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Models of language comprehension:
N400, P600 and their significance during childhood and beyond

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Introduction

To understand language comprehension, we need to grasp how the brain processes meaning. To understand how the brain processes meaning, we need to explore which language comprehension processes are happening in the so-called "anatomy of language" areas in the brain and pinpoint the order of these processes.

To achieve these goals, we can use brain imaging methods. Moreover, if we want to understand and learn about language comprehension during development, especially infant and early childhood development, our best possible option now are ERP (event-related potential) measurements. ERPs enable us to monitor what is happening in the brain while a sentence is processed, also called an online method. Looking at some of the other available options, functional resonance imaging(fMRI) does not have sufficient temporal resolution and applying magnetoencephalography (MEG) might pose a challenge when working with children. ERPs allow us to follow both the linguistic stimuli while the brain is processing them and thus pinpoint the specific brain activations happening during that time and their order. To get a complete picture of language comprehension, the ERP data and its interpretation would need to be bound to a method that provides brain-location data, like the fMRI method mentioned above. Nevertheless, even before achieving this kind of integrative model of language comprehension, it is possible to theorise solely based on the ERP data itself.

ERPs represent the neural correlates that occur during the processing of certain stimuli. Neural correlates are a specific pattern of brain activity that corresponds with an experience, in this case presumably, language comprehension upon being presented with linguistic stimuli. ERPs are time locked. They can be positive or negative deflections, and we will discuss both kinds in this essay. N400 and P600 are the most researched neural correlates when it comes to language and language comprehension. Interpreting these neural correlates, researchers have been building models of language comprehension. In the last decade, more opinions of what the plausible models incorporating them had emerged. In addition, as I will mention in the later sections of this essay, additional components like the late frontal positivity (or the alpha and theta waves) have appeared in studies that modify the meaning and function of these neural correlates in the models of language comprehension.

Comparing the corpus of studies on adult and infant/early childhood populations concerning ERP data and consequently models of language comprehension, we may find the second somewhat side lacking in data. However, there is a rising body of studies that shed light on how comprehension changes throughout development. Some ERP related research is also aiding the quest of understanding language acquisition. In this essay, I will present how the ERP component measurements change from infanthood to adulthood. Ultimately, this all binds into the larger models of language comprehension that aim to give a unified view, including all the separate ERP components.

The neural correlates of language

The two most prominent neural correlates in the literature researching language comprehension are N400 and P600. However, in the following sections, more than these two neural correlates are featured. Understanding the bigger picture than just these two is crucial to understanding newer models of language comprehension. In this section, I will give a brief introduction to each.

The research about what the neural correlates signify is still ongoing. Newer studies challenge the widespread acceptance that N400 is related exclusively to semantics and P600 to syntax. With this change of paradigm, new models of interpretation have emerged. Diverging opinions still exist, and therefore, it is impossible to give a well-rounded description without raising some debate.

N400 is a neural correlate that is associated with the processing of meaning/semantics. Kutas and Federmeier (2011), in their paper outlining the 30 years of research related to the ERP component, explain that the name comes from recording N400 as relative negativity peaking at 400ms. They go on to clarify that the N400 response doesn't need to be negative per se and that researchers routinely calculate it by point-to-point subtraction from side-by-side comparisons from a baseline ERP (for whatever examined condition). This difference, the N400 effect, "is a monophasic negativity between 200 and 600ms, largest over centro-parietal sites, with a slightly right hemisphere bias." (Kutas and Federmeier, 2011).

N400 is not elicited only after linguistic input. Infant studies show that the action-perception paradigms, in which expectancies of meaningful actions can be violated, elicit infant N400(Junge et al. 2021). Furthermore, N400 is found with sign language and pseudowords (1994, Kutas & Van Petten) and music (Calma-Roddin and Drury, 2020) input. However, it is necessary to keep in mind that the role that N400 has when it comes to language comprehension might not be the same when it comes to other input and modalities.

P600, or the late posterior positivity, is a positive waveform peaking at around 600ms, first discovered in 1992 while inspecting syntactic violations (Osterhout and Holcomb, 1993). In research that followed this initial discovery, different models of language comprehension have assigned different roles and meanings to it, like reanalysis and revision of syntactic structure or difficulty of syntactic integration (Kuperberg, 2007). Nonetheless, the idea that it is related to syntax processing remained in the lead.

Early on, some researchers considered P600 to be part of the P300(P3) group, more specifically, that P600 is related to P3b. In those theories, P600 "reflects a general-purpose response to low-probability target events often associated with some form of categorisation and/or binary decision" (Schacht et al., 2014). However, a large body of research suggests that despite those early assumptions, the P600 response is language-specific, at least in some respects (example: (Friederici, 2011).

