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## **EARLY AND LATE BRAIN INDEXES OF LANGUAGE AND COGNITION (WP1)**

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### ABSTRACT

Cognitive science is dominated by theories of modular seriality and interactive parallelism. These competing approaches make conflicting predictions on neurophysiological brain activation testable in MEG and EEG experiments. Seriality of lexical, semantic and syntactic processes receives support from late (latency  $\sim 1/2$ s) sequential neurophysiological responses, especially N350, N400, and P600. However, parallelism is substantiated by early near-simultaneous brain indexes of a range of psycholinguistic processes, up to the level of semantic access and context integration, emerging already 100-200ms after critical stimulus information is present. Crucially, there are reliable latency differences of 10-50ms between early cortical area activations reflecting lexical, semantic and syntactic processes, which are left unexplained by both serial and parallel models. We here offer a new mechanistic model building upon neuroanatomical and neurophysiological knowledge. A key concept are discrete distributed cortical circuits with specific inter-area topographies, in which cortico-cortical conduction times determine activation delays. Activity spreading in these circuits accounts for comprehension-related regional activation differences in the millisecond range.

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Two main views are dominating cognitive science. Modular seriality posits serial or cascaded processing of different types of information extracted from a stimulus in autonomous subcomponents, whereas interactive parallelism proposes simultaneous access to information of different kinds in a distributed interconnected system (box 1). Behavioural experiments capitalising on reaction times and performance accuracy have not been conclusive in deciding between the two competing views, as available evidence could be interpreted in favour of both<sup>1,2</sup>. It is also well-known that neurophysiological double dissociations, once used to argue in favour of a modular perspective, can, in fact, also be explained by a distributed systems account<sup>3-5</sup>. A great opportunity is opened by looking at the brain's on-line response to materials that signify specific semantic and conceptual information. These brain responses unfold in time millisecond by millisecond and their activation dynamics are picked up with neurophysiological imaging using EEG and MEG (Electro- and Magnetoencephalography). Neurophysiological source localisation, in conjunction with metabolic brain imaging using functional magnetic resonance imaging (fMRI), can even identify critical areas whose activation is modulated by the processing of specific types of stimulus information.

Here, we review neurophysiological evidence for cognitive seriality, which is clearest in the psycholinguistic field, in the area of spoken and written language comprehension. However, the review also shows that different information types have early (100-200ms) and near-simultaneous brain correlates. Early near-simultaneity provides objective support for parallelism in written and spoken language processing. Late seriality and early near-simultaneity of cognitive processes are then integrated on the bases of a mechanistic model of cognitive functions

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grounded in discrete distributed neuronal circuits. Importantly, the new mechanistic model also explains specific fine-grained activation time differences that breach the early simultaneity of cognitive information access.

### LATE SERIALITY

In terms of brain function, where action potentials can propagate along axons within milliseconds<sup>6</sup>, half a second is already an extremely long time period. In this context, the most well-known language components appear to arise extremely late. The N400<sup>7</sup> is maximal  $\frac{1}{3}$  to  $\frac{1}{2}$  of a second after onset of the critical stimulus word. Typically, the N400 is elicited by words that appear in sentences where they do not fit semantically, as in the example below (mismatching critical word is in italics).

The fish swam in the *bed*.

The N400 also appears to single words following each other in random order<sup>8</sup> and to language stimuli whose phonological features are unexpected in a given context<sup>9</sup>. It may also reflect nonlinguistic processes, as suggested by its appearance to pictures<sup>10</sup>, sounds<sup>11</sup>, and odours<sup>12</sup>. The scalp topography of the N400 with its parietal negativity maximum may be generated in left fronto-temporal cortex<sup>13</sup>, but deeper bilateral sources have also been discussed<sup>14</sup>. Given the range of possible generators and the variety of conditions that lead to an enhanced N400, attempts have been made to dissect the N400 into subcomponents. One proposal is that an early part, called N350, reflects lexical or phonological processing<sup>15,16</sup>, and can be separated from the N400 proper, which is best characterised as an index of semantic memory processes and context integration<sup>17</sup>.

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An even later component of the event-related potential, ERP, which is positive-going and, like the N400, maximal at parietal leads, has somewhat unclear brain origin, and is related to syntax and grammar processing. It is elicited by a critical word that renders a sentence ungrammatical, as, for example, “from” in the string below.

The man sold the *from* house.

The late positive brain wave, called P600, can be elicited by a range of violations of grammar rules, including rules of phrase structure, agreement and subadjacency. A P600 wave can even emerge to sentences that are grammatically correct, but in most individuals would first elicit a garden path effect associated with the temporary (incorrect) impression that the string is ungrammatical<sup>18-20</sup>.

