

# 511-cognition-language

Rick Gilmore

2021-11-05 13:30:56

- The emergence of complex behavior
  - Cambrian Explosion
  - Sparked by behavioral imperatives? (Fox, 2016)
    - Behaviors realized through...
  - Complex behavior ~ Nervous systems
- Cognition
  - Cognition and the cerebral cortex
    - Macrostructure
    - Microstructure
    - Processing networks
    - Data-driven dynamics
      - (Shine et al., 2019)
  - Summing up
- Language and the brain
  - Language behavior
  - Hierarchical structure of language information
  - Wernicke-Geschwind (WG) model
    - Wernicke's area (Brodmann Area or BA 42)
    - Broca's area
  - Dual streams (Hickok & Poeppel, 2007)
    - Metaanalytic evidence (Hagoort & Indefrey, 2014)
  - Summing up
- References

## The emergence of complex behavior

### Cambrian Explosion

What caused the Cambrian explosion? | The Economist



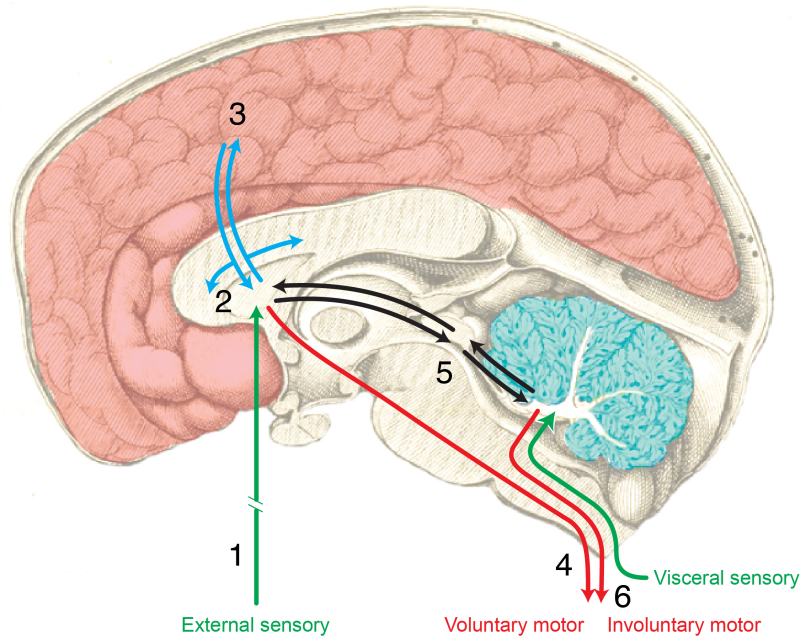
Sparked by behavioral imperatives? (Fox, 2016)  
(<http://doi.org/10.1038/530268a>)

- Behavior requires energy
- Behavior requires perception at a distance
- Behavior requires action
- Actions require
  - Problem solving, (sequence) planning
  - Current + stored information (memory)

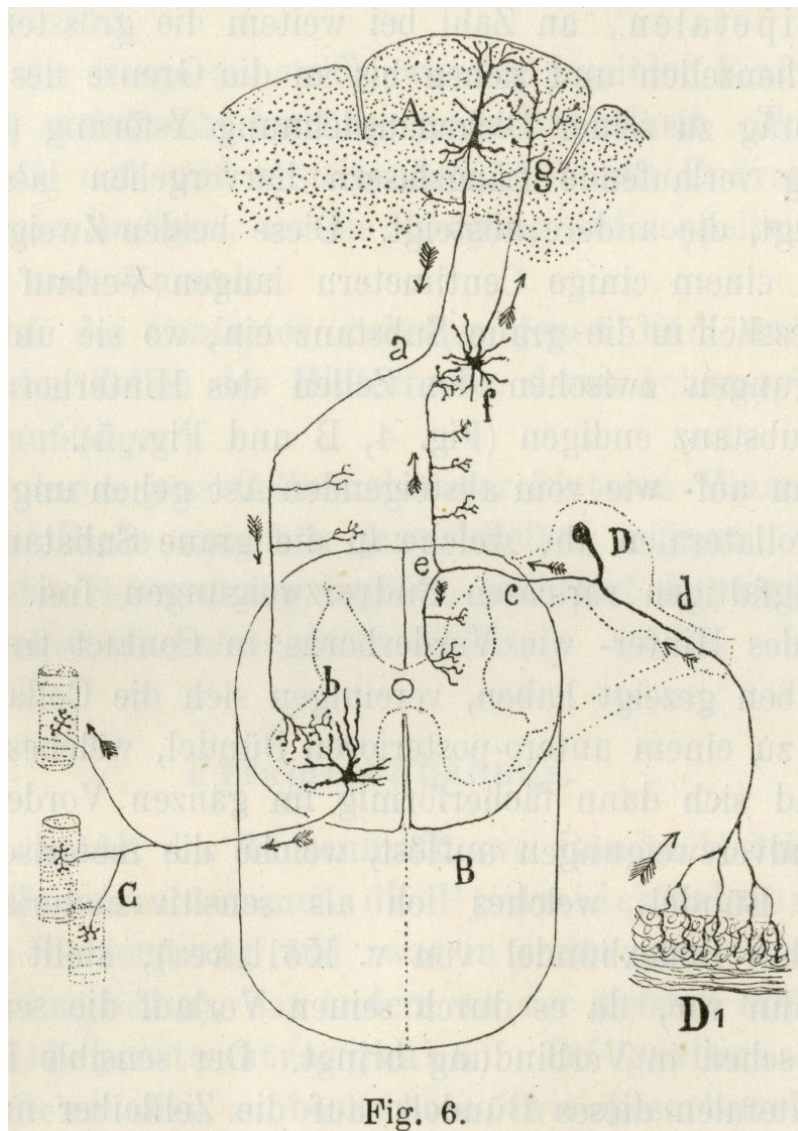
Behaviors realized through...

