Wherefore art thou N400?

Ellen Lau - Linguistics

A cortical network for semantics: (de)constructing the N400

Ellen F. Lau, Colin Phillips*‡ and David Poeppel*‡§||*

Abstract | Measuring event-related potentials (ERPs) has been fundamental to our understanding of how language is encoded in the brain. One particular ERP response, the N400 response, has been especially influential as an index of lexical and semantic processing. However, there remains a lack of consensus on the interpretation of this component. Resolving this issue has important consequences for neural models of language comprehension. Here we show that evidence bearing on where the N400 response is generated provides key insights into what it reflects. A neuroanatomical model of semantic processing is used as a guide to interpret the pattern of activated regions in functional MRI, magnetoencephalography and intracranial recordings that are associated with contextual semantic manipulations that lead to N400 effects.

And now

- What is interpretation, and how can neuroscientists study it?
  - Mental particulars
  - Acquiring long-term knowledge

2003:

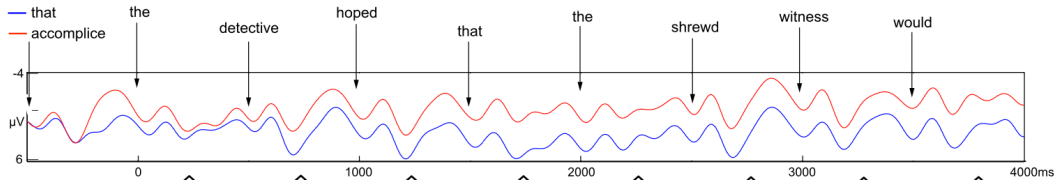
What about the brain is such that human language is the way it is?

2005:

My kingdom for a reliable neural measure of syntactic computation…

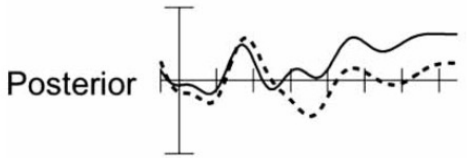
ERP effects of the processing of syntactic long-distance dependencies

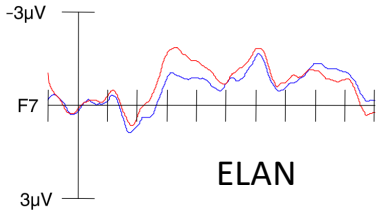
Colin Phillips[a,b,*], Nina Kazanina[a], Shani H. Abada[c]



The linguistic processes underlying the P600

Ana C. Gouvea, Colin Phillips, Nina Kazanina & David Poeppel



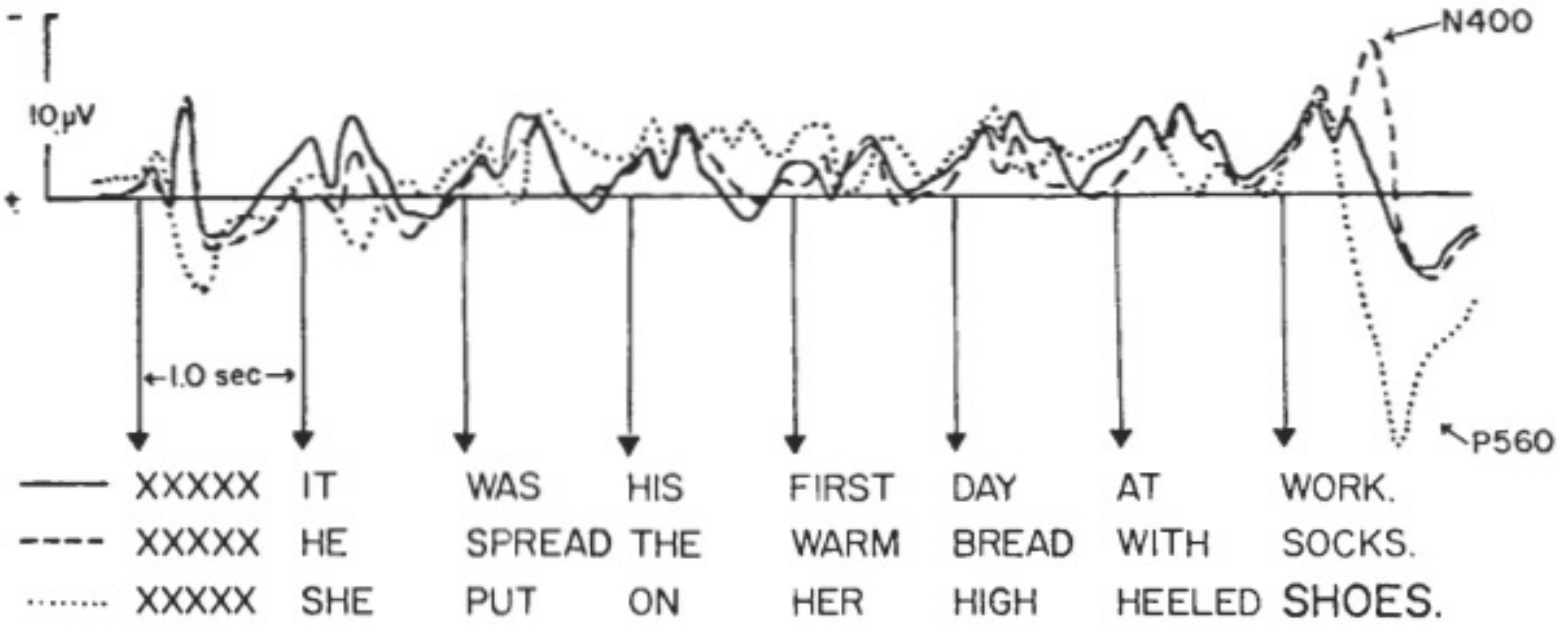


The role of structural prediction in rapid syntactic analysis

Ellen Lau, Clare Stroud, Silke Plesch, Colin Phillips *

Reading Senseless Sentences: Brain Potentials Reflect Semantic Incongruity

MARTA KUTAS
STEVEN A. HILLYARD
Department of Neurosciences,
University of California, San Diego,
La Jolla 92093



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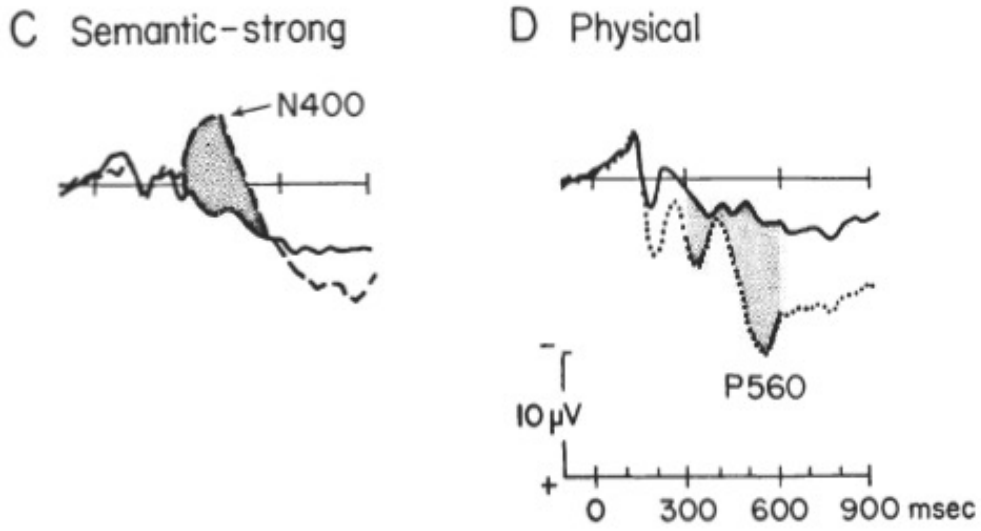
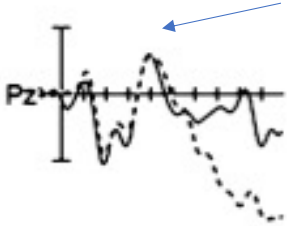


Does lack of N400 effect mean you didn't compute the implausibility?

Semantic incongruity...but no N400!



— **Passive Control**

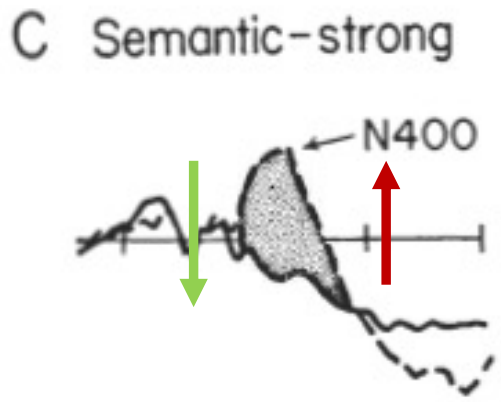
The hearty meal was devoured ...

----- **Violation**

The hearty meal was devouring ...

Lee & Osterhout 2005

N400: Anomaly boggle, or primed facilitation?



IT	WAS	HIS	FIRST	DAY	AT	WORK.
HE	SPREAD	THE	WARM	BREAD	WITH	SOCKS.

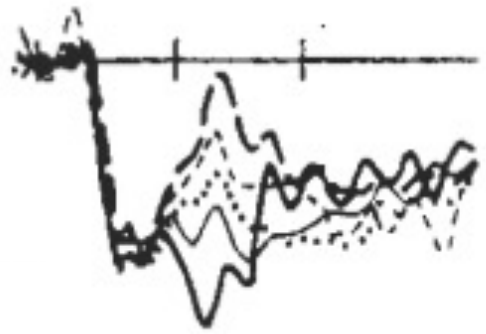
Brain potentials during reading reflect word expectancy and semantic association

Marta Kutas & Steven A. Hillyard

Department of Neurosciences, M-008, University of California, La Jolla, California 92093, USA

1984: N400 modulated by predictability in congruous sentences

Kutas & Hillyard, 1984



------	lo/hi	There was nothing wrong with the car.
.....	med/med	Too many men are out of jobs.
——	med/hi	She locked the valuables in the safe.
——	hi/hi	He mailed the letter without a stamp.

Van Petten, 1991; Federmeier & Kutas, 1999; Federmeier et al., 2007

Brain potentials during reading reflect word expectancy and semantic association

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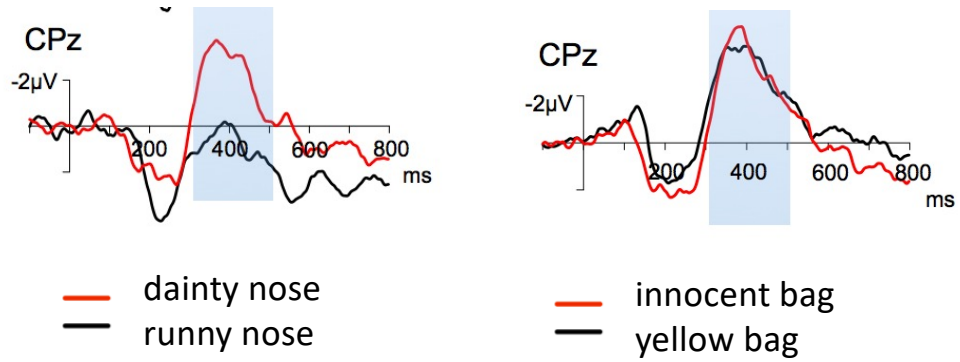
'These findings suggest N400 may reflect processes of semantic priming or activation'

N400: Anomaly boggle, or primed facilitation?