Earlier lexical and syntactic effects have been described in the N125 ERP component, which peaks at 100-250ms and has a left anterior maximum (early left anterior negativity, ELAN)<sup>21,22</sup>. Like the P600, this early effect was seen with a range of syntactic violations, including those of phrase structure and agreement rules<sup>23,24</sup>. As the same time range also revealed differences in cortical activation between lexical categories, for example between nouns and verbs<sup>25-27</sup>, it may reflect an early stage of grammar processing where the information about a word’s lexical category is accessed and a phrase structure representation is being built. This early access to lexico-syntactic structure was distinguished from later, and possibly deeper, syntactic analysis reflected by the P600<sup>28</sup>.

The serial perspective emerging from these data is the following: After initial analysis of physical features of critical word stimuli, lexical category information is retrieved and an elementary syntactic structure is built (N125). Subsequently, lexical

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processing (N350) and semantic access and context integration (N400) predominate. Finally, there is an optional second step of in-depth syntactic analysis or re-parsing (P600, box 1).

### **EARLY NEAR-SIMULTANEITY**

Neurophysiological indexes of psycholinguistic processes have also been found early, within 200 milliseconds after the sensory information was sufficient for identifying the critical stimulus word or morpheme. In the visual modality, critical words are flashed on a screen and the full information for identifying the stimulus item is therefore available at the very onset of stimulus presentation. In the auditory modality, spoken words unfold in time and it can take several hundred milliseconds until the available information about the stimulus is sufficient for identifying the word<sup>29</sup>. Latencies of brain responses in speech comprehension are relative to this critical recognition point.

### **Written language**

Psycholinguistic processes are reflected early by the syntactic N125 and lexical-category responses (last section). For example, grammatical function words elicited a left-lateralised component very similar in scalp topography to the syntactic negativity, with latencies as early as 160 milliseconds, whereas content words elicited a bilateral early negativity with the same latency<sup>30</sup>. Apart from other neurophysiological differences between grammatical word types, further work also documented early reflections of additional psycholinguistic variables, including the frequency with which words occur in normal text (word frequency), word length, and

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typicality (the likelihood with which letters of a word occur together)<sup>31-33</sup>. Word meaning (semantics) and even affective-emotional properties of words were reflected in early brain responses as well<sup>34-36</sup>. In summary, all types of information bound to single written words, be they physical, orthographic, lexical or semantic in nature, appear to be reflected by neurophysiological indicators within the first 200ms after word onset.

But would context processing become manifest similarly early or only at a later stage? Sereno and collaborators were the first to report neurophysiological indexes of semantic context integration within a sentence before 200 milliseconds after visual word onset<sup>37</sup>, and Penolazzi et al. confirmed these results also demonstrating that the early semantic effects critically depended on the length of written words<sup>38</sup>. These results argue in favour of early near-simultaneity of a wide range of psycholinguistic and cognitive processes in written language comprehension (box 2).

### Speech

When, relative to the point in time at which a critical word can first be uniquely recognised, would spoken language give rise to meaning-related effects? As word recognition latencies are reflected in early MEG activity<sup>39</sup>, it became important to relate access to a wider range of psycholinguistic information to early magnetic and electric brain activation. This work demonstrated the early near-simultaneous manifestation of phonological, lexical, semantic and syntactic processing, for example in a brain response known as the mismatch negativity, MMN<sup>40,41</sup> (box 3), a difference potential overlying early components of the ERP. The

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MMN is elicited in the so-called oddball paradigm where a frequent so-called standard stimulus is randomly replaced by rare deviant stimuli<sup>42</sup>. The MMN difference potential recorded in the EEG has a latency of 100-250ms and a fronto-central maximum with major sources in superior-temporal cortex of both hemispheres. Additional sources in fronto-central cortex may reflect stimulus characteristics and cortical circuits activated by specific stimuli. The MMN is of greatest interest for cognitive scientists, because its magnitude reflects the activation of memory circuits, for example for phonemes and spoken words. A sound, which distinguishes between meaningful words in a language the subject is proficient in, shows a stronger left superior-temporal MMN activation compared with similar but unfamiliar sounds<sup>43</sup>. In the very same way, lexical items elicit stronger superior-temporal MMN generators compared with meaningless pseudowords<sup>44-46</sup>. The existence of memory circuits at different levels (phonological, lexical) is therefore reflected by the MMN.