The choice of tasks influences P600. In a study that examines precisely that, Schacht et al. (2014) open a great discussion about what role P600 plays in the overall language comprehension framework. I will mention more of this in the model discussion section.

Another neural correlate is the late frontal positivity or late frontally distributed positivity. It is less prominent in the language-specific research than N400 and P600, but it has its place in more recent language comprehension models. The late frontal positivity is maximal at the prefrontal and frontal sites and is a positive response elicited post-N400, between 500–900ms. What differentiates the late frontal positivity from the P600 is the location. P600 is maximal in parietal and occipital sites. DeLong et al. (2011) give a thorough, comprehensive overview of this component in their study.

Lastly, I would like to mention the theta and beta waves. In their study, "one of the first to use time frequency analysis of the EEG to investigate the neural oscillations that underlie language comprehension in children", Schneider and Maguire (2019) feature the theta and beta waves. The theta and beta waves signify possibly more subtle aspects of semantic and syntactic processing. In line with the study, Schneider and Maguire (2019) found that theta increases for semantic errors and beta decreases for grammatical errors are in line with the adult studies(Bastiaansen et al. 2005, 2010). However, the theta and beta waves are not commonly featured in the proposed models of language comprehension. As we can see from this very recent study, data that shows their changes over the course of development is also lacking.

The neural correlates of language throughout childhood development

When comparing the adult and infant/child population, it is evident that there is much less research in the second group. Furthermore, the available findings are rarely integrated into the unified theories of language comprehension.

Different underlying mechanisms/processes may be responsible for language comprehension in children when compared to adults, and they may rely on other parts of the brain for it. As the details in the remaining text of this section will show, the ERP components manifest differently in children. Despite that, there is considerable consistency with adult findings. Understanding how language comprehension differs in children and adults can help us understand language acquisition, the prodigious language learning abilities that children demonstrate and bring us to a better overall understanding of cognition.

In their systematic review of the N400 component for word learning in the first two years of life, Junge et al. (2021) call the N400 the "direct neural index of word meaning". Considering all the previous discussion and the different models we discover in the next section; it may be a bold statement. However, we must remember that when we talk about researching N400 in infants, we talk about the onset of comprehension and language acquisition. The integrative sentence processing models are for this age range are possibly not applicable as such.

Furthermore, Junge et al. (2021) find that the N400 is present in infants, albeit often delayed. They found that the window and distribution of N400 for infants is possibly modulated by age, reaching adult-like presentation with time, usually stabilising around 13 years of age. According to their review, "developmental studies on different sorts of cognitive processing all seem to suggest that while infants display distinct ERP components similar to adults, it is not fully matured." Some critique raised is that infancy might be too short of a period to notice development and that individual differences are of great importance.

The size of the infant's vocabulary is one of the crucial individual differences mentioned in Junge et al. (2021). Their results "suggest that the N400 amplitude increases as a function of vocabulary size when age is held constant." Moreover, although N400 is found in infants for similar tasks like adults, it is not consistently elicited. Interestingly, infants didn't elicit N400 when listening to non-words or pseudowords, unlike adults. Instead, the N200-500 component was registered, connected with the familiarity of the word form. Junge et al. (2021) discuss that the lack of consistency when defining the infant component makes studies hard to compare. The lack of consistency also leads to inconsistencies in recording whether N400 or the N2000-500 was elicited.

Friedrich and Friederici (2004) researched if the mechanisms indexed by N400 are already working during early language acquisition. They found that "both lexical expectations facilitating early phonological processing and mechanisms of semantic priming facilitating integration into semantic context are already present in 19-month-olds." These children were shown images and simultaneously were presented with the corresponding matching or non-matching words acoustically. Supporting the findings in the review discussed above, the individual differences or the child's specific skills were noticeable in the "strength, latency, and hemispheric differences of the semantic incongruity effect". In their view, the existence of N400 at this age shows that the mechanisms that adults use to integrate word meaning into semantic context are already present at this age. Friederici and Friedrich have contributed a wealth of studies that explore language acquisition in infants. The scope of this essay unfortunately too narrow to mention all (for word meanings in infants see: Friedrich and Friederici, 2011, 2017).