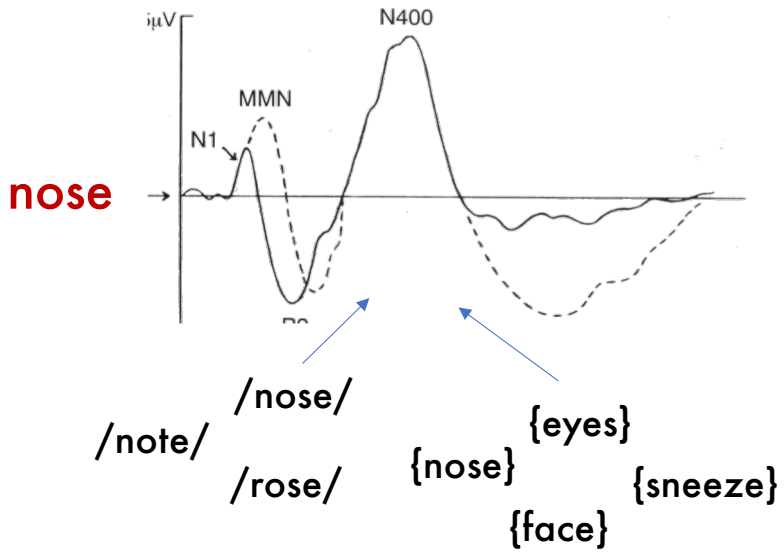
N400 often actually more sensitive to lexical-semantic predictability than to meaning anomaly



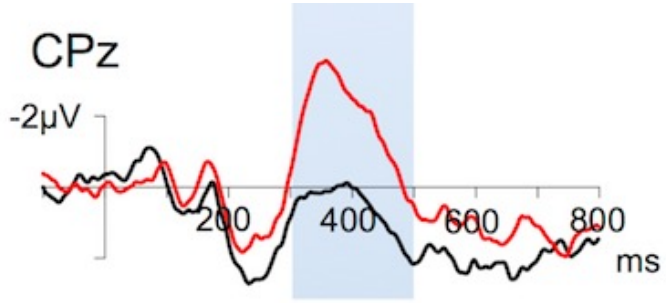
Lau, Namyst, Fogel & Delgado, 2016

N400 *linking hypothesis*

- the N400 response to a word out of context reflects the activation of a neighborhood of concepts and words (Laszlo & Federmeier, Holcomb et al. 2002)



N400 *linking hypothesis* – **pre-activation**



runny nose (highly predicted)

dainty nose (not predicted)

- If the word/concept was predictively activated by context, then when it is presented, these irrelevant neighbors will be rapidly suppressed, resulting in N400 reduction

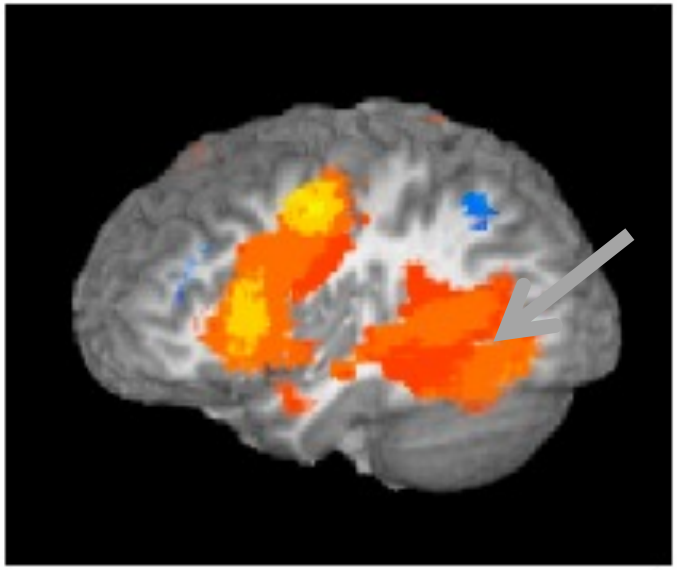
Lau, Namyst, Fogel & Delgado, 2016

A cortical network for semantics: (de)constructing the N400

Ellen F. Lau, Colin Phillips*‡ and David Poeppel*‡§||*

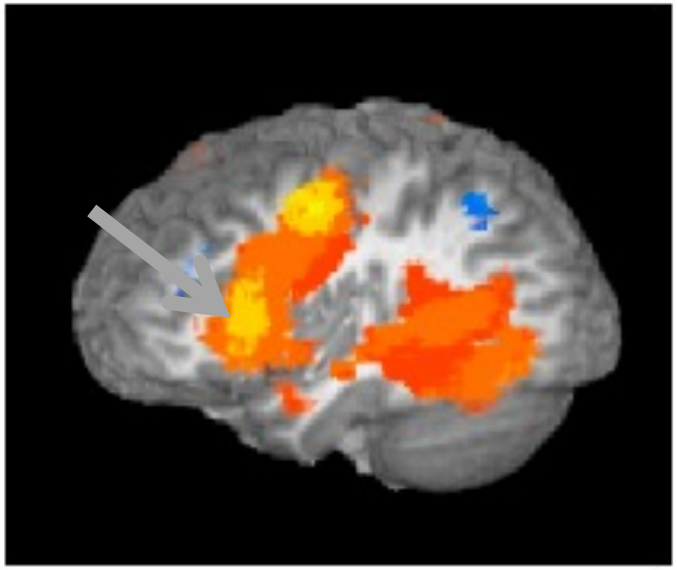
Abstract | Measuring event-related potentials (ERPs) has been fundamental to our understanding of how language is encoded in the brain. One particular ERP response, the N400 response, has been especially influential as an index of lexical and semantic processing. However, there remains a lack of consensus on the interpretation of this component. Resolving this issue has important consequences for neural models of language comprehension. Here we show that evidence bearing on where the N400 response is generated provides key insights into what it reflects. A neuroanatomical model of semantic processing is used as a guide to interpret the pattern of activated regions in functional MRI, magnetoencephalography and intracranial recordings that are associated with contextual semantic manipulations that lead to N400 effects.

Localizing Predictive Access



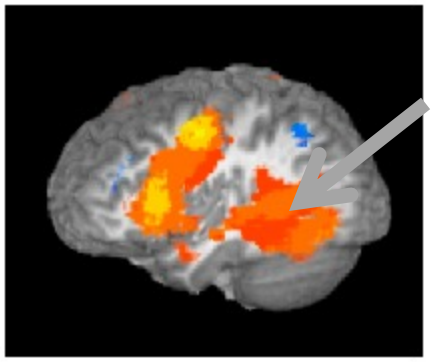
- Left **posterior temporal** cortex is associated with long-term storage of lexical-conceptual information

Localizing Predictive Access



- Left **inferior frontal** cortex associated with a lot of higher-level computations

Localizing Predictive Access



Refs	Modality	Task	SOA	IFG			IT	MTG		
				BA47	BA45	BA44	BA37	BA21		
Short-SOA studies										
177	V	Lexical decision	33					✓		
54*	V	Lexical decision	150				✓	✓		
128*	V	Lexical decision	200							
54*	V	Lexical decision	250				✓	✓		
178*	V	Naming target	250				✓			
Long-SOA studies										
131*	V	Lexical decision	600	✓	✓					
92	A	Lexical decision	600					✓	✓	
179	A	Lexical decision	650		✓	✓			✓	
180	A	Lexical decision	750		✓			✓	✓	
181	V	Relatedness	800	✓	✓			✓		
54*	V	Lexical decision	1,000	✓	✓	✓		✓		
54*	V	Lexical decision	1,000	✓	✓	✓		✓		
128*	V	Lexical decision	1,000							✓

Lau, Phillips, & Poeppel, 2008 Nat. Rev. Neurosci.

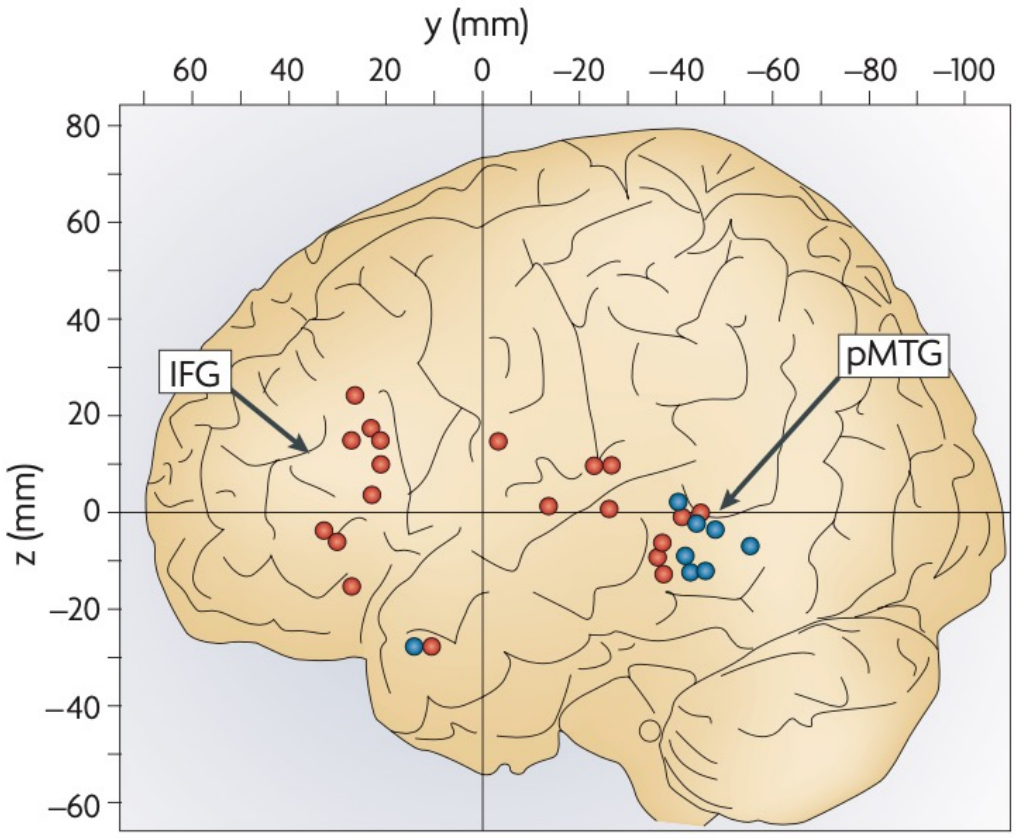


Figure 3 | **A visual summary of the results of semantic- priming manipulations in functional MRI.**