Semantic effects could also be demonstrated in the MMN response, for example in the differential activation of motor areas elicited by action words referring to different parts of the body: Surprisingly, words that refer to actions also activate the motor system when being perceived<sup>47</sup>. Furthermore, this motor activation even reflects fine-grained referential meaning of the action-related words: Words referring to actions performed with the legs, arms or face activate the motor system, pre-motor and motor cortex, in a somatotopic manner<sup>48</sup>. A leg-related word such as “kick” activates dorsal parts, where leg actions are represented and processed, whereas arm-related words such as “pick” or face related words such as “lick”, activates lateral or inferior frontal motor areas. The semantic somatotopy of action words documented



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by fMRI calls for neurophysiological research into the time course of category-specific semantic activation. MMN experiments showed that motor regions are being sparked rapidly, within the first 140-170 milliseconds after the word recognition point. There was also evidence for fine-grained latency differences, as face- and arm-words tended to activate inferior frontal cortex earlier than leg words activated the centro-dorsal leg region<sup>49,50</sup>. This is support for a near-simultaneous early reflection of phonological, lexical and semantic information immanent to a spoken word within the first ~150 milliseconds after the auditory input allows for word identification.

Syntactic effects very similar in both scalp topography and cortical generators to the syntactic N125 could also be revealed in the MMN response, with latencies similar to those of lexical and semantic MMN effects<sup>51-53</sup> (box 3). According to recent work, also semantic context integration is reflected by the MMN at early latencies<sup>54</sup>. Neurophysiological work on spoken language had earlier shown that semantic expectancy violation at the level of discourse can also lead to early manifestations in the ERP<sup>55</sup>. These results are consistent with the early semantic context integration effects seen to written words in sentence context (previous section).

## SUMMARY AND INTEGRATION

These summarized data show that brain processes indexing lexical, semantic and syntactic processes first occur early, within 200 milliseconds after stimulus information allows for unambiguous identification of critical words. Phonological and orthographic information is also brain-reflected in the same time range. This early near-simultaneity appears largely consistent with parallel models of language

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and cognitive processing. As the late responses (N400, P600) starting after 200ms are preceded by early indicators of the same types of stimulus information, they cannot reflect the first, initial stages of information access. In the light of their early precursors, they must reflect secondary processes following syntactic, lexical or semantic information access and context integration. It is possible that secondary stages are necessary to parse and understand a meaningful sentence. A different possibility is that comprehension processes terminate early, within 200 ms, and late brain responses reflect post-comprehension processes<sup>56</sup> specifically triggered by failure of semantic or syntactic integration of a word into its context. A range of post-comprehension processes may be relevant here, for example attempts to rephrase the "inaccurate" word or phrase. In this context, the longer latency of the P600, as compared with the N400, might arise from the reprocessing of several lexical units, which is relatively time demanding. In contrast, typical semantic incongruencies are best resolved by replacing a single critical word.

The data summarised so far can be integrated as follows. Access to phonological, lexical and semantic word features along with semantic and syntactic context integration and parsing are early near-simultaneous processes reflected by brain responses with latencies between 100 and 200ms. N400 and P600 reflect the reprocessing of lexical/semantic and syntactic information or might indicate specific linguistic or non-linguistic post-comprehension processes.

### **MILLISECOND DELAYS**

A strict parallelism approach is consistent with the near-simultaneity of psycholinguistic information access in the first 200 milliseconds. However, 200

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milliseconds is still a long time period, as brain physiology operates on a millisecond time scale. The lag with which sensory stimuli elicit the first neuronal activation in primary auditory and visual cortex is in the range of 20-50ms<sup>57,58</sup> and conduction times between distant cortical areas are, as far as the most frequent myelinated axons are concerned, in the range of 10-50ms<sup>6</sup>. To understand the brain processes of language at the mechanistic level of nerve cell circuits, it is essential to ask whether the *near*-simultaneous early language processes in the brain still include regular fine-grained activation time differences.

Near-simultaneity of auditory perceptual, acoustic-phonological, and lexical-morphological processes can be inferred from the similar latencies of electric and magnetic components to stimuli that trigger these cognitive processes specifically (box 3). However these data come from different studies and it is necessary to investigate the issue in experiments where the critical brain responses were elicited by well-matched stimuli. The best way to control exactly for stimulus features may be the use of *identical stimuli placed in contexts*. Certain speech stimuli, for example stop consonants, can be perceived as noise if placed in a noise context, and are comprehended as phonemes only if presented in appropriate speech context. These speech sounds can have the role of affixes and meaningful language units, morphemes, so that their context not only determines whether they are perceived as noise or speech but also whether they carry meaning or not. Presented in noise, phonemic and morphemic conditions, such critical identical stimuli elicited specific brain responses, with significant left-laterality only arising in the morphemic condition<sup>59</sup>. Remarkably, the latency of the brain response (136-155ms) did not differ significantly between conditions. This result is consistent with strict simultaneity and

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parallelism of acoustic, phonological and lexical information access in speech processing.