When children are above infant age, we can move from word to sentence comprehension level. Strotseva-Feinschmidt et al. (2019) used ERP measurements to check the awareness of the functional meaning of syntactic cues, like case markings in German children aged 2 to 3 years old. The results confirmed their thesis that this awareness happens somewhere between 2 and 3 years old. 2-year-olds were unable to correctly interpret accusative, case-marked, object-first structures at an above-chance level. Although children start to use syntactic strategies around this age, they still rely on the lexico-semantic features even if they are not their main drive for their interpretation. If we look at the ERP data from the study in a "rawer" analysis, we can see that although some of the tasks elicit adult-like components, they are neither the same in characteristics nor are always found in the matching brain locations. These results are in line with the studies presented above and speak of a maturing comprehension system.

It seems that the youngest, although differently manifested, already show some adult-like semantic and syntax processing and integration. What if we continue to follow the development, does this change for older children?

The study by Schneider and Maguire (2019) examined 8/9-year-olds and 12/13-year-olds and the correlates elicitation during language comprehension. Their findings show that the neural correlates related to semantic processing (like N400) reach adult-like levels at a younger age when compared to the syntax related correlates (like P600). Furthermore, they underline that they are the first study to show that "the semantic processes necessary to comprehend complex, natural auditory speech are still developing late into childhood." Comparing the study results, one can notice continual improvement stemming from the younger group of children to the older group and eventually the adult baseline. Another interesting observation is that the P600 has a different, frontally distributed effect in children. In their view, this means that the children process the syntactic error differently than the adults and "the ongoing localisation changes underline syntactic development." An older study by Atchley et al. (2006) supports these results as well. They examined 8-13-year-olds and found that while N400 reached adult-like presentation, P600 differed.

According to these studies, syntactic processing takes longer to mature and reach adult-like levels. Additionally, the semantic-related ERP components show maturity around 13 years of age already. Looking over from infanthood over to young children and teens, we see that the intensity, speed and location of the ERP components change continuously. However, there is an interesting question that remains. When does development stop? Do the components change and develop beyond the adult-like manifestations?

A study examined the N400 component over six decades (Kutas and Petten. 1998). The participants were aged 20-80 years old. The findings showed that as people progress into adulthood, the N400 weakened and got delayed. As possible reasons for these demonstrated changes, the authors mention the reduced working memory capacity, less efficient inhibitory mechanisms and slowed processing as documented issues. Some other explanations offered were the size of the semantic memory and its interconnectedness hindering easy access. The more difficult access, together with the ageing effects mentioned in the previous sentence, possibly leads to poorer integration thus poorer N400.

All these studies interpret the findings through some model of language comprehension. To put the component results in context, we must make assumptions about what they signify. Traditionally, N400 and P600 were thought to process semantic/meaning and syntax, respectively. More recent research has questioned this explicit division and has introduced more subtle interpretations. I will discuss some of these findings in the next section. Improving the language comprehension models for adults will also bring value to the study of language acquisition, as the early language development can then be put in a starker, more realistic context.

Models of language comprehension

Studies in the last decade have been taking the interpretation of the N400 and P600 beyond the semantic-syntactic division, giving rise to more complex language comprehension models. Moreover, besides the dynamic meaning of the elicited main components, the late frontal positivity and the theta and beta waves have been added to these unifying interpretations.

Discussing and re-evaluating the models of language comprehension is very important from the developmental perspective too. Currently, the studies take the adult-like responses as the baseline, surrounding them with the context of the existing leading models. The tasks confirm or negate these model assumptions and are then scaled to infant/child level or modified to fit. In the previous section, we learned that the ERP components manifest differently in children. A better understanding of the adult-like processing could boost the search for pinpointing the exact times of any emerging language skills, as well as measuring their impact.

The "Semantic illusion" sentences are a great point to start the discussion about the role of the language-specific neural correlates. These sentences are semantically anomalous, but instead of an N400 response, they elicit a P600/"semantic P600". The "Semantic illusion" refers to these findings in the related literature (some examples: Kolk et al., 2003; Kuperberg et al., 2003). These sentences puzzle researchers and are not compatible with the older models of language comprehension.

Originally, N400 was thought to signify semantic integration processes (Kutas and Federmeier, 2011). We can elicit N400 after presenting a person with a surprising/incongruous word that doesn't fit with the context presented until that point. On the other hand, P600 was thought to signify syntactic reanalysis or repair (DeLong et al., 2014). Unlike the semantic context like N400, P600 is sensitive to syntactic violations.

In semantic illusion sentences, the N400 effect is absent (or attenuated) to semantically incongruous or anomalous words (Kuperberg 2007). Instead, there is a P600 component. In this case, it seems that the P600 is somehow performing a semantic function. It is still an ongoing question as to why and research groups differ in their explanations. Their findings give fascinating insights into how humans might be processing language comprehension.