- Perception at a distance of what/where
- Locomotion
  - Approach/avoid/explore
- Object manipulation/consumption
- Signaling/communication
- Physiological regulation

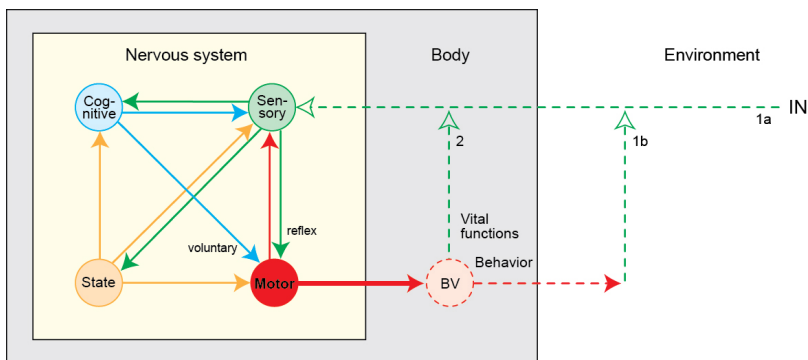
Complex behavior ~ Nervous systems



<http://larryswanson.com> (<http://larryswanson.com>)



<http://larryswanson.com> (<http://larryswanson.com>)



<http://larryswanson.com> (<http://larryswanson.com>)

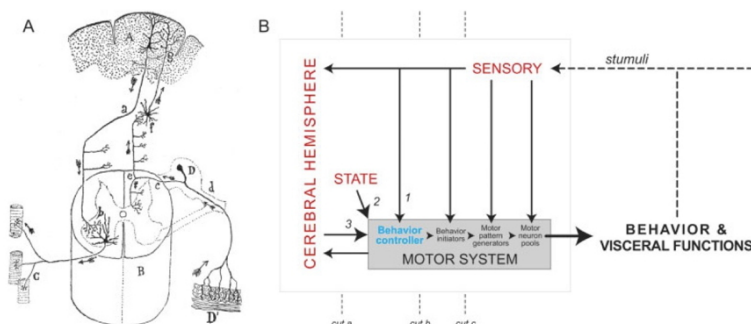


Fig. 1. **A:** Perhaps the first diagram illustrating the cellular organization of a vertebrate spinal reflex, based on the neuron doctrine and law of functional polarity, published by Cajal in 1890 (see Cajal, 1894). Note that he emphasized two interconnected sources of motor neuron (b) control: dorsal root ganglion cells (D) and cerebral cortical pyramidal (or psychomotor) neurons (A). For clarity, he showed sensory input to the right side of the spinal cord, and motor output from the left side. **B:** A modern version of the basic plan of nervous system organization, adding behavioral state inputs (2) to sensory or voluntary (1) and cerebral hemisphere/cognitive or voluntary (3) inputs to the motor system hierarchy; see text for details (adapted from Swanson, 2000a).

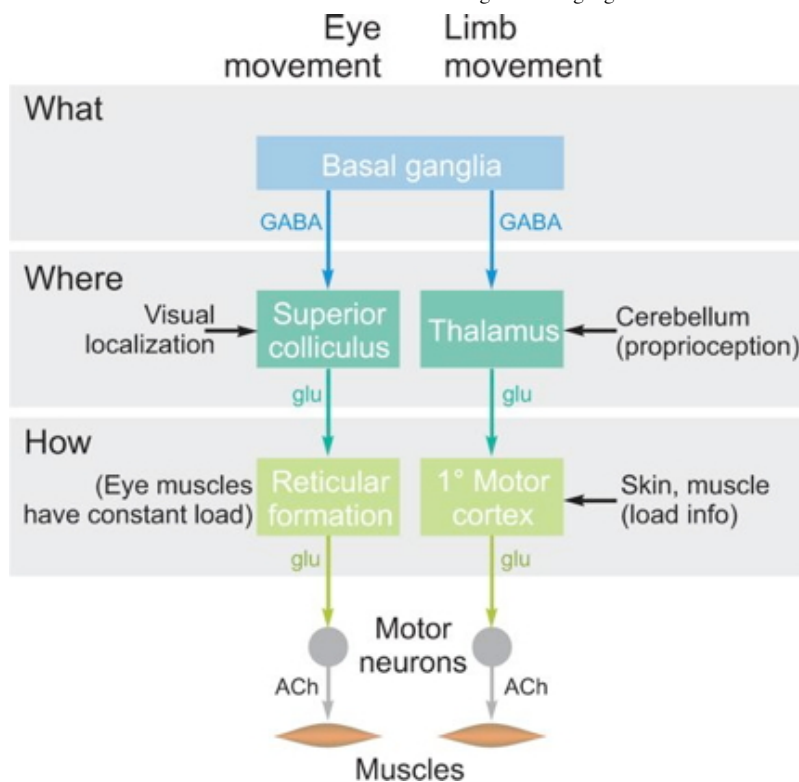
(Swanson, 2005) (<http://dx.doi.org10.1002/cne.20733>)

Cortico-striatopallidal differentiations for:

- Motivated behaviors
- Locomotion and posture
- Orienting movements (eyes, head)
- Reaching, grasping, manipulating
- Orofaciopharyngeal movements
- facial expression
- vocalization
- licking, chewing, swallowing
- Breathing
- Autonomic responses
- Neuroendocrine responses

Fig. 8. Hypothesized differentiations of the cerebral cortico-nuclear system (cortico-striatopallidal system) for all major classes of motor responses or behavior (adapted from Swanson, 2003a).

(Swanson, 2005) (<http://dx.doi.org10.1002/cne.20733>)



(Swanson, 2012) ([https://books.google.com/books?](https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh)

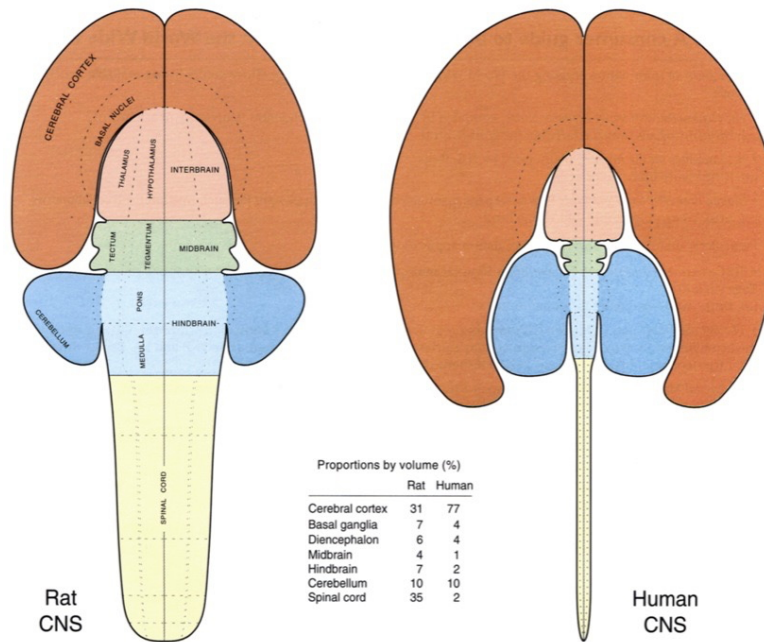
[hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh](https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh).