Written word processing has disclosed an early time course indexing minimal delays between the brain indicators of physical and higher linguistic-conceptual processes<sup>32,33,60</sup>. In one study exploiting regression analysis to disclose relationships between the magnitude of ERPs and psycholinguistic variables, there was an early reflection of word length and typicality (100ms), followed by indexes of lexical and semantic processing (150ms)<sup>31</sup>. This suggests a 50ms delay between processing onset of written word form and lexico-semantic information. Interestingly, the earliest effect related to word form processing was present in inferior-temporal cortex, whereas the 150ms effects of lexicality and semantics were seen in a more distributed system including also perisylvian cortex. Around 200ms, additional lexicality effects arose in inferior-temporal areas, consistent with reactivation of this area<sup>61</sup> (box 2).

Fine-grained differences in cortical activation times were seen between lexical brain processes. The first brain responses distinguishing between spoken words and pseudowords arose around 130 milliseconds after the critical stimulus information was present. The word-evoked activation pattern, however, consisted of at least two parts, a source in activation in superior-temporal cortex closely followed by a second source activation in inferior-frontal cortex. This second inferior-frontal generator was sparked at the same time (140-150 ms) when also meaning-related brain activation emerges<sup>59,62</sup>.

Fine-grained latency differences between meaning-related brain responses were seen in studies on category-specific semantic processing, especially investigations of different types of action-related words. When MEG and EEG were

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used to investigate the physiological basis of the comprehension process in real time, the activation of specific parts of the sensorimotor cortex by action words related to the face, arm and leg led to different activation times. Both for spoken and written word stimuli, the leg area activation to leg-related words was found to be delayed relative to the inferior frontal face-related semantic activation<sup>49,50,63</sup>. That these activations were indeed a manifestation of semantic word features was confirmed by significant correlation between semantic ratings of stimulus words and the magnitude of local activation in leg and face regions<sup>50</sup>. It is important, in the present context, that different types of semantic information were brain-reflected with different latencies, thus arguing in favour of distinct category-specific semantic systems with different brain loci and activation times.

In sum, in spite of near-simultaneity of early brain responses reflecting access to different linguistic information types, there are reliable fine-grained delays. One may argue that these delays could be explained by seriality, only at a much finer time scale than previously stipulated, with tens rather than hundreds of milliseconds as the relevant grain size. However, such fast seriality would leave unexplained a range of observations including

- the lack of reliable differences between neurophysiological processes elicited by noise, phonemes and meaningful units of speech,
- the reliable difference in activation time between word form and lexico-semantic processes in written word processing, along with the reactivation of inferior-temporal areas,
- the fine-grained latency differences between cortical area activations reflecting category-specific semantic processes.

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### **TOPOGRAPHY AND CONDUCTION DELAYS IN LINGUISTIC MEMORY CIRCUITS AS THE KEY**

To provide an account of early near-simultaneity and the critical latency differences, a model is necessary that spells out language and conceptual processes in terms of mechanistic neuronal circuits and their activation. The neuronal circuit model in box 4 (diagram a) explains this strict simultaneity of acoustic, phonological and lexical processing by differential activation of phonological and word form-related circuits in fronto-temporal perisylvian cortex. Still, as acoustic information enters the cortex in superior-temporal areas, spreading within perisylvian circuits accounts for the ~20ms delay of inferior-frontal upon superior-temporal activations.

The circuit model also accounts for different functional contributions of inferior-temporal cortex at 100 milliseconds, where its activation reflects typicality, and at 150-200 milliseconds, where lexicality effects are reflected. Early bottom-up processes in lexico-orthographic circuits related to typicality (100ms; box 4, diagram b) would accordingly be followed by processing in lexico-semantic networks in perisylvian and anterior-temporal areas (150ms) leading to differential top-down semantic activation in inferior-temporal cortex (diagrams c, d). This explanation of inferior-temporal reactivation capitalises on the postulate that word form and semantic circuits are spread out over the same areas.

More difficult to explain are the fine-grained latency differences that cut across traditional processing subcomponents. Most notably the different activation time lags of semantic activation constitute a challenge. The neuronal circuit model explains such differences in terms of conduction delays within neuronal assemblies.

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As semantic networks for action-related words connect lexical representations in perisylvian cortex and semantic networks, for example in arm and leg motor cortex, it is conceivable that different time demands arise for activity to travel the short distance from perisylvian cortex to arm representation as compared with the longer distance from the same perisylvian networks to the dorsal leg representation (box 4, diagram f, g). Therefore, the mechanistic model provides an account of category-specificity in the time course of semantic brain activation.

