuss important aspects of syntactic encoding, which was not the topic of the target article. We discuss their well-taken proposal that multiple syntactic frames for a single verb lemma are represented as independent nodes, which can be shared with other verbs, such as accounting for syntactic priming in speech production. We also discuss how, in principle, the alternative multiple-frame-multiple-lemma account can be tested empirically. The available evidence does not seem to support that account.

Pulvermüller discusses possible neural mechanisms for the implementation of our computational model of lexical access (Pulvermüller 1999, reprinted here). His starting point is clear and correct: The processing model is not a theory about brain mechanisms. It is not a "'neural model" or anything of the sort. It is a psychological processing model formalized in terms of a rather classical spreading activation architecture. The issue of the model's potential neurological underpinnings is of great importance. On the one hand, the model should not be incompatible with existing neuroscience. For instance, WEAVER's chronometric properties should not violate known neurological limitations. Providing potential neural mechanisms for implementing fragments of the model amounts to providing existence proofs for compatibility. On the other hand, the theory of access can be a guide or tool for exploring the patterns of cerebral activations obtained in neuroimaging studies of word production, which involve tasks ranging from picture naming and verb generation to word and nonword reading. A rather coherent pattern of mappings between processing mechanisms in the theory and brain localizations emerges from study.

The first issue addressed by **Pulvermüller** concerns inhibition. Clearly, neuronal functioning would get disrupted without inhibitory regulation. How can this be compatible with the absence of inhibitory connection in the WEAVER model? Here Pulvermüller correctly observes that WEAVER incorporates an equivalent of inhibition, namely, in the lexical competition governed by Luce's rule.

Next, **Pulvermüller** addresses the issue of the brain loci corresponding to various computations in the model and we agree with several of his proposals. To shortcut somewhat, we refer to the above-mentioned meta-analysis by Indefrey and Levelt (2000). There each word production task used in the literature was analyzed as the combination of a "core" process and a "lead-in" process. A core process is any consecutive subset of stages in the target article's theory, ranging from conceptual preparation to articulation. The lead-in process for a given task is the task-specific initiation of these core processes. For instance, picture naming has visual object recognition as its lead-in process, followed by a core process consisting of all stages of word production. Word reading has visual word recognition as the lead-in process. It is followed by core processes from phonological code retrieval, via syllabification down to articulation. Nonword reading has some form of grapheme-phoneme conversion as the lead-in process. There is no phonological word code retrieval here; the core process begins with syllabification and is completed with articulation.

By comparing observed cerebral activations between critical pairs of task, and using a statistical criterion, the various core processes in the theory could be related to smaller or larger foci. For instance, the critical difference between word and nonword reading resides in accessing a word's phonological code. The meta-analysis indicates Wernicke's area as being involved in this core operation. Similarly, the studies indicate that syllabification involves the left inferior frontal gyrus, whereas phonetic encoding and articulation show the expected bilateral involvement of ventral sensorimotor areas. The tasks used in the imaging literature did not allow us to distinguish between conceptual preparation and lemma access. The statistically common region in the imaging studies relating to this pair of processes turned out to be in the midpart of the left middle temporal gyrus. However, the subtraction logic of the meta-analysis would necessarily miss the variability in cortical representation for different semantic fields, such as tools, vegetables, and animals. **Pulvermüller** correctly points to this issue, which has become a hot topic in imaging and patient studies of

https://doi.org/10.1017/S0140525X04260071 Published online by Cambridge University Press