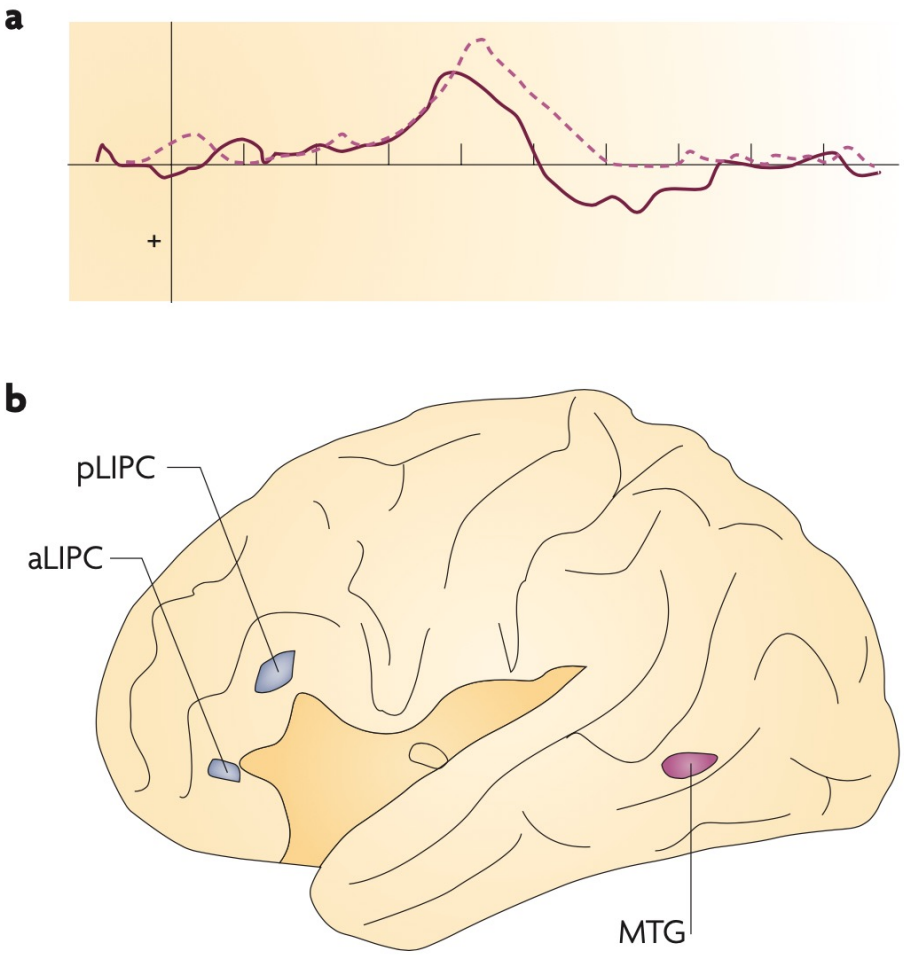
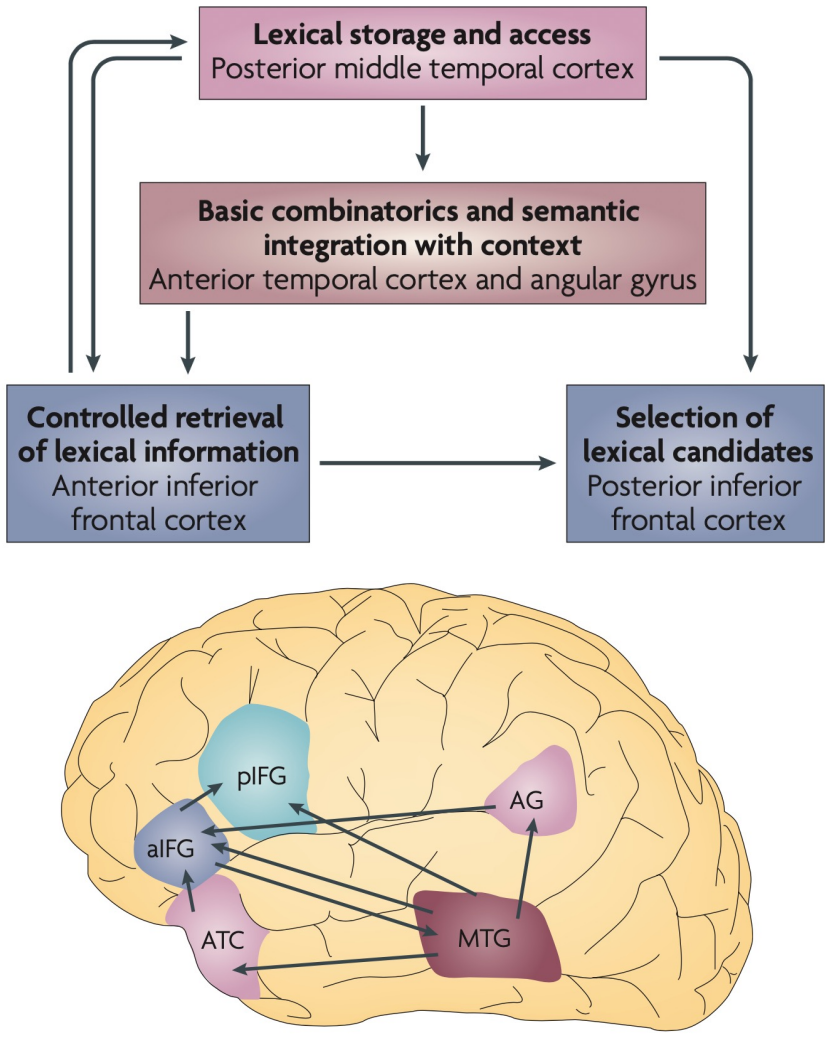


Figure 4 | **Semantic priming at short and long SOAs.**



The data reviewed here support the framework for semantic processing that is presented in FIG. 5. Amodal lexical representations, linked to distributed semantic representations throughout the cortex, are stored and activated in the posterior middle temporal cortex and in parts of the neighbouring STS and IT. These representations are more easily accessed in predictive or priming contexts, leading to a reduction of activation that is reflected in the N400 effect and in corresponding BOLD signal reductions. During sentence processing, these lexical representations are accessed by the anterior temporal cortex and angular gyrus, which integrate the current input into the semantic and syntactic context that is under construction. The anterior inferior frontal cortex mediates top-down controlled semantic retrieval of lexical representations, which is partially based on the updated representation of the global semantic structure that is provided by integration areas. This top-down retrieval facilitates lexical access, indirectly contributing to a reduction in MTG activity. The posterior inferior frontal cortex mediates selection among highly activated lexical representations, partially based on the current global semantic representation.

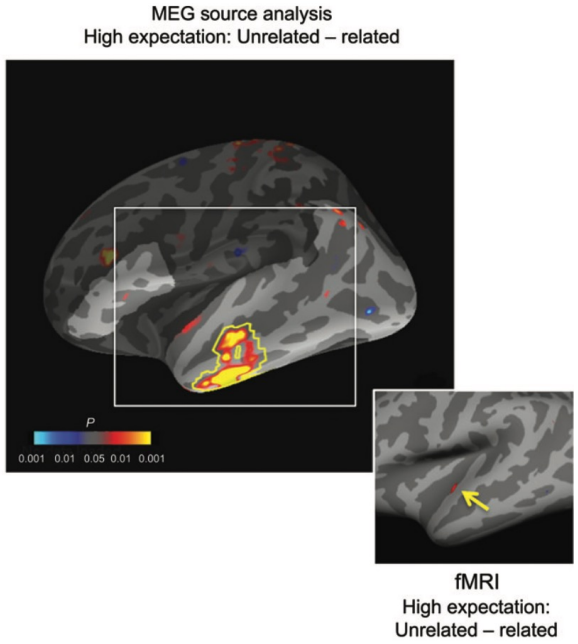
What made this paper resonate?

- Putting ERP and neuroimaging literatures in conversation
- Honesty about particular blindnesses of each method and why they wouldn't converge perfectly
- A simple, clear linking hypothesis from cognitive mechanism to neural measure

- And prediction just happened to be getting really, really hot!

What I did next

- Lots of MEG/fMRI work on N400 localization



Automatic Semantic Facilitation in Anterior Temporal Cortex Revealed through Multimodal Neuroimaging

Ellen F. Lau,[1,3,4] Alexandre Gramfort,[2,5] Matti S. Hämäläinen,[2,6] and Gina R. Kuperberg[1,4]

Spatiotemporal Signatures of Lexical–Semantic Prediction

Ellen F. Lau[1,3,4], Kirsten Weber[1,4], Alexandre Gramfort[2,5], Matti S. Hämäläinen[2,6] and Gina R. Kuperberg[1,4]

Short communication

fMRI evidence that left posterior temporal cortex contributes to N400 effects of predictability independent of congruity

Ellen F. Lau[a,*], Anna Namyst[a,b]

What I did next

- Using N400 effect as a 'tool' to see whether readers had computed all the implications of the linguistic context on lexical likelihood

A "bag-of-arguments" mechanism for initial verb predictions

Wing-Yee Chow[a,b], Cybelle Smith[a,c], Ellen Lau[a] and Colin Phillips[a]

Antecedent access mechanisms in pronoun processing: evidence from the N400

Sol Lago [a], Anna Namyst [b], Lena A. Jäger [a] and Ellen Lau[b]

Enough time to get results? An ERP investigation of prediction with complex events

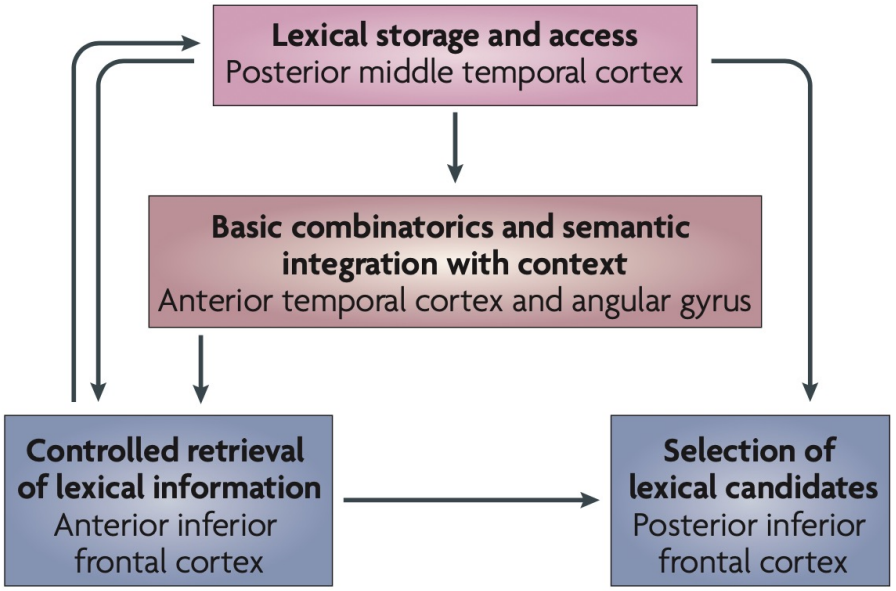
Chia-Hsuan Liao and Ellen Lau

Re-vision today

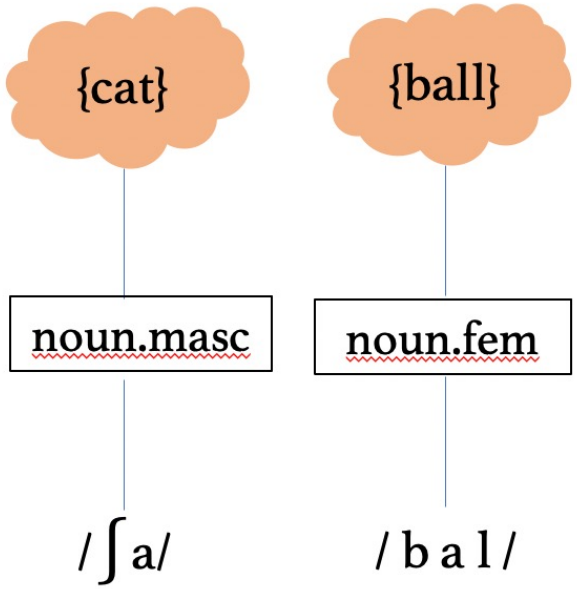
- 15 years later, what was wrong with my foundational assumptions?