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### FUTURE TRENDS AND DIRECTIONS

As many psycholinguistic and conceptual processes seem to be brain-reflected both early and late, it is important to clarify the relation between the two. Are the early semantic, syntactic and lexical effects just the beginning of late effects? Differential dynamics such as the ones summarised in box 2 speak against this possibility. Would the late processes just repeat the early ones, or occur only if the early ones are unsuccessful? Here, our own data indicate that the early near-simultaneous processes exhibit surprising specificity to information types, both topographically and in terms of cortical generators, whereas the late ones, e.g. N400, seem equally modulated by different linguistic features<sup>31,41</sup>. Still, are the late components reflections of prolonged specifically linguistic processes or would they rather reflect post-comprehension processes<sup>56</sup> following completed psycholinguistic information access and context integration? And how fixed are the lags anyway? Kutas and colleagues have recently shown that stimulus context can modulate the time lag of brain responses indexing word and object processing<sup>64</sup>. Such context dependence and flexibility is of greatest relevance in the study of cognitive processes and points the way to fruitful future research. The relationship between specific brain area activations on the one hand and specific cognitive processes on the other is one of the most exciting topics in cognitive neuroscience at present. Addressing this issue using MEG/EEG and source localisation has only become possible very recently. If successful, the new available methods will make it possible to read the activation signatures of cortical circuits processing language and concepts in the human brain, therefore propelling the science of behavioral-physiological correlation into a new era.



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### **BOX 1: Modular seriality versus interactive parallelism**

When recognising an object or understanding a word, there is access to long-term memory traces in our brains. In one view, this access process is a chain of subprocesses starting sequentially, with process-onset-asynchronies of hundreds of milliseconds. One postulate has been that phonological and lexico-syntactic features of a word are accessed first (150ms) later followed by semantic access and context integration (400ms). Such serial or cascaded processing is usually attributed to separate processing subcomponents, modules, that each are envisaged to process independently their share of the input information (modular seriality).<sup>3,28,65,66</sup> A serial model with a time scale indexing the time range when after stimulus presentation component processes might occur in the brain, is given on the left in the diagram below.

As an alternative to seriality, different types of information may be accessed in parallel in the perception and recognition process. Upon analysis of the physical features and form of a stimulus or symbol, processing of linguistic-conceptual information, for example phonological, lexical, syntactic and semantic information, does accordingly occur early and at roughly the same time. The idea of parallelism has been connected with that of an interactive system allowing for free information exchange between processing subcomponents (interactive parallelism).<sup>67-70</sup> The figure at the bottom right shows an example of a parallel model of psycholinguistic information access and relates it to time after critical stimulus information is present.

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### **BOX 2: Near-simultaneous early brain-reflections of psycholinguistic information types in word reading.**

Written words that differ in their form, frequency and meaning lead to different brain responses early-on. Variables related to the make-up of the written word form (word length, typicality) tended to become manifest before those of higher cognitive variables were first measurable (word frequency, lexicality, semantics). This supports at least two stages in lexical processing, a form-related process at 100ms and a lexico-semantic process at 150-200ms. The figure at the bottom indicates that these stages can draw upon the same brain areas. The typicality effect at 100ms was localised in posterior inferior-temporal cortex (cf. fusiform visual word form area<sup>71,72</sup>) and the subsequent lexico-semantic effect involved the same area, consistent with its reactivation in lexico-semantic processing<sup>61</sup>.

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### **BOX 3: Near-simultaneous early brain-reflection of psycholinguistic information types in speech comprehension**

On-line speech comprehension processes have been studied using the mismatch negativity, MMN, a brain response to acoustic change detection which also reflects the activation of memory traces in the human brain<sup>42</sup>. Phonological processing became manifest in a modulation of the MMN around 140ms<sup>59</sup> and lexicality was reflected by two sources in superior-temporal and inferior frontal cortex, sparked, respectively, at 136 and 158ms<sup>43,44</sup>. Syntactic violations elicited a syntactic MMN at about the same time, with sources in inferior frontal and superior-temporal cortex<sup>51,53</sup>. Semantic effects were seen at 140-170ms when the same syllables were presented in words that indicated face/arm movements, arm or leg actions<sup>50</sup>. These results are consistent with near-simultaneous early access to different types of psycholinguistic information. Critically, there were fine-grained time lag differences, especially in the semantic domain: Leg-related words (e.g., "kick") activated the central-dorsal sensorimotor leg representation 30ms later than inferior-frontal areas were sparked by face/arm-related words ("eat", "pick"). This shows category-specificity in the temporal structure of semantic brain activation.

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### **BOX 4: Lexicon and semantics at the mechanistic level of cortical circuits**

An integration of neuroimaging results on language and conceptual processing requires a mechanistic theory spelt out in terms of nerve cell circuits. As word learning implies linking spoken word forms to their respective articulatory patterns, the abstract articulatory acoustic pattern of a spoken word form is stored by strongly connected lexical circuits distributed over superior-temporal and inferior-frontal cortex (perisylvian cell assemblies, figure part a). In literate speakers, information about writing gestures and written word forms are bound to spoken word form representations; this binding of knowledge is cortically grounded by a perisylvian cell assembly with a halo extending into hand-related motor and premotor cortex and fusiform gyrus (b). Meaningful words bind, in an arbitrary manner, information about their form and the concepts they refer to. Abstract semantic links may be realised, in part, by the multiple connections between perisylvian cell assemblies and modality-specific semantic circuits in various parts of the cortex, for example in anterior inferior-temporal cortex (animal, colour concepts, figure part c), posterior-inferior and middle temporal cortex (tools, shapes, d), inferior-frontal cortex (face and articulatory actions, e), dorso-lateral fronto-central cortex (arm actions, f), and dorsal central cortex (leg actions, g).