## Cognition

Combines...

- Perception (<https://neurosynth.org/analyses/terms/perception/>)
- Attention (<https://neurosynth.org/analyses/terms/attention/>)
- Imagery (<https://neurosynth.org/analyses/terms/imagery/>)
- Learning (<https://neurosynth.org/analyses/terms/learning/>) and conditioning (<https://neurosynth.org/analyses/terms/conditioning/>)
- Memory
  - Episodic (events) (<https://neurosynth.org/analyses/terms/episodic%20memory/>)
  - Semantic (facts, things, entities) (<https://neurosynth.org/analyses/terms/semantic%20memory/>)
  - Procedural (actions (<https://neurosynth.org/analyses/terms/action/>))
  - Working (<https://neurosynth.org/analyses/terms/working%20memory/>)
- Problem-solving
- Language (<https://neurosynth.org/analyses/terms/language/>)

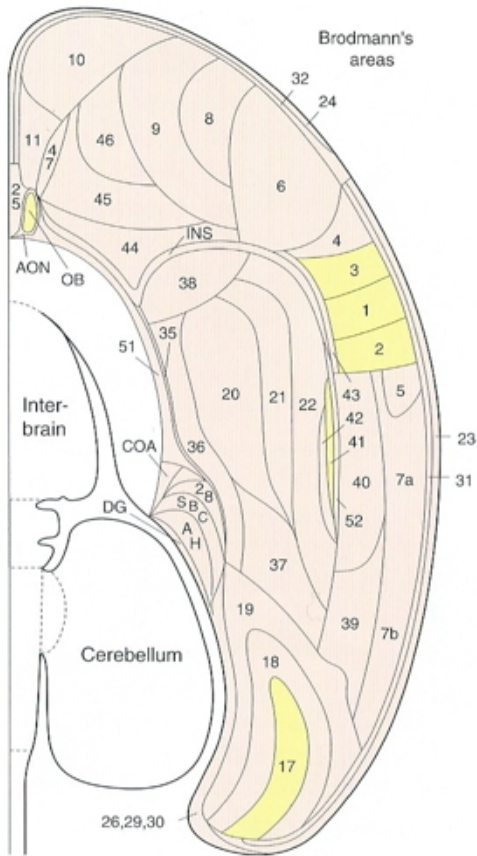
## Cognition and the cerebral cortex



(Swanson, 2012) (<https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh>

## Macrostructure

- Areas
  - Unimodal sensory
  - Polymodal association
  - Motor
- Connections
  - Association
  - Commissural



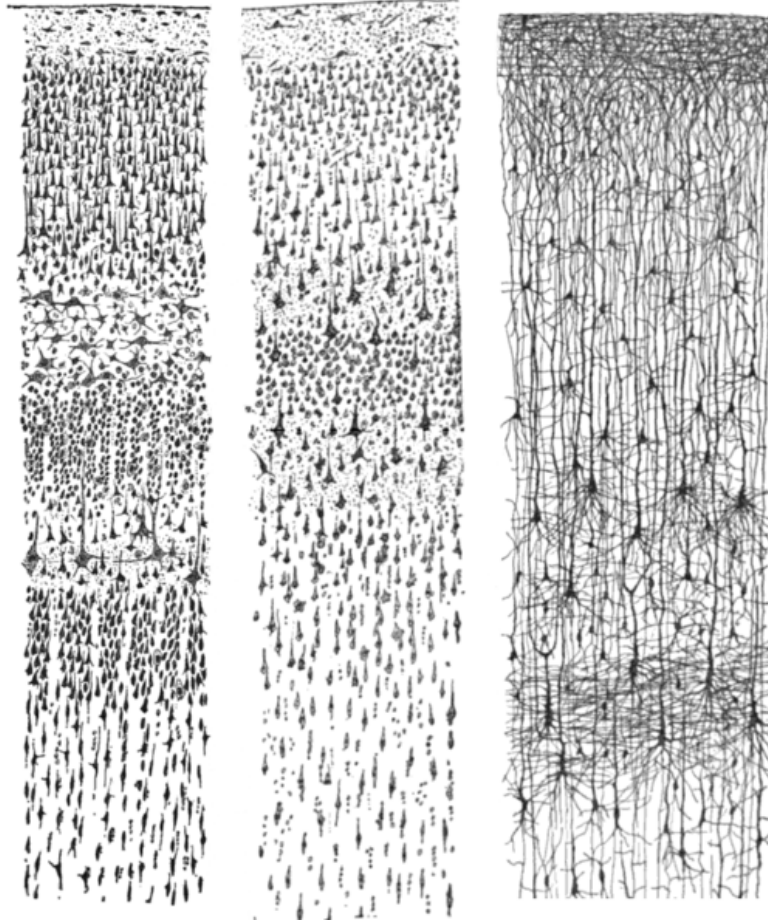
**Figure 10.5** A topological representation of Brodmann's regionalization of the cerebral cortex (light red) into areas is shown on this flatmap of the human brain (see Figs. 10.3 and 10.4). Primary sensory cortical areas are indicated in yellow. Compare with Figures 6.7 and 10.1. Key: 1-3, somatic sensory; 17, visual; 41, auditory; AH, Ammon's horn; AON, anterior olfactory area, COA, cortical amygdalar area; DG, dentate gyrus; INS, insular area; OB, olfactory bulb; SBC, subicular complex. Adapted with permission from L.W. Swanson, Mapping the human brain: past, present, and future, *Trends Neurosci.* 1995, vol. 18, poster accompanying p. 471.