What is ‘lexical access’, and what is a lexical item?

These data strongly suggest that at least some substantial part of the N400 effect reflects facilitated lexical access, and thus that the N400 effect cannot be attributed only to post-access processes. These data do not provide any conclusive evidence to support the integration account of the N400 effect, but they also do not rule out the possibility that the effect reflects a combination of



What is ‘lexical access’, and what is a lexical item?



What is ‘lexical access’, and what is a lexical item?

Nanualutsiutunga

nanu	-alut	-siu	-tu	-nga
bear	-big/terrible	-look.for	-INDI	-1sg

‘I am looking for a big bear.’

Beach (2012)

The alarm went off

Báicài → cabbage

white vegetable

Tu m’as vu

Haspelmath, 2017

What is interpretation?

What is interpretation?

- Is it successfully '**activating**' the concepts that correspond to the wordforms?

- This description leaves out the computational goals. What is the activation in service of? What larger process would concept activation be a step in?

What is interpretation?

- Is it **conceptual combination**, a representation of relations between concepts that allows deductions and inferences?

What is interpretation?

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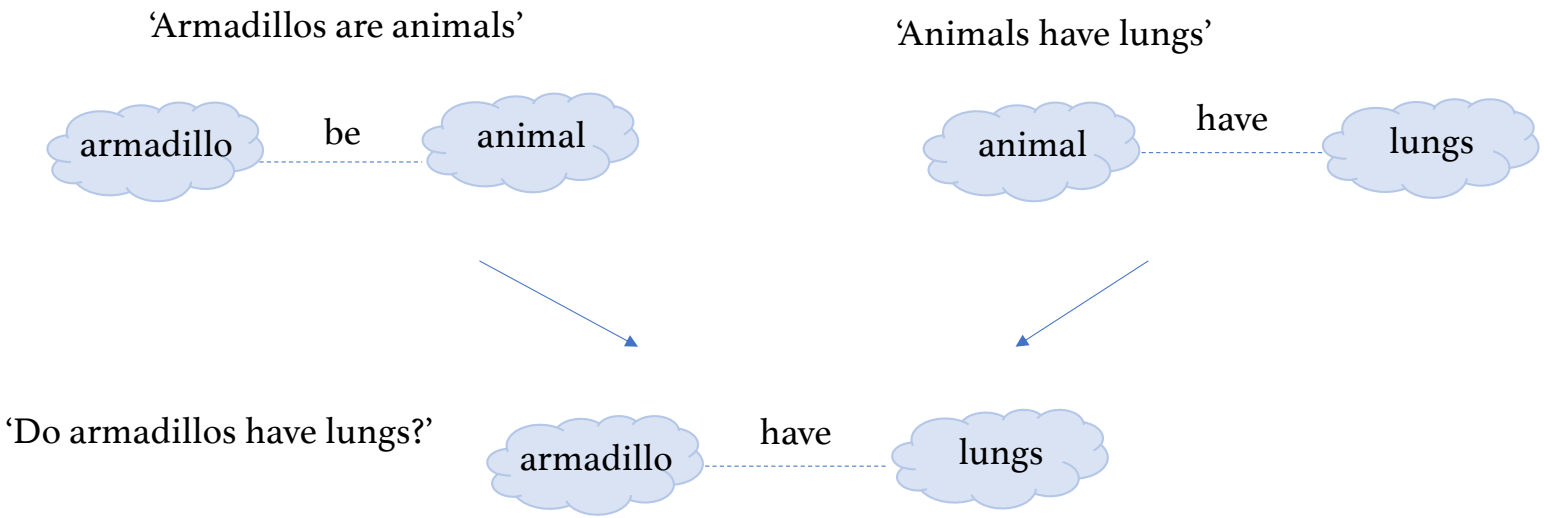


What is interpretation?

- Is it **conceptual combination**, a representation of relations between concepts that allows deductions and inferences?

- Yes, but…

What is interpretation?

- Not just general concepts…but also **mental particulars**
- Not just deductions/inferences on current context…but also **acquiring long-term knowledge**

What is interpretation?

- **Mental particulars**
- **Acquiring long-term knowledge**

Non-linguistic concepts

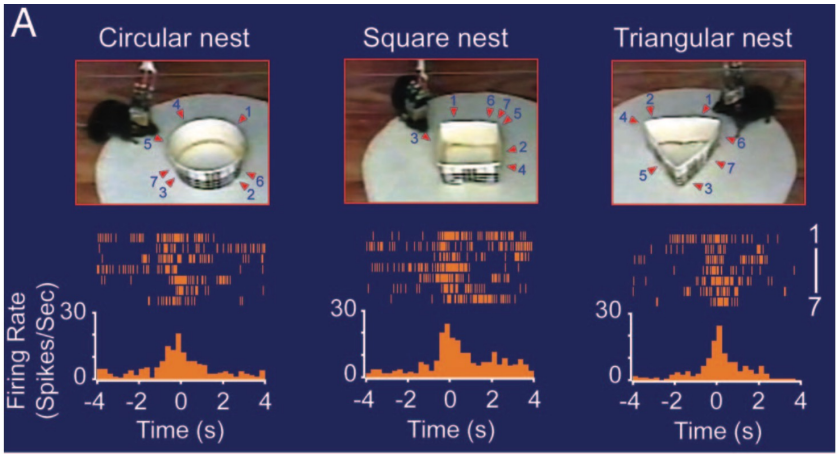
- Let's think about the non-linguistic cognition that our ancestors and other non-linguistic animals have for representing the world

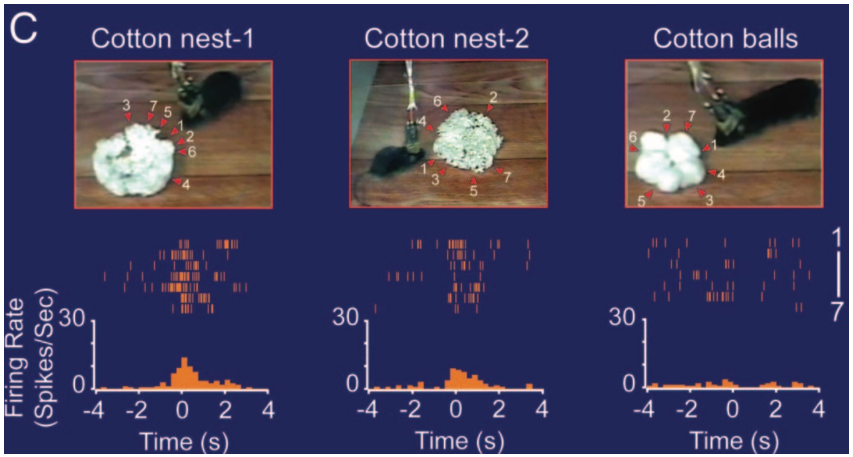
- These organisms surely have lots of mental representations that stand for general properties of stuff in the world, like 'dangerous', 'red', 'wet', 'shelter', and can participate in a variety of computations—what arguably qualify as **concepts**

Fitch, 2019; Gallistel, 2011

Neural encoding of the concept of nest in the mouse brain

Longnian Lin*†‡, Guifen Chen†, Hui Kuang†, Dong Wang*, and Joe Z. Tsien*†‡





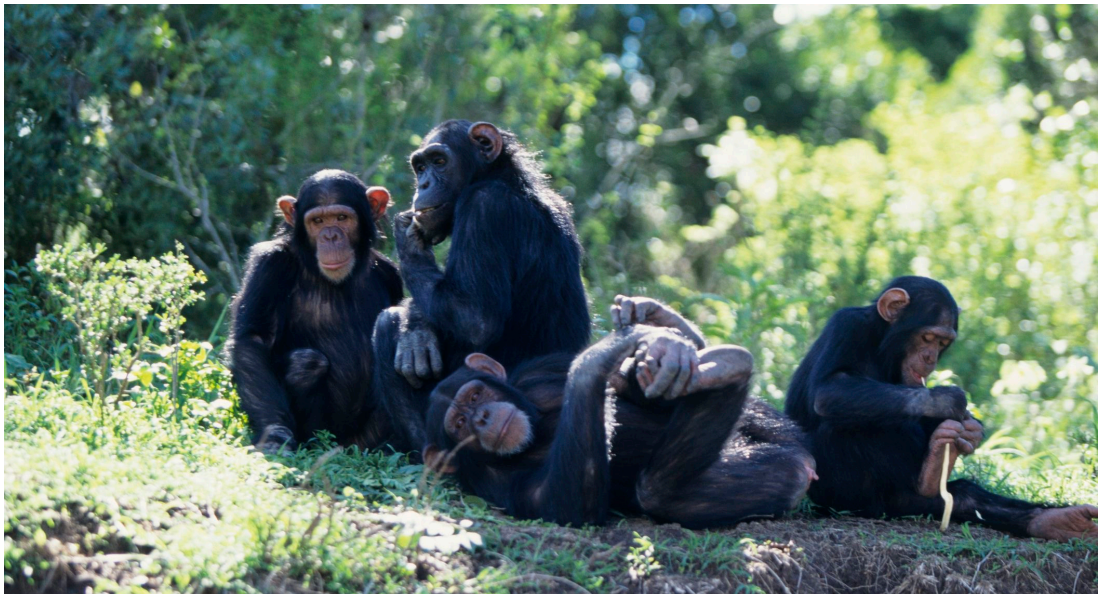
Fitch, 2019; Gallistel, 2011

Mental particulars

- But humans and many other social animals also have mental representations that stand in for particular instances

Mental particulars

- Conspecific representations for complex social interactions

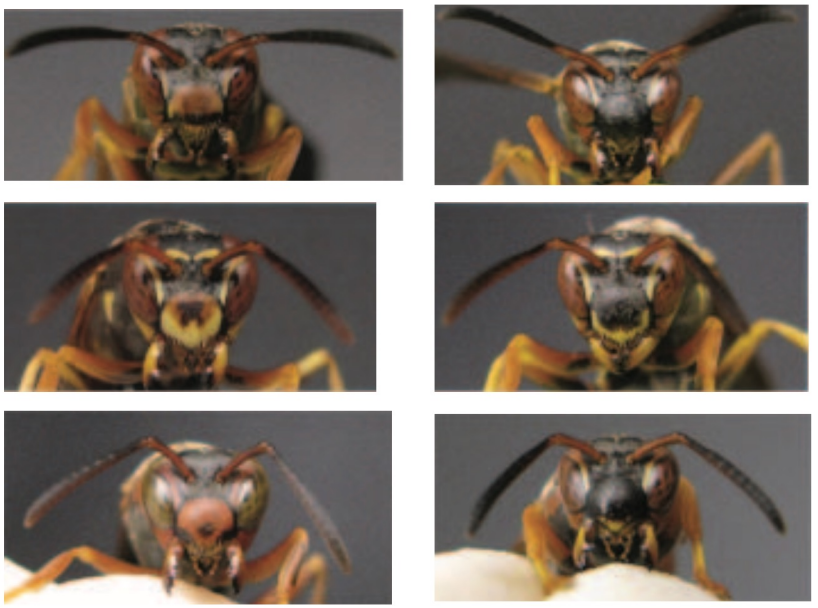


Mental particulars

- Conspecific representations for social interactions

Specialized Face Learning Is Associated with Individual Recognition in Paper Wasps