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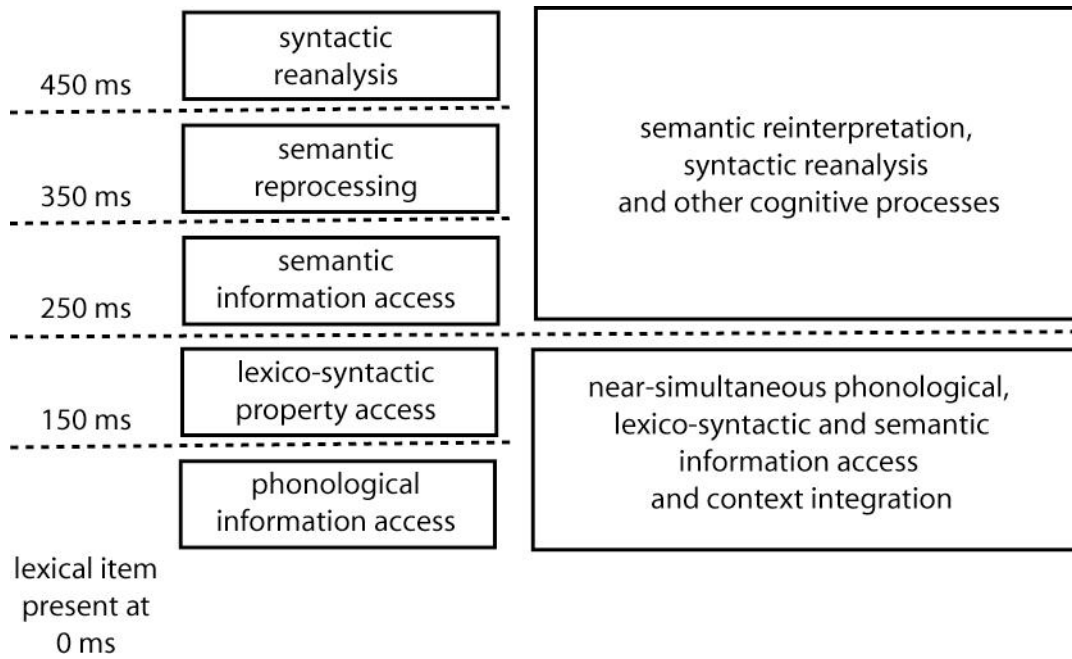