(Swanson, 2012) (<https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh>.

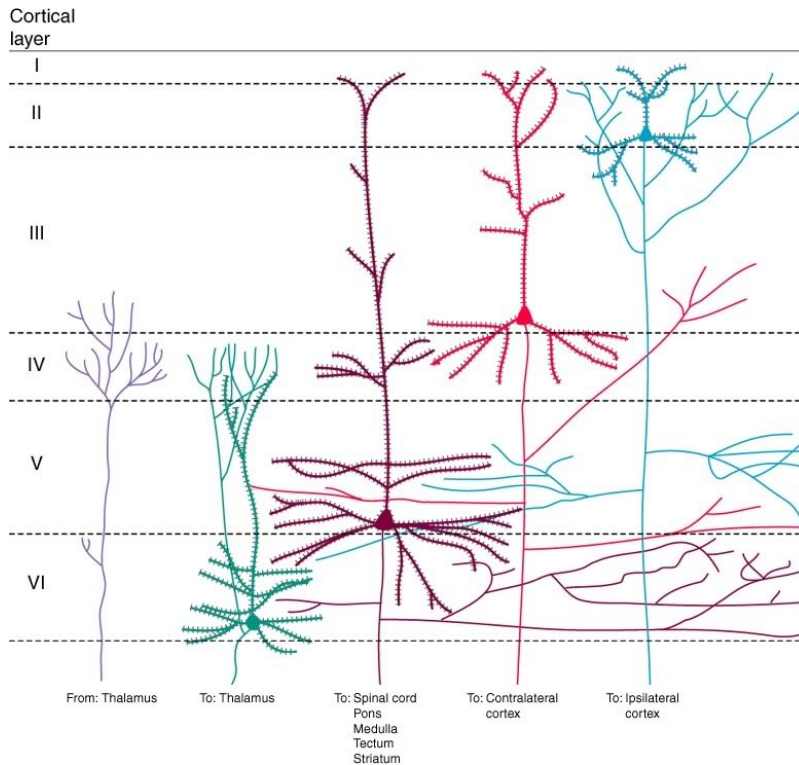
[hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh](https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh).

## Microstructure

- Columnar structure
- Cytoarchitectonic differences (e.g. Brodmann)



Wikipedia



Copyright © 2002, Elsevier Science (USA). All rights reserved.

**Layer**

**Connection type**

**Comments**

I

Few cell bodies



Layer	Connection type	Comments
II	Efferent	Ipsilateral association via large pyramidal cells
III	Efferent	Contralateral commissural
IV	Afferent	from thalamus; small stellate & granular cells; V1 has sublayers
V	Efferent	Superficial -> Basal ganglia; Deep -> brainstem, spinal cord; pyramidal cells
VI	Efferent	Thalamus

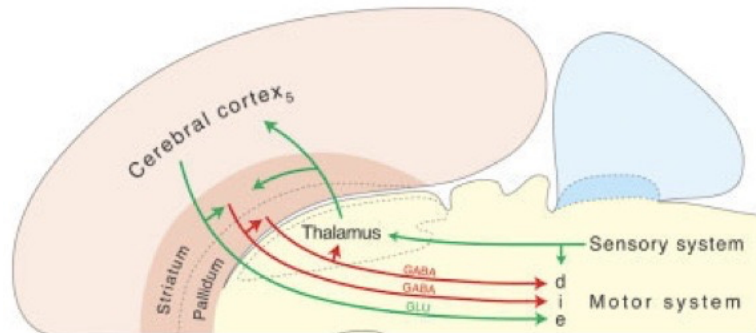


Fig. 2. A model of the elementary or minimal circuit element characteristic of almost all parts of the cerebral hemispheres (pink). It consists of a triple descending projection to the motor system of the brainstem and spinal cord (see Fig. 1B), with feedback to cerebral hemisphere via thalamus. The model predicts that the cerebral hemisphere provides a direct excitatory input (e) to motor system via glutamatergic (GLU), layer 5 (for isocortex), cortical pyramidal neurons that generate a collateral in the striatum (lateral cerebral nuclei), which sends an inhibitory input (i) to motor system via GABAergic (GABA) medium spiny stellate neurons providing a collateral to pallidum (medial cerebral nuclei). The latter then sends a disinhibitory (d), GABAergic projection to motor system, with collaterals to dorsal thalamus, which then projects back to cortex via glutamatergic neurons (and of course receives various classes of sensory input). Many thalamic nuclei also project to striatum (Smith et al., 2004). This minimal circuit element is topographically organized and differentially elaborated regionally.

(Swanson, 2012) ([https://books.google.com/books?](https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh)

[hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh](https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh)

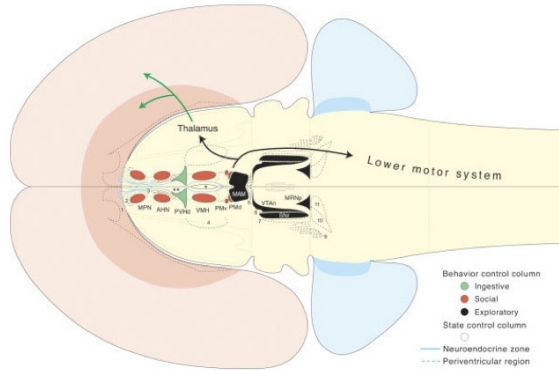
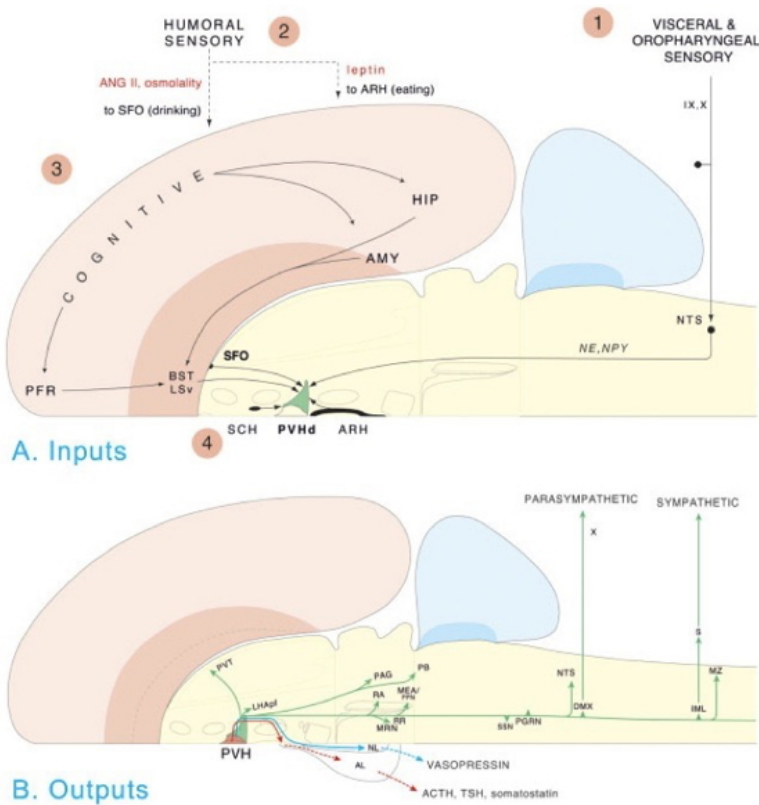