DeLong et al. (2014) and Schacht et al. (2014) have conducted intriguing studies that expand the original assumptions about N400 and P600.

In the study by Schacht et al. (2014), the researchers question how the tasks performed impact the P600 response. They examine the semantic and the syntactic P600 response. Their findings show that both P600 and their combination are diminished when the word relationships are irrelevant for the task. In their view, this suggests that, independently of the nature of P600 being syntactic or reflecting general-purpose processes (being part of the P300 group), the underlying processes are dependent and non-automatic. Furthermore, they found that while the semantic P600 depends on central attention and is open to external information, the syntactic P600 is more robust.

The study by DeLong et al. (2014) also gives some ideas about the role of P600 and N400. They also prominently feature the "late frontal positivity" mentioned in the section above. It is important to note that they examined written sentence comprehension. In their findings, this third component is elicited by lexically unexpected words, but only if they are plausible continuations. Moreover, they "speculate that this frontal positivity may relate to a necessary suppression of mental representations arising from pre-activation of highly probable but not presented sentence continuations, when a plausible alternative is encountered". In that sense, (the incongruous) plausible and unlikely endings are disparately processed, engage different brain regions and have partially overlapping temporal dynamics.

Many studies centre on different questions, like autonomy or plausibility, and thus push the boundaries of our understanding of what the language-specific components signify. The studies above are just examples (see Kutas and Federmeier (2011) for a comprehensive historical overview).

The goal of this section was to show that our understanding of the components is a work in progress. Before finishing, I would like to add at least one of the very recent attempts of unifying the correlates into a model of language comprehension.

Kuperberg et al. (2020) propose a generative framework of language comprehension. In this framework, comprehension is hierarchical, propagated through layers (situation model, event structure, semantic features). A higher-level change will be usually small, and changes will accumulate over time. Some situations will induce a more significant and sudden change, thus more detectable. What does this type of organisation mean for the individual components and their role?

In the view of Kuperberg et al. (2020), their generative framework is designed to make the debate if N400 reflects lexical access or integration obsolete. In their view, comprehenders can "use their situation model to predict event structures and their associated semantic features, even when these predictions do not correspond to the pre-activation of specific individual lexical items". In other words, when a comprehender creates a situation model, this model can include items that were not yet lexically included till that point. When the comprehender encounters another word, and its semantic and syntactic features are already consistent with the previous context, very little work is needed to integrate it. In the other case, when a word strongly violates the previous context and predictions, we would expect an N400 effect. They also address the plausibility that DeLong et al. (2014) centred. In their view, the changes in animacy (when unexpected), for example, trigger changes in the event layer instead since the broader picture need to be updated.

For the late frontal positivity, it is believed that it reflects either inhibition of the expected word continuations or the re-integration process. In their framework, these processes happen simultaneously, and there is no separation. Lastly, they address the late posterior positivity(P600). In the study by DeLong et al. (2014), we learned that contrasting the late frontal positivity reflects incongruous but plausible words, while P600 reflects the incongruous and impossible. Other researchers have had slightly different interpretations, but the consensus is that there must be conflict "between alternative representations that are computed during language comprehension" (more: Kuperberg, 2007). In their framework, P600's main task is to detect this conflict. When it comes to the underlying processes, they mention detection of high-level conflict, repeated making sense of the new input (reanalysis and/or repair) or a revised interpretation. They, however, make no confident claims for P600. The researchers mention that P600 might be very well connected to P300, as many studies discussed above have proposed.

The above-presented research in this section is only an example of the differing opinions and newest ideas about the possible models of language comprehension, and thus the meaning of the language-specific neural correlates. There are more competing theories and quality assumptions in literature.

Conclusion

Understanding how the brain processes language comprehension is an ongoing research topic. The language-specific neural correlates and EPR analysis are helping researchers understand it better. Different models interpret the ERP components differently. That sparks multiple views of what underlying processes they represent and in what order they take place. Furthermore, grounding these processes in the physical language centres in the brain is necessary.

The same analysis in children helps us understand the developmental trajectory of language comprehension, its onset and ultimately, complete language acquisition. The infant/child ERP research available tells us that when we speak of maturing, developing systems that differ from the ones found in adults in many ways. However, a lot of the ERP responses seem to be consistent with the adult ones too. In the youngest, we move from comprehending words and wordforms to phrases and, lastly, sentences. We expect that the processes behind comprehension at that age will be different.

It is necessary to relate the infant and child findings to the adult ones. With the growing efforts of building better models of language comprehension for adults, we will be able to interpret the early life results more successfully. With the constantly improving rate of neuroimaging technology, exciting decades are upon us for language acquisition research.

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