Figure for box 1

### BRAIN INDEXES OF LANGUAGE AND COGNITION

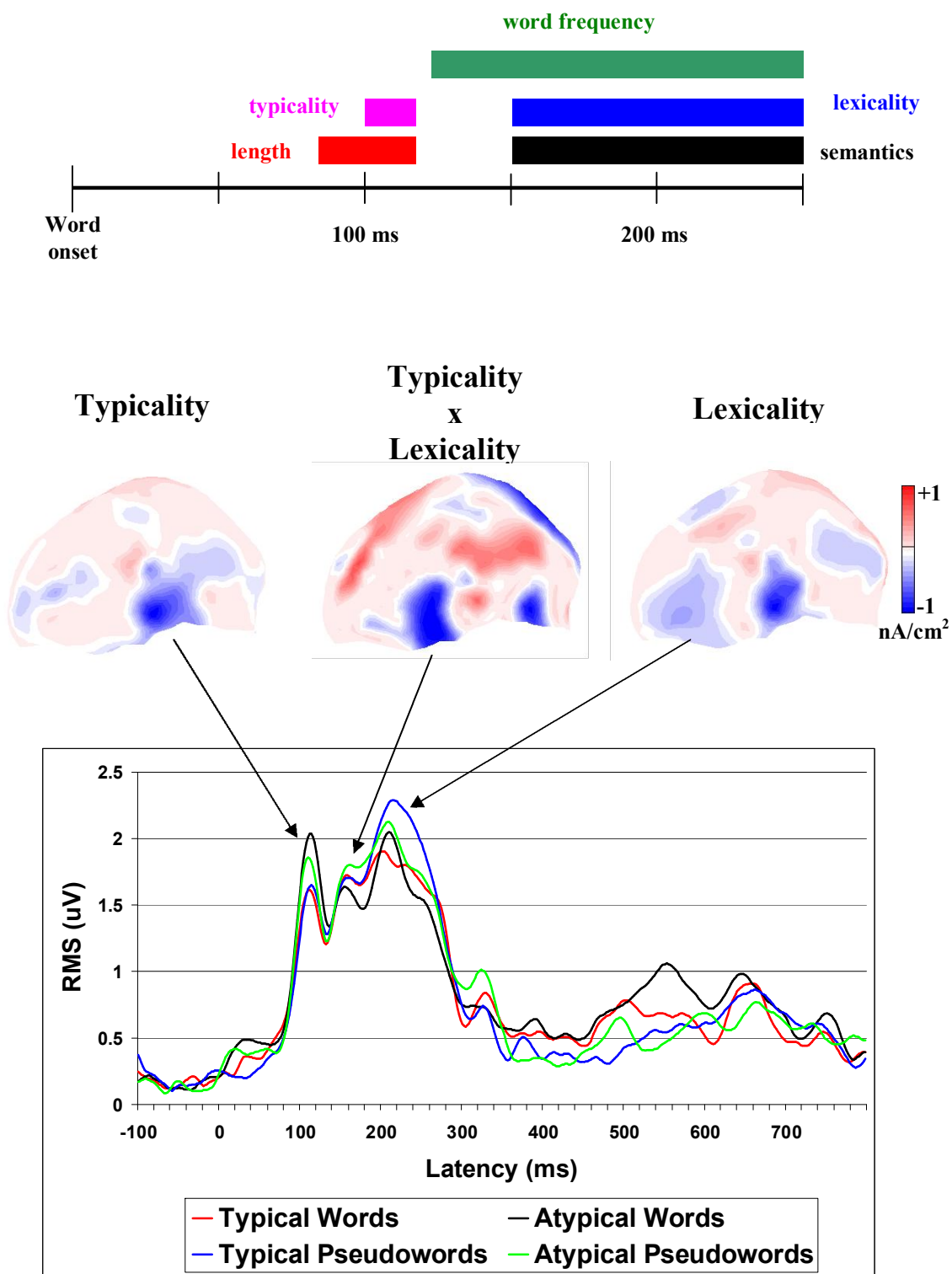


Figure for box 2

## BRAIN INDEXES OF LANGUAGE AND COGNITION