Fig. 3. Basic topography of the behavior control column (BCC) in ventromedial regions of the upper brainstem as viewed on a flatmap of the rat central nervous system. Each component minimally generates a dual projection to the lower motor system (primarily motor pattern generator networks and motoneuron pools) and dorsal thalamus. Where analyzed experimentally (dorsal premammillary nucleus, PMd; mammillary body, MAM; and reticular substantia nigra, SNr), the thalamic projection is a collateral of the descending projection to motor system. This dual projection may be either glutamatergic (e.g., MAM) or GABAergic (e.g., SNr). The BCC caudal segment contains MAM, nondopaminergic ventral tegmental area (VTAn), SNr, and parvocellular midbrain reticular nucleus (MRNp). The BCC rostral segment contains medial preoptic nucleus (MPN), anterior hypothalamic nucleus (AHN), ventromedial nucleus (VMH), ventral premammillary nucleus (PMv), and PMd. Two critical functional regions lie between the BCC rostral segment and third ventricle (midline): the median eminence (\*, asterisk) and surrounding neuroendocrine motor zone (solid blue line), and the periventricular region (dashed blue line and \*\*, double asterisks), which contains visceromotor pattern generator and circadian rhythm generator networks. The behavioral state control column, running parallel to the BCC, is indicated by dashed outlines (see text for more information).

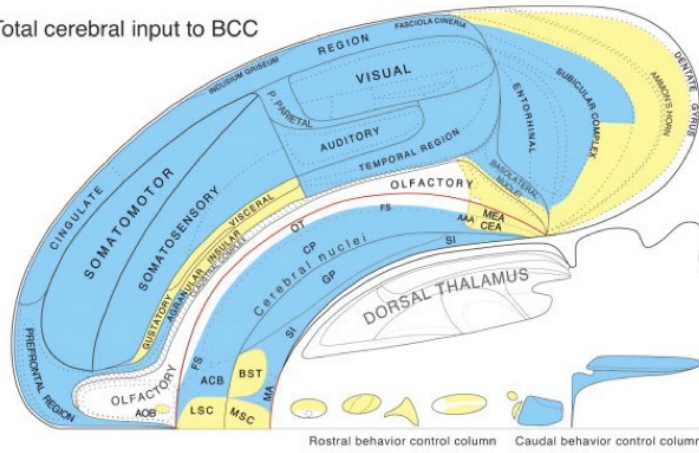
(Swanson, 2012) ([https://books.google.com/books?](https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh)

[hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh](https://books.google.com/books?hl=en&lr=&id=tAk8Rr00kykC&oi=fnd&pg=PP2&dq=larry+swanson+book&ots=5F7nEnts45&sig=DJLKh)).



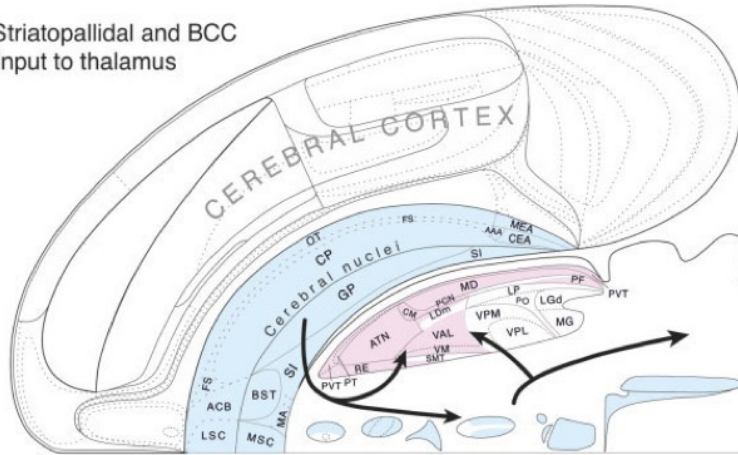
(Swanson, 2005) (<http://dx.doi.org10.1002/cne.20733>)

A. Total cerebral input to BCC



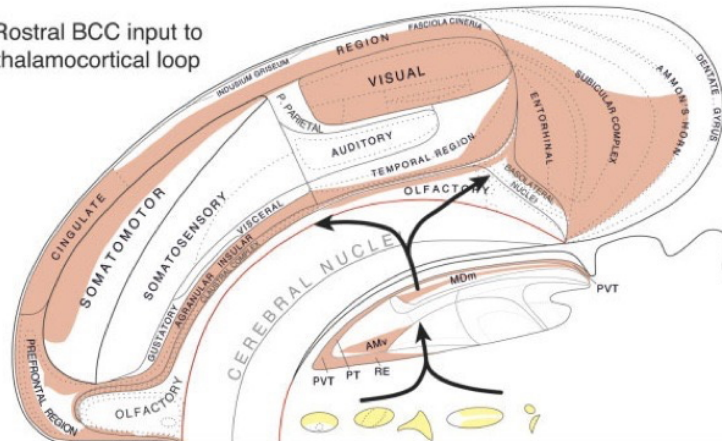
(Swanson, 2005) (<http://dx.doi.org10.1002/cne.20733>)