Michael J. Sheehan* and Elizabeth A. Tibbetts

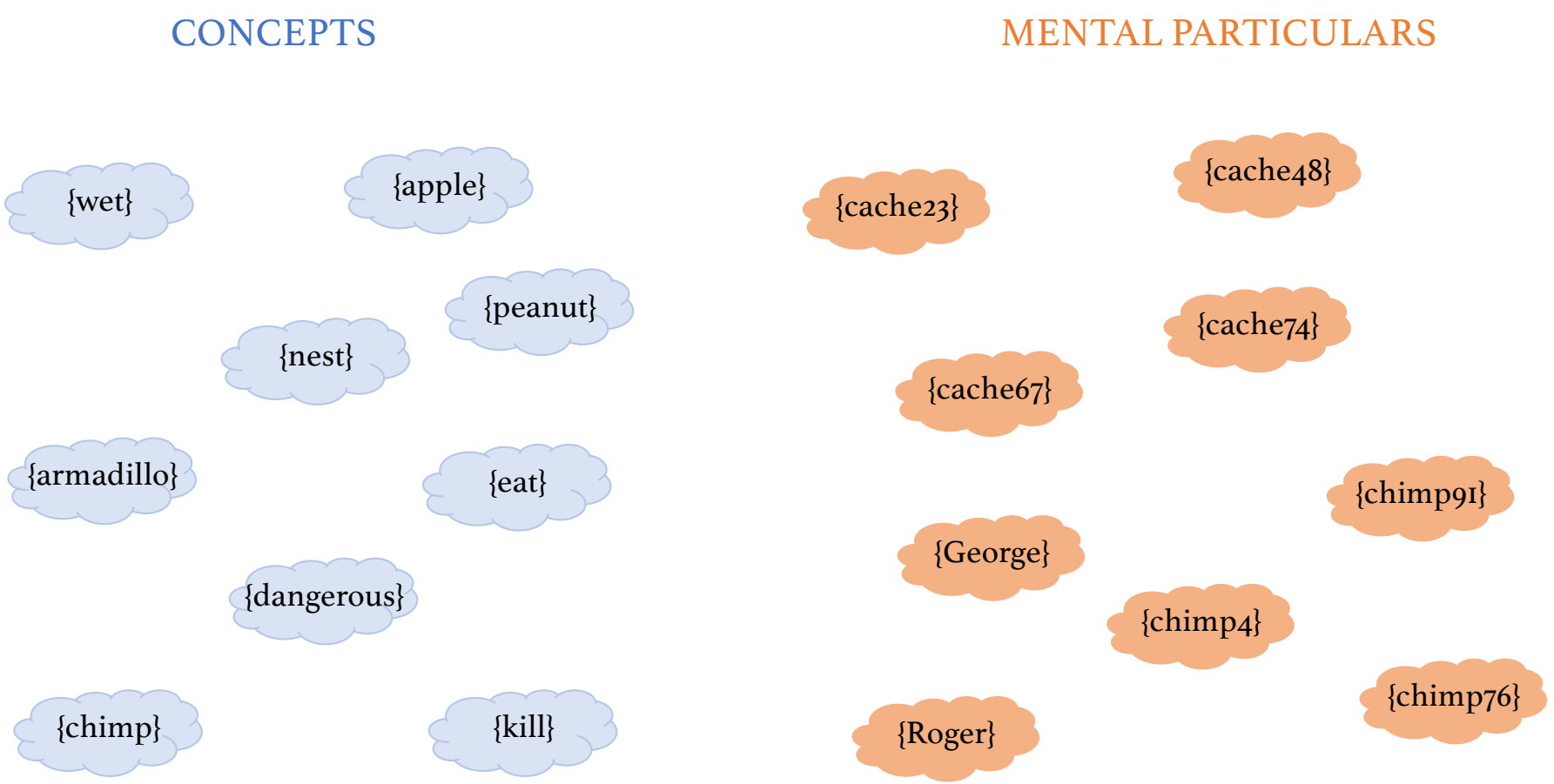


See Tibbetts & Dale, 2007 for cross-species review

Mental particulars

- Another kind of particular is locations, as in animals who hide food and can remember the *kind* of food they hid in each particular cache, among hundreds

Clayton & Dickinson, 1998


CONCEPTS
{wet}
{apple}
{peanut}
{nest}
{armadillo}
{eat}
{dangerous}
{chimp}
{kill}
MENTAL PARTICULARS
{cache23}
{cache48}
{cache74}
{cache67}
{chimp91}
{George}
{chimp4}
{chimp76}
{Roger}

Mental particulars

- We can get a little tangled up sometimes in thinking about the distinction between concepts and mental particulars
  - Couldn't you have a general concept that just happens to apply to one thing in the world, like {Pinta-Island-tortoise}?

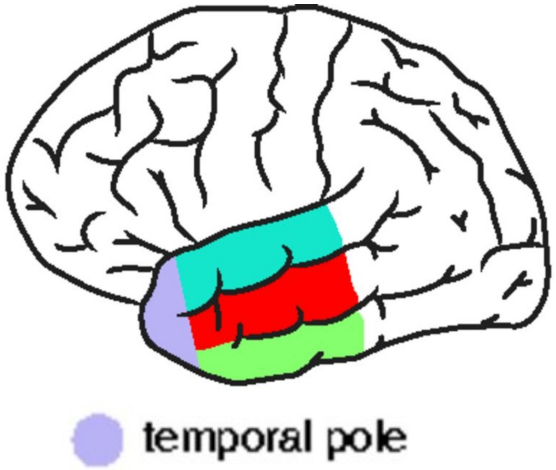
'Lonesome George'
1910-2012

Mental particulars

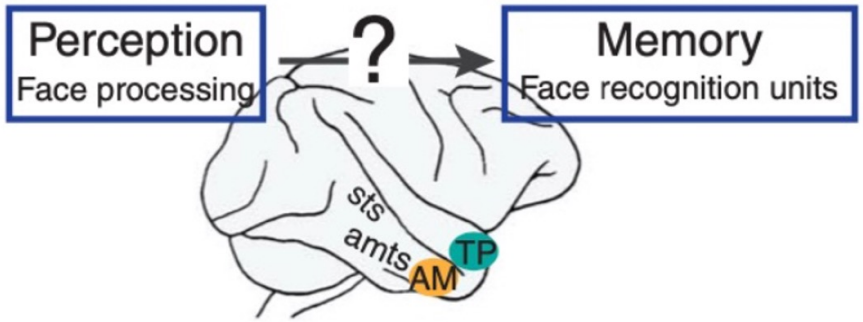
- We need to hold onto **the computational goal of a system** (vs. what you can *do* with the system once you have it)

- The goal that general concept representations are designed to serve is allowing generalization of properties **across** instances in the world

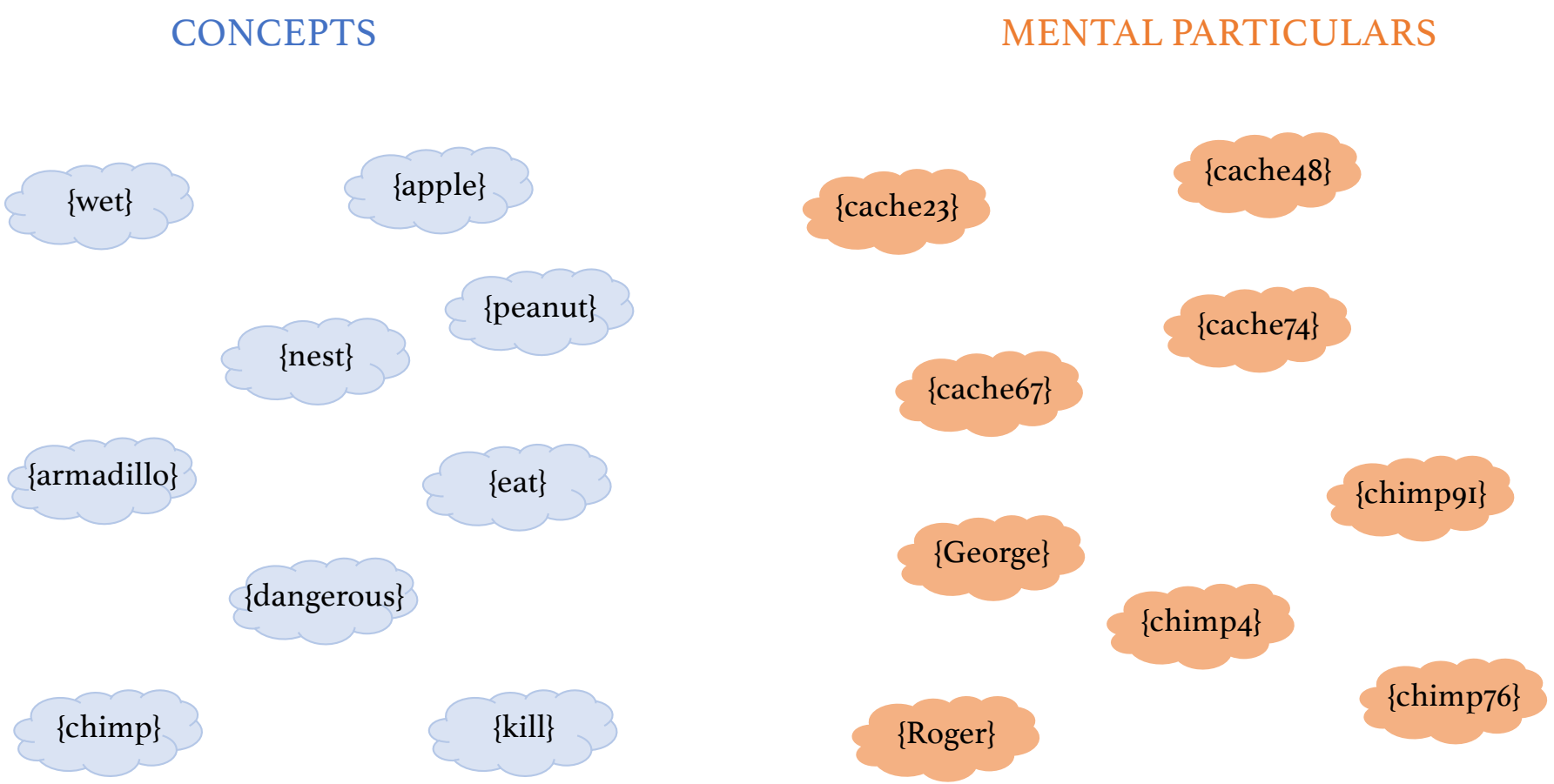
- The goal that mental particular representations are designed to serve is to **encode unique properties** of instances in the world



- Neuroimaging studies show **temporal pole** activity when retrieving knowledge about known individuals or buildings
- Patients with temporal pole damage lose access to this knowledge
- Macaques show pathway from ventral face perception to temporal pole individual recognition



e.g. Damasio et al. 1996; Gorno-Tempini and Price, 2001; Olson et al. 2013; Schneider et al. 2018; Landi et al. 2021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{dangerous}
{chimp}
{kill}
MENTAL PARTICULARS
{cache23}
{cache48}
{cache74}
{cache67}
{chimp91}
{George}
{chimp4}
{chimp76}
{Roger}

What is interpretation?