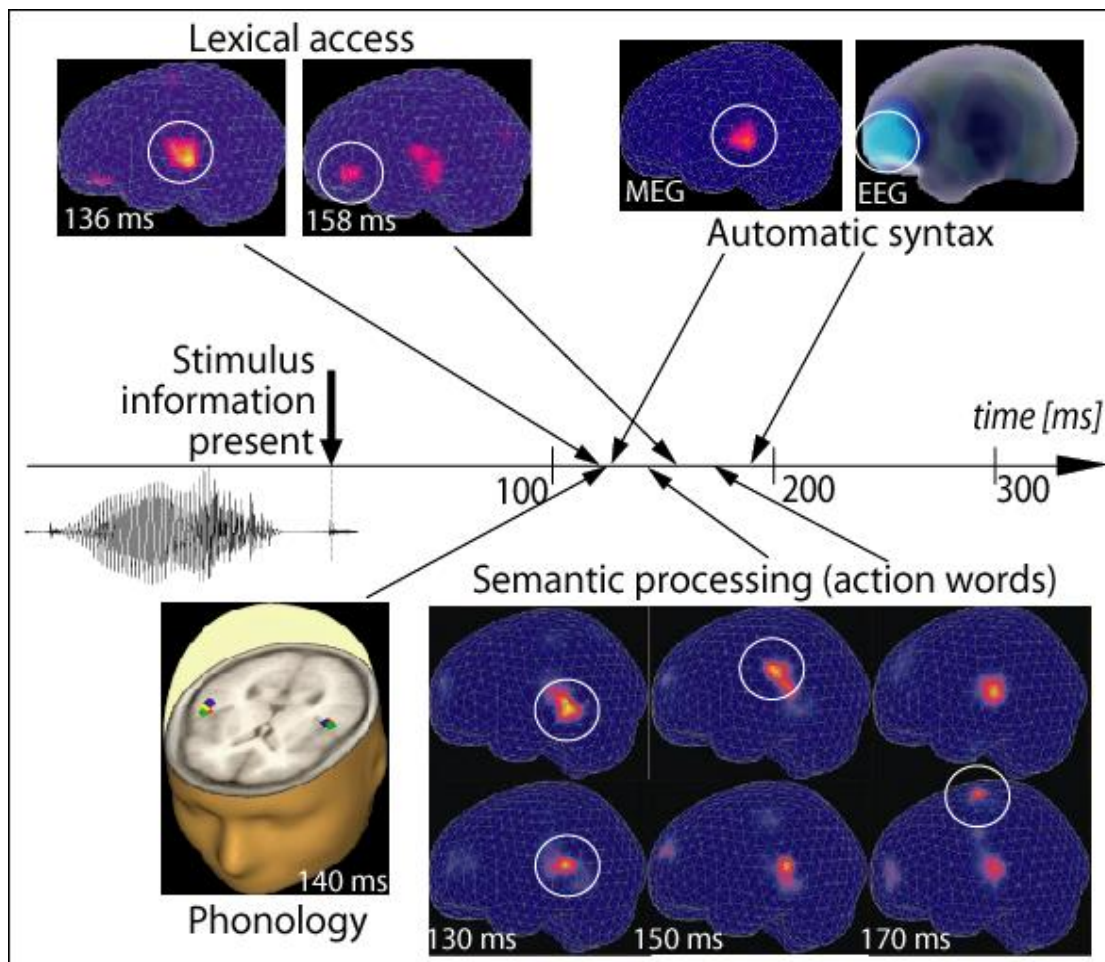


Figure for box 3

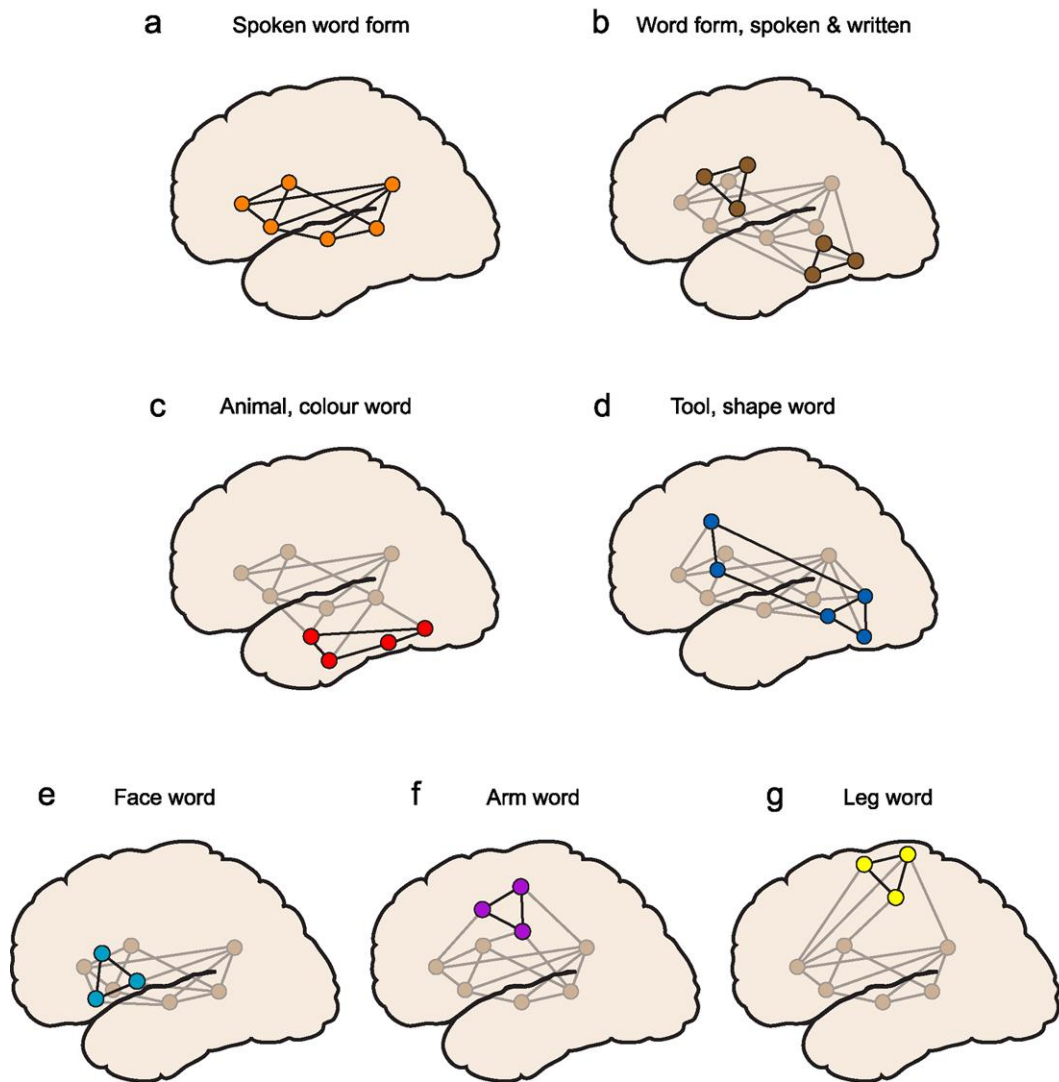
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Figure for box 4