B. Striatopallidal and BCC input to thalamus



(Swanson, 2005) (<http://dx.doi.org10.1002/cne.20733>)

C. Rostral BCC input to thalamocortical loop

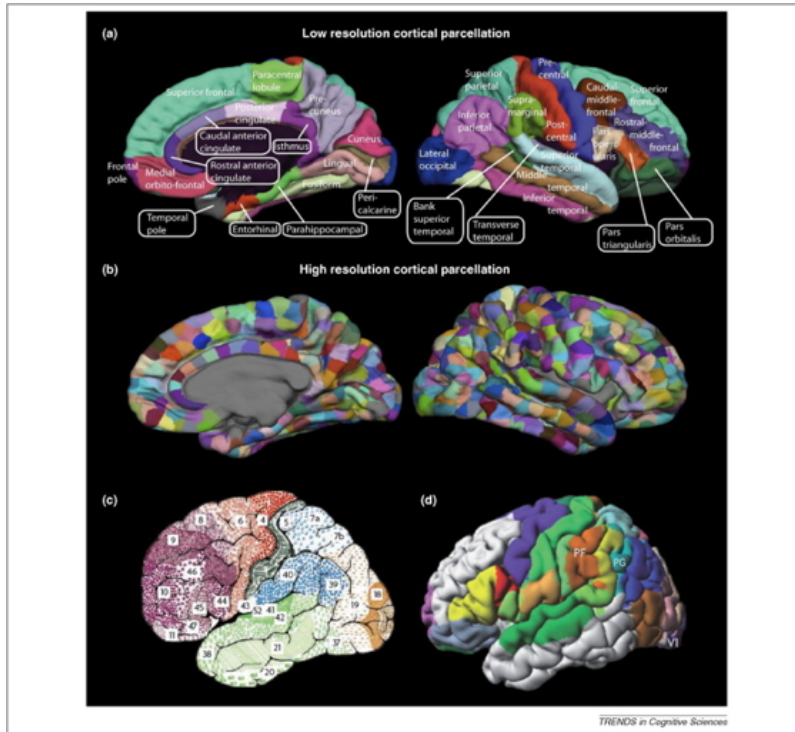


(Swanson, 2005) (<http://dx.doi.org10.1002/cne.20733>)

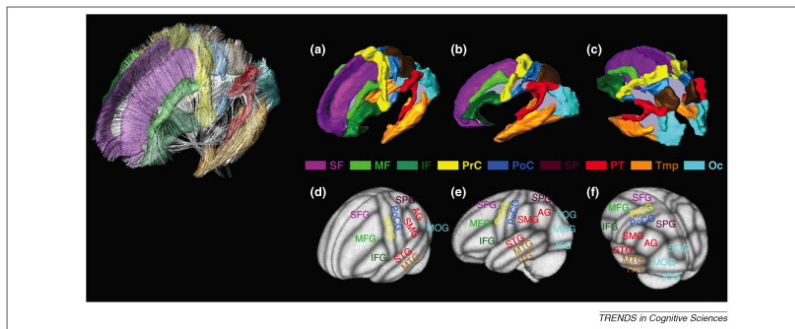
### Processing networks

*“Although it has long been assumed that cognitive functions are attributable to the isolated operations of single brain areas, we demonstrate that the weight of evidence has now shifted in support of the view that cognition results from the dynamic interactions of distributed brain areas operating in large-scale networks...”*

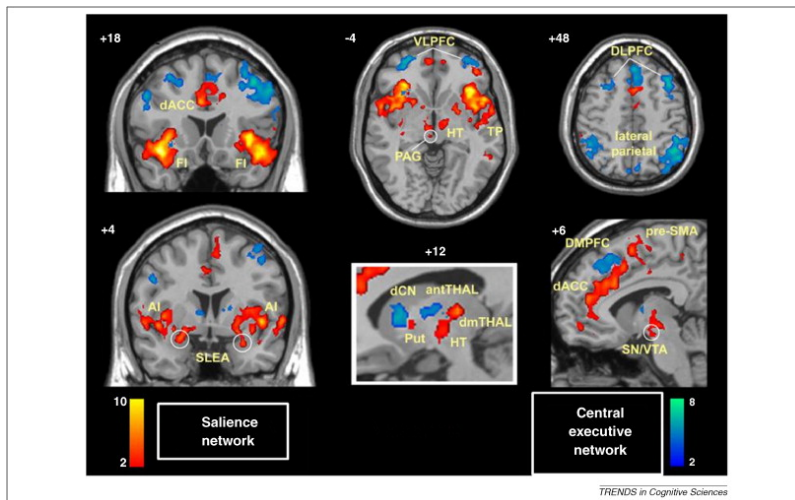
(Bressler & Menon, 2010) (<http://dx.doi.org/10.1016/j.tics.2010.04.004>)



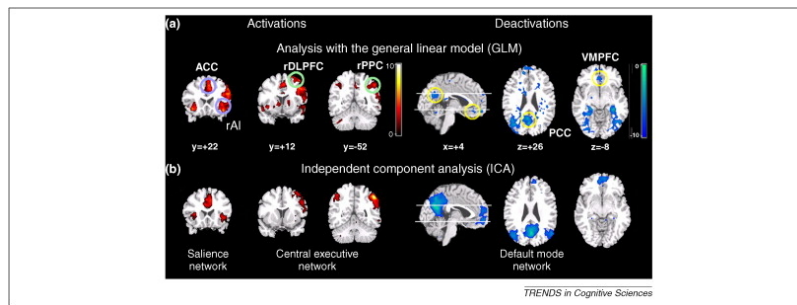
(Bressler & Menon, 2010) (<http://dx.doi.org/10.1016/j.tics.2010.04.004>)



(Bressler & Menon, 2010) (<http://dx.doi.org/10.1016/j.tics.2010.04.004>)



(Bressler & Menon, 2010) (<http://dx.doi.org/10.1016/j.tics.2010.04.004>)