- For animals that have mental particulars, scene interpretation will involve representing relations between these particulars as well as between general concepts

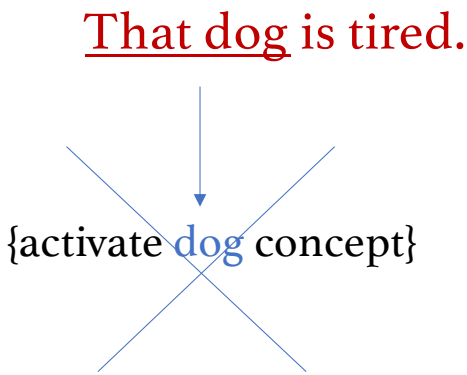
{groom}

{chimp91}

{chimp4}

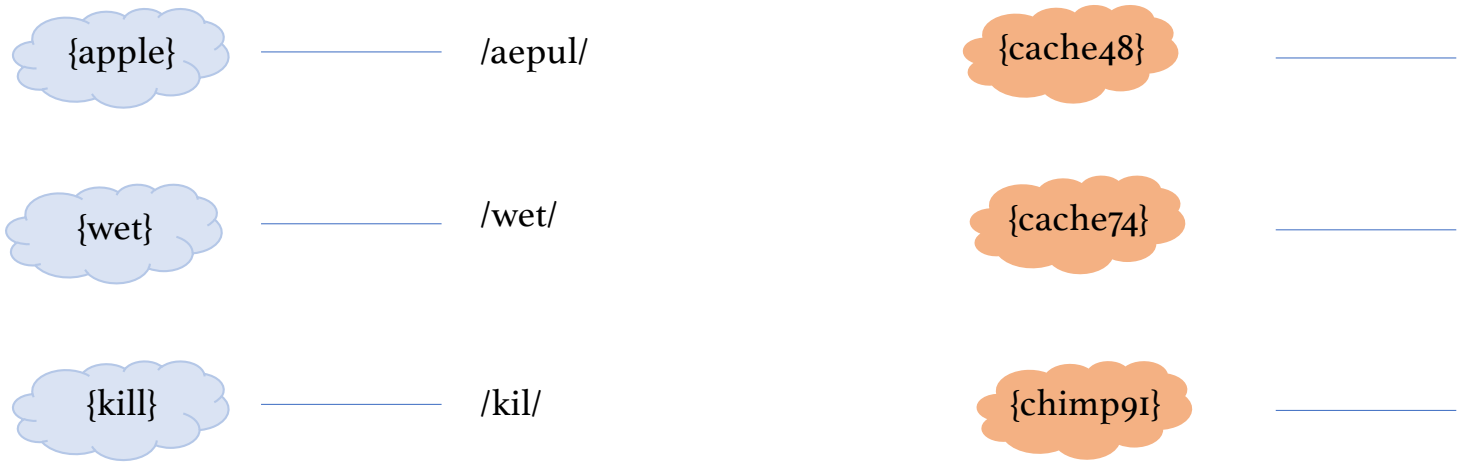
Mental particulars

- Analogously, we don't want to think of sentence interpretation as centered around *conceptual* activation and combination only



Mental particulars and language

- Language vocabularies mostly contain names for general concepts, not for the particulars



Mental particulars and language

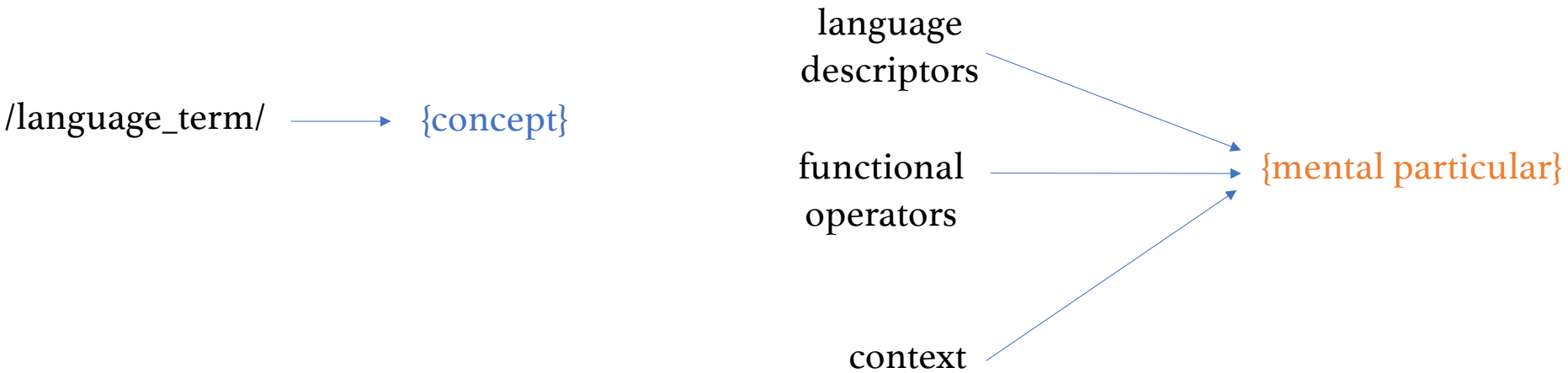
- But we still want to talk about particulars—in fact often we want to assert conceptual properties to hold for particulars just as we do for general kinds:

That dog is dangerous.

Armadillos are dangerous.

Mental particulars and language

- This means there's a built-in non-isomorphism between language units and non-linguistic cognition units that has to be overcome for successful communication and interpretation
- Which is likely to require distinct subroutines in comprehension



Mental particulars and ERPs

- If N400 amplitude is really a neural correlate of 'conceptual activation' or 'conceptual integration', we're not yet studying this equally fundamental component of interpretation: **using language to enter mental particulars into the combinatorial representation**

- What exists already and what could we do next?

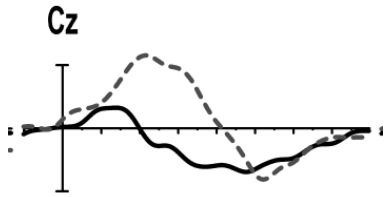
Mental particulars and ERPs

- Nieuwland and Van Berkum (2006) used ERPs to show that mental particular knowledge affects interpretation rapidly

A woman saw a dancing peanut who had a big smile on his face…The peanut was

--- salted

— in love

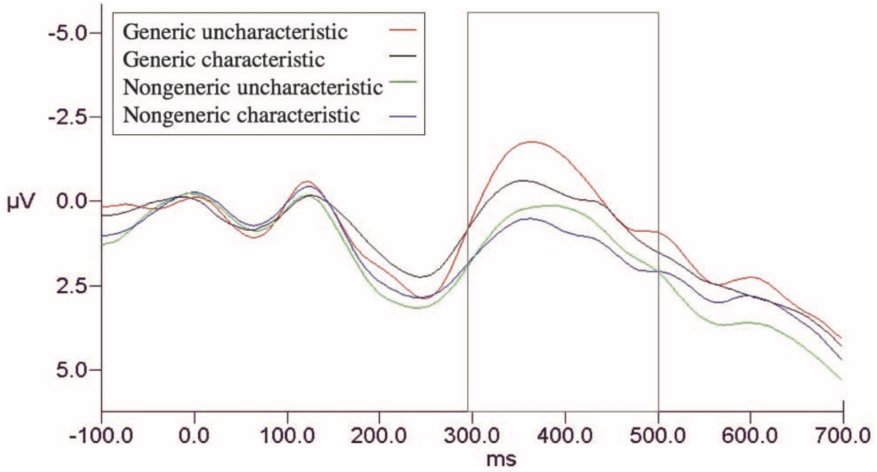


Mental particulars and ERPs

- Prasada, Poeppel and colleagues (2008) similarly showed with N400 amplitude that the difference between a mental particular vs. a general concept rapidly affected subsequent processing

Bananas are yellow.
This banana is yellow.

Bananas are green.
This banana is green.

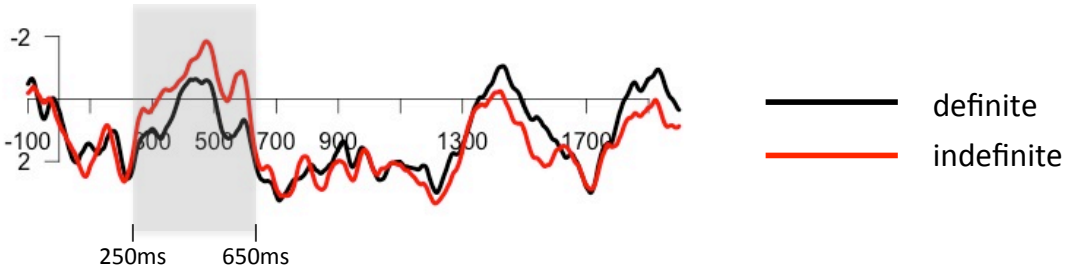


Mental particulars and ERPs

- We showed evidence that people's expectations about reference to a particular entity rapidly affected responses to a definite vs. indefinite article

Anna wore a necklace to her friend's party.