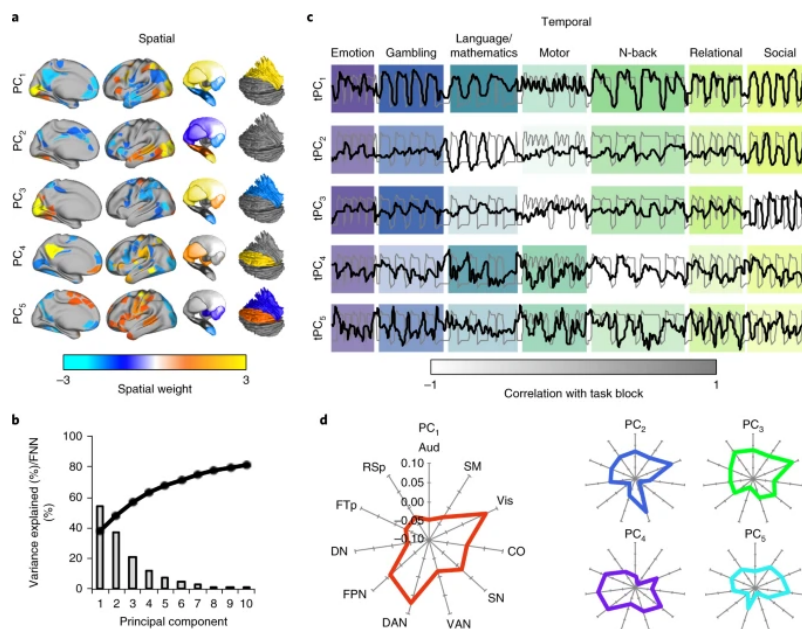
(Bressler & Menon, 2010) (<http://dx.doi.org/10.1016/j.tics.2010.04.004>)

## Data-driven dynamics

- Cortical states have high dimensionality
- Is there a lower-dimensional space that maps onto behavior?

(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

- Data from  $n = 200$  adult participants in Human Connectome Project (HCP) (<https://www.humanconnectome.org>)
- 7 cognitive tasks
- Dimension reduction via principal components analysis (PCA)

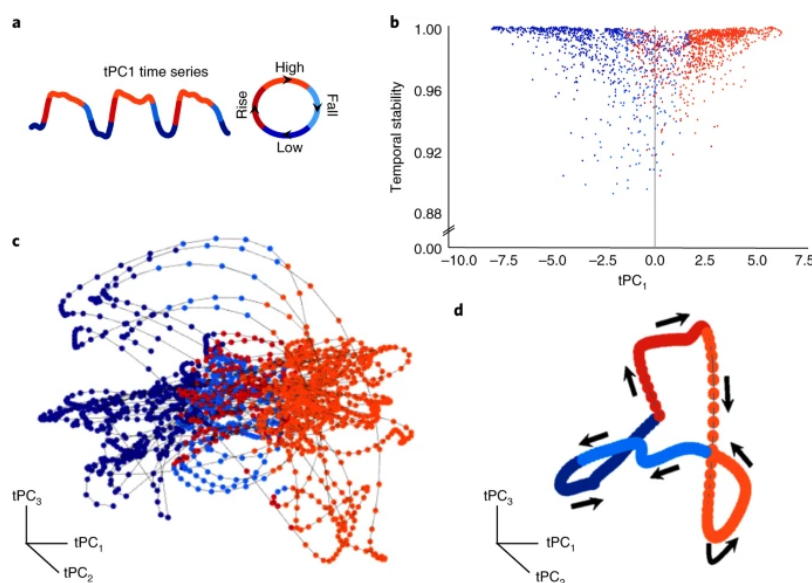


(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

Fig. 1: Spatiotemporal PCA across multiple cognitive tasks. a, Spatial maps for the first five principal components (colored according to spatial weight; thresholded for visualization). b, Line plot representing the percentage of variance explained by first ten principal components; bar plot depicting the percentage (single value per component) of false nearest neighbors for first ten principal components. FNN, false nearest neighbors. c, Correspondence between convolved, concatenated task block regressor (gray) and the time course of the first five tPCs (black); color intensities of the blocks reflect the Pearson's correlation between tPC1-5 and each of the unique task blocks ( $n = 100$  subjects). d, Mean spatial loading of first five PCs, organized according to a set of predefined networks. DAN, dorsal attention; Vis, visual; FPN, frontoparietal; SN, salience; CO, cingulo-opercular; VAN, ventral attention; SM, somatomotor; RSp, retrosplenial; FTP, frontotemporal; DN, default mode; Aud, auditory.

(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

- Map PCAs to time series...

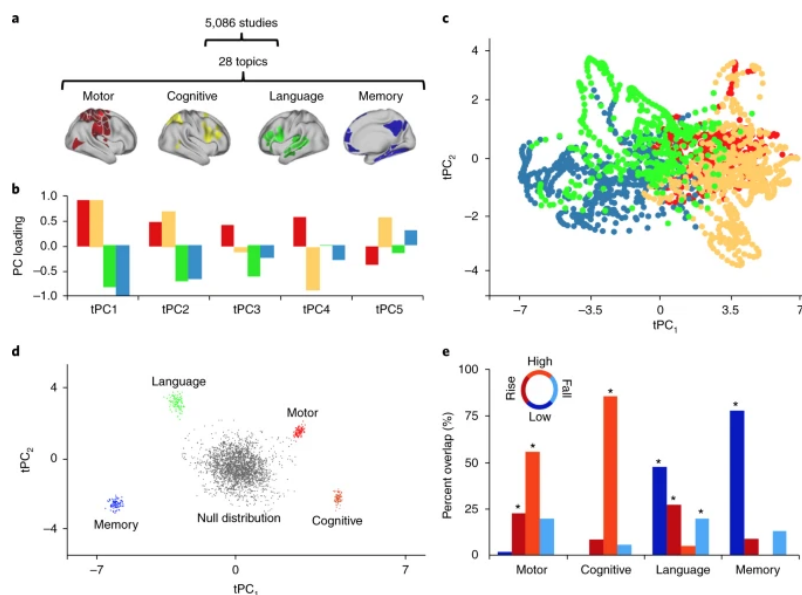


(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

Fig. 2: The low-dimensional signature across cognitive tasks. a, The procedure used to partition tPC1 into unique phases: low (blue), rise (red), high (orange), and fall (light blue). b, Scatter plot comparing the loading of tPC1 (colored according to the partition defined in a) with a temporal stability measure (defined by the similarity of the BOLD response at adjacent time points); we observed a significant positive Pearson's correlation ( $r = 0.58$ ) between  $|tPC1|$  and temporal stability ( $n=1,939$  time points), providing heuristic evidence for attractor basins at the extremes of tPC1 engagement. c, A three-dimensional scatter plot comparing the first three tPCs; each node represents one time point (colored according to the phase of tPC1), with time implicitly unfolding across the embedding space (contiguous points connected by black line). d, The low-dimensional manifold traversed by the global brain state across the first three dimensions, with arrows depicting the direction of flow along the manifold.

(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

- How do these brain states map to cognition?
  - Explore overlap with NeuroSynth (<https://neurosynth.org>) 'topic families'



(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

Fig. 3: The cognitive relevance of the low-dimensional embedding space. a, Four NeuroSynth ‘topic families’: motor (red), cognition (yellow), language (green), and memory (blue). b, Bar plot demonstrating loading (single-value) of topic families onto top five principal components. c, Scatter plot of time points of the first two tPCs, colored according to their loading onto each of the four NeuroSynth topic families. d, Mean value (resampled 100 times) of tPC1–2 for each topic family compared with a block resampled null distribution (5,000 iterations). e, Temporal conjunction between the topic families and the four phases of the tPC1 manifold; bar plots designate a single value (%) and asterisks denote  $P < 0.01$  (block resampled null model;  $n=5,000$  iterations).

(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

*The results of our multimodal analysis revealed that the neural activity required for the execution of cognitive tasks corresponds to flow within a low-dimensional state space<sup>43</sup>. Across multiple, diverse cognitive tasks, the dynamics of large-scale brain activity engage an integrative core of brain regions that maximizes information-processing complexity and facilitates cognitive performance; only to then dissipate as the tasks conclude, flowing towards a more segregated architecture...Across multiple cognitive tasks with markedly different behavioral requirements, the dynamics of human brain activity were found to occupy a low-dimensional state space embedding that may form the functional backbone of cognition in the human brain.*

(Shine et al., 2019) (<http://dx.doi.org/10.1038/s41593-018-0312-0>)

## Summing up

- Cognition involves
  - Do what, where, when, and how
- The “cognitive” cortex
- Processing networks
  - Functional specialization
  - Dynamic interaction
  - Low dimensional dynamics
  - Nested feedback control loops



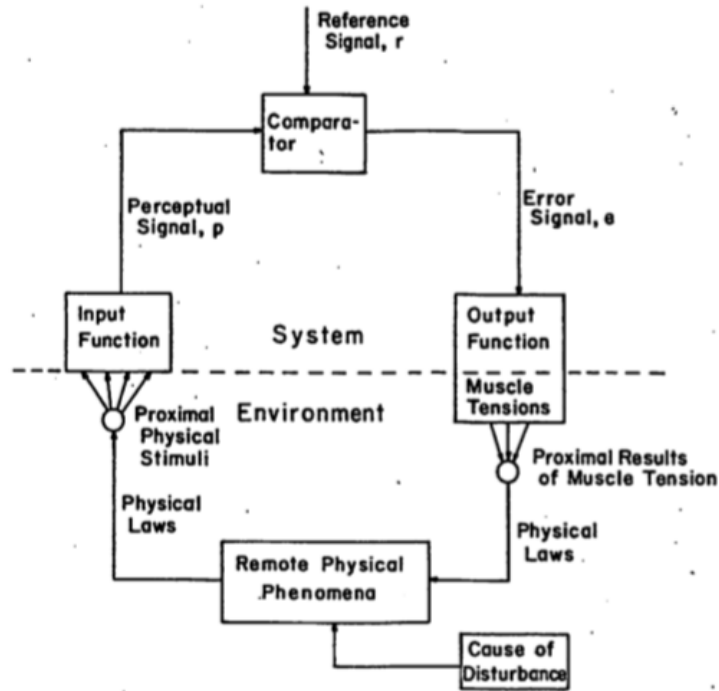


FIGURE 5.2. General model of a feedback control system and its local environment.

(Powers, 1973)

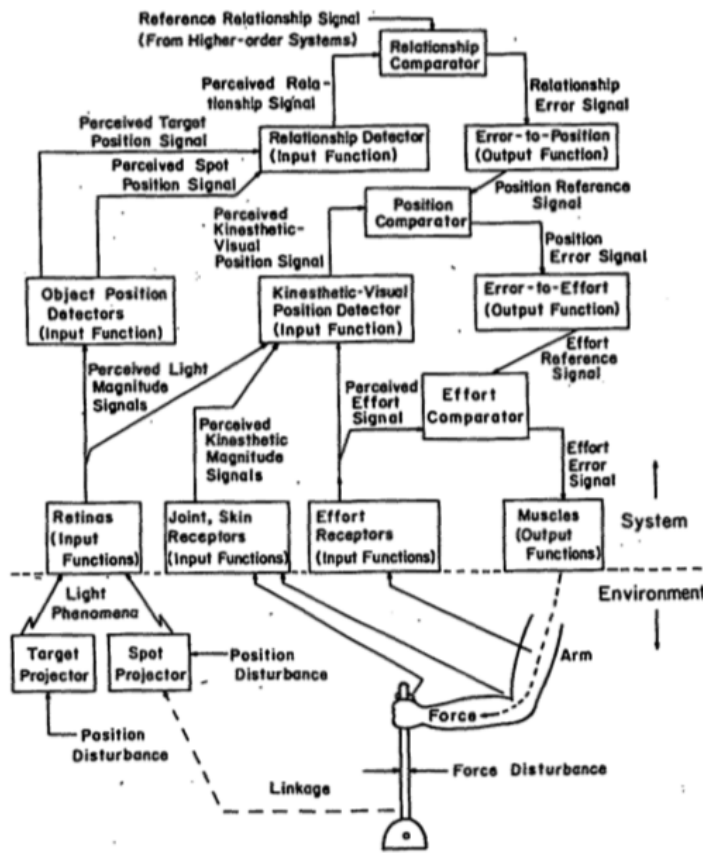