She told everyone that the / a …



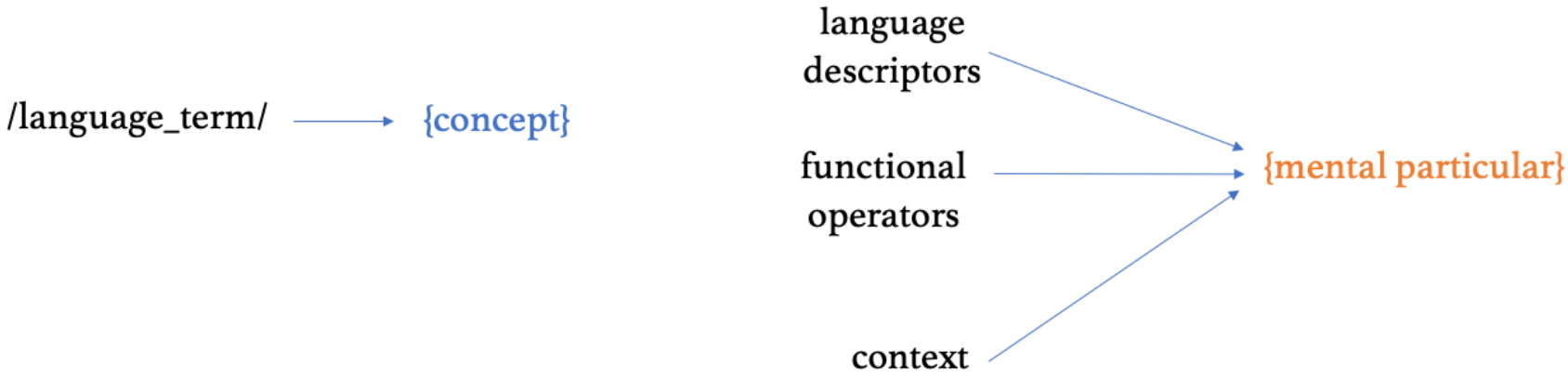
Schlueter, Williams, & Lau 2015 CUNY

Mental particulars and ERPs

- But so far, doesn't really get at the computations that actually identify or establish the mental particular from the language input

Mental particulars and ERPs

- Looking for neural correlates of the different processes required to identify mental particulars vs. general concepts, and the brain circuits for storing new information about each



Mental particulars and ERPs

- This would mean more comparisons between the responses to noun phrases that trigger these different subroutines

I love sunlit ponds

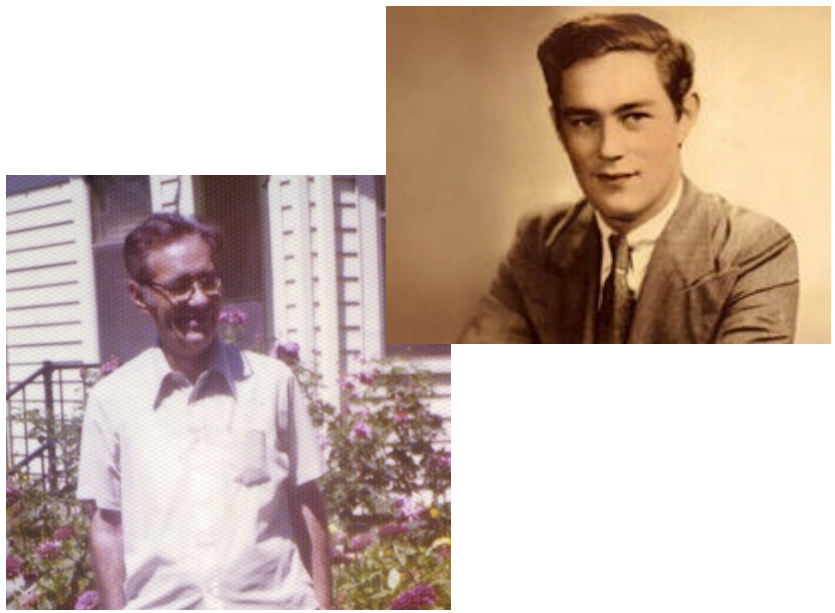
I love the sunlit ponds

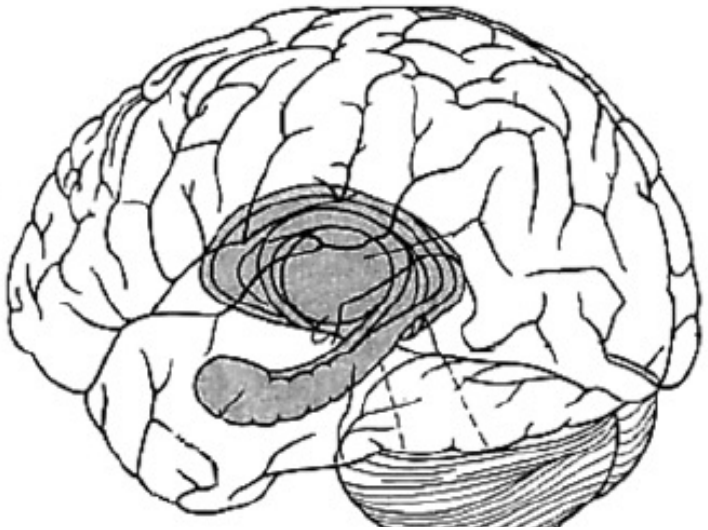
What is interpretation?

- **Mental particulars**
- **Acquiring long-term knowledge**

Short-term vs. long-term knowledge

- Hippocampal amnesia





‘Preserved language comprehension’

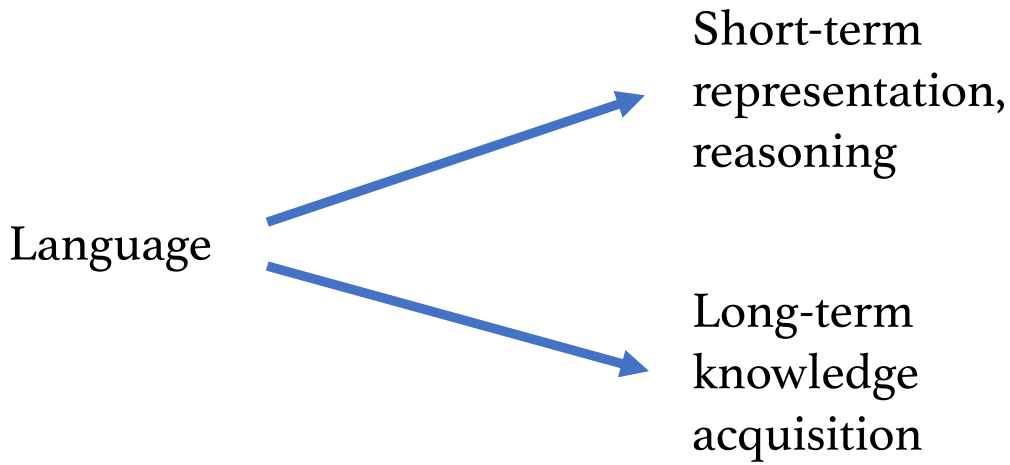
- Patients with hippocampal amnesia can carry on a conversation or engage in counterfactual reasoning about a described situation

Conversations about crossword puzzles

Speaker	Transcript
Conversation 1 (Day 1):	
Interv 2:	So you love puzzles?
H.M.:	Yeah.
Interv 2:	You’ve done them all your life?
H.M.:	Yes . . . most of my life.
Interv 2:	And did you do them when you were . . . aah . . . did you start doing them when you were in school?
H.M.:	I started doing them mostly when I was after school.
Interv 2:	Uh-huh. Did you do them out of a newspaper or did you
H.M.:	<<jumping in>> Started in the newspaper.
Interv 1:	What newspaper?
H.M.:	Well, didn’t make any difference . . . mostly *The Times*.

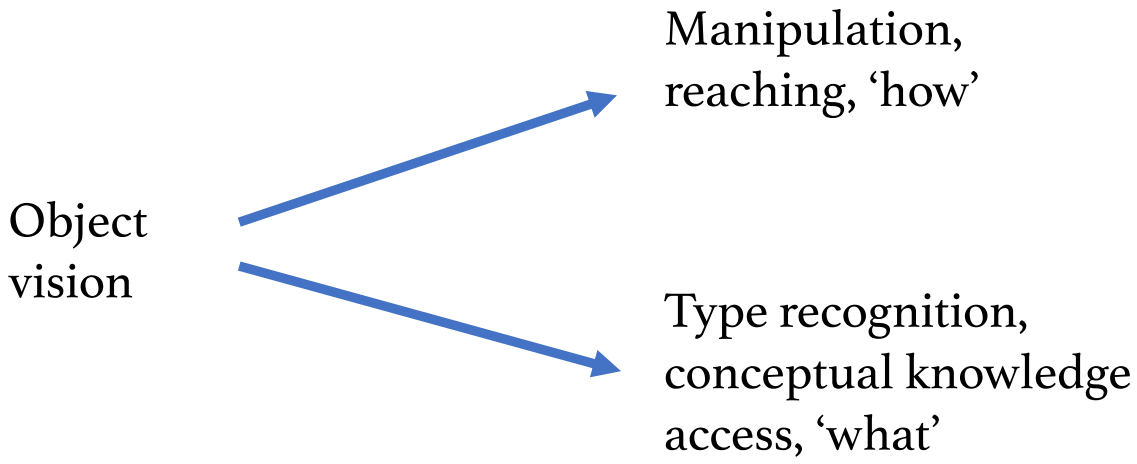
Short-term vs. long-term knowledge

- But these could rather be two equally important goals of the language comprehension system



Object vision: recognition vs. manipulation

- Just like we think object type recognition and object manipulation are two equally important goals of the visual system



Ungerleider & Mishkin, 1982

Acquiring long-term knowledge

- What functional considerations make long-term memory different from working memory?

Acquiring long-term knowledge

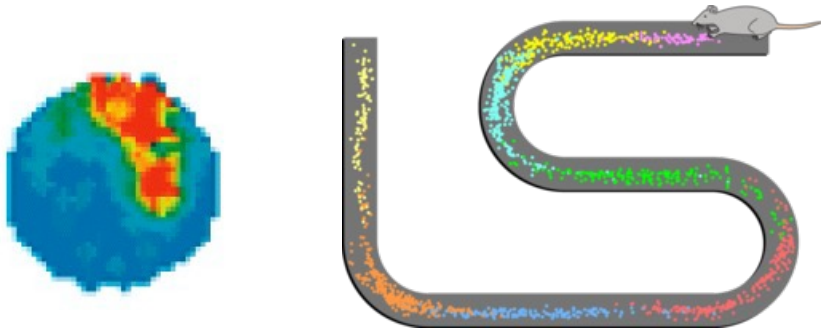
- RECOVERABILITY!

Long-term memories need to be stored in a way that they can be recovered later when needed (otherwise they might as well not be stored)

Acquiring long-term knowledge

- Hippocampus originally evolved in early vertebrates to solve this problem for navigation--indexing properties of particular places

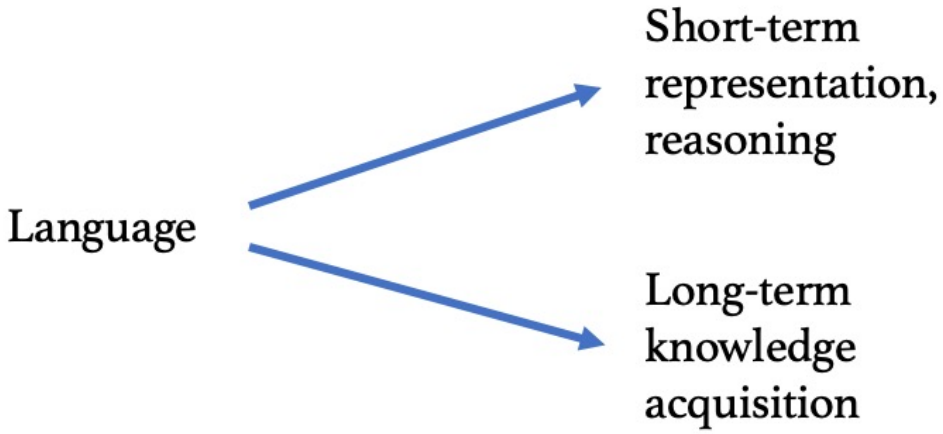
- Solution: sophisticated system for rapid indexing, encoding, updating, re-identifying, and relating to a mental map



hippocampal place cell receptive fields

Acquiring long-term knowledge

- If this is a key function of language comprehension, we can expect it to have shaped the format of language



Clauses and long-term memory

- Why don't most languages allow you to say things like 'A dragon.' but require instead forms like 'Once there was a dragon.'?

- Somewhat mysterious for working memory—'A dragon' would be a straightforward way to introduce a new entity into the current scene

- Makes more sense if sentence representation is shaped for long-term knowledge acquisition—'A dragon' is not a well-formed command for indexing a new piece of information in a recoverable way

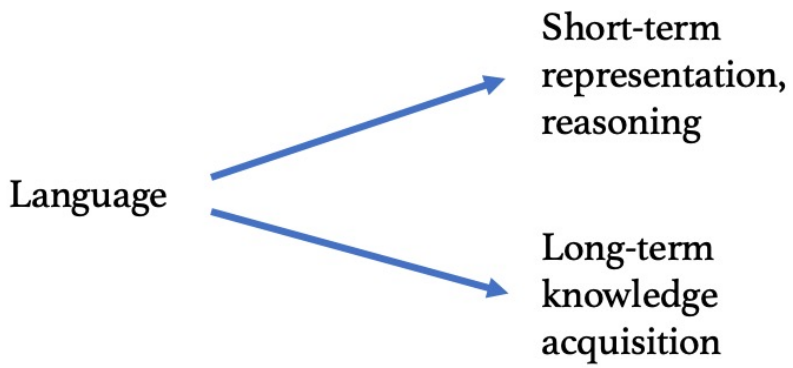
Clauses and long-term memory

- Perhaps in the default case, the clause corresponds to the basic unit size of hippocampal memory updates

- And classical subject – predicate logic was capturing something important about how sentences get translated into long-term hippocampal memory for later recovery

Acquiring long-term knowledge and ERPs

- So again, interpretation is **not just conceptual combination**—it is also the process of encoding relations between particulars and general concepts in a way that makes possible **a functional long-term knowledge system**



Acquiring long-term knowledge and ERPs

- If N400 amplitude is a neural correlate of 'conceptual activation' or 'conceptual integration', we're not yet studying this equally fundamental component of interpretation: updating long-term knowledge representations in hippocampal memory

- In fact, we already know that N400 repetition effects are preserved in hippocampal amnesia patients (Olichney et al. 2000)

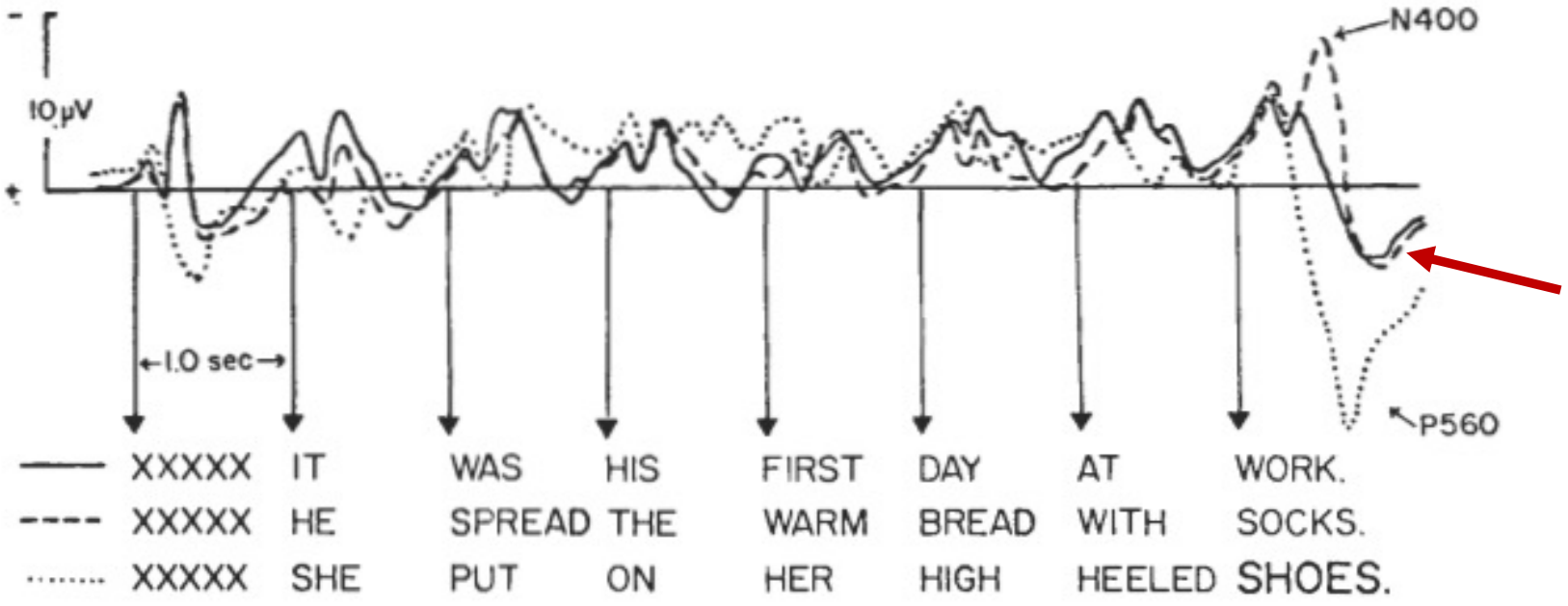
Acquiring long-term knowledge and ERPs

- If clauses approximately correspond to the units of hippocampal memory, we should more seriously investigate **neural responses tied to clause boundaries**

- Existing evidence for such ‘wrap-up’ effects (Stowe et al., 2018)

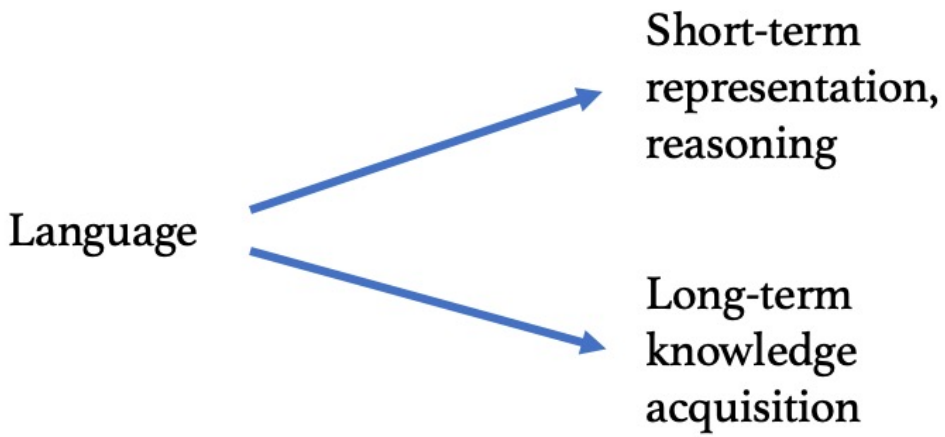
Reading Senseless Sentences: Brain Potentials Reflect Semantic Incongruity

MARTA KUTAS
STEVEN A. HILLYARD
Department of Neurosciences,
University of California, San Diego,
La Jolla 92093



Acquiring long-term knowledge and ERPs

- We should stop thinking of hippocampal memory or long-term memory as a separate, independent domain which language scientists don't really need to know about



What is interpretation?

- Creating combinatorial representations of **general concepts** AND **mental particulars**

- Combinatorial representations for deduction and inference in **working memory** AND for **addressable long-term knowledge**

And what is the N400 effect anyway?

- Marta Kutas may have been right in cautioning me not to seek a simple answer to this

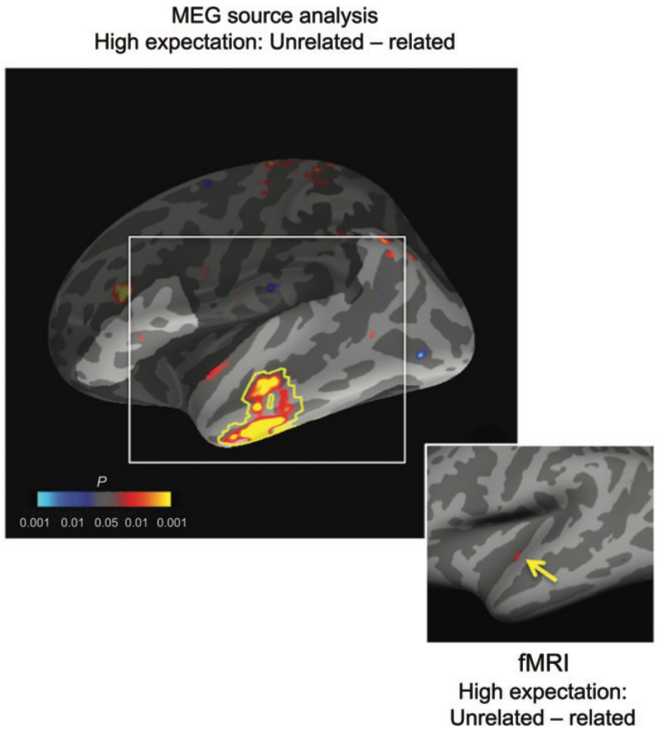
- ERP effects index large changes **in quantity of information being transmitted**

- Perhaps all such **changes in information transfer** in the temporal lobe in the 200-500ms time-window will surface as N400 effects, with slightly different scalp distributions

- Can still be a useful measure, without corresponding to a single type of representation

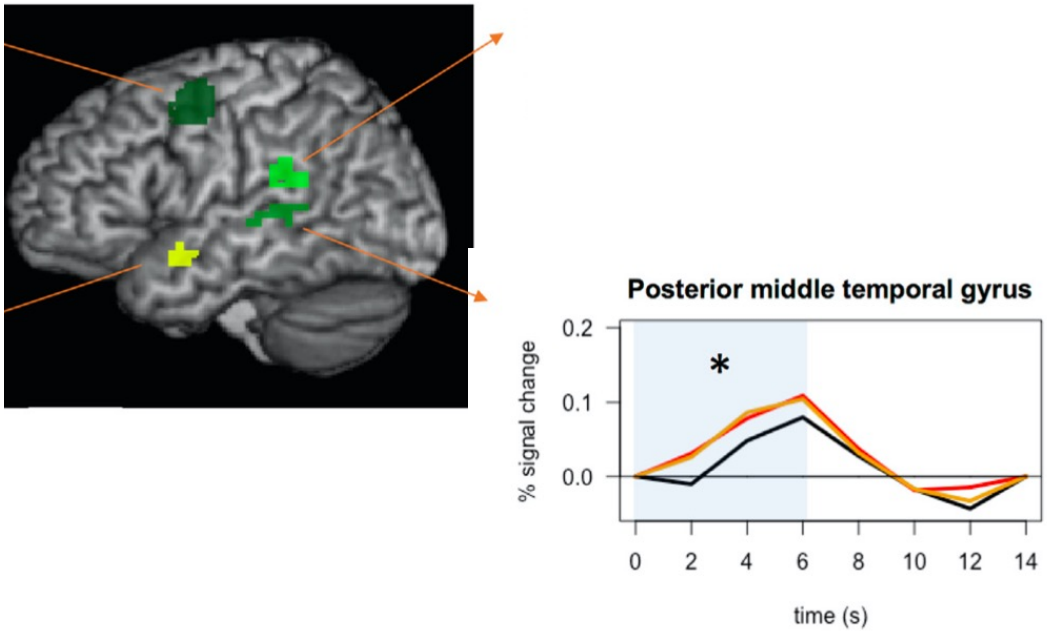
Semantic associates
cat – dog

anterior temporal



Adj-N collocation
runny – nose

posterior temporal



Scholar Moms

Thank you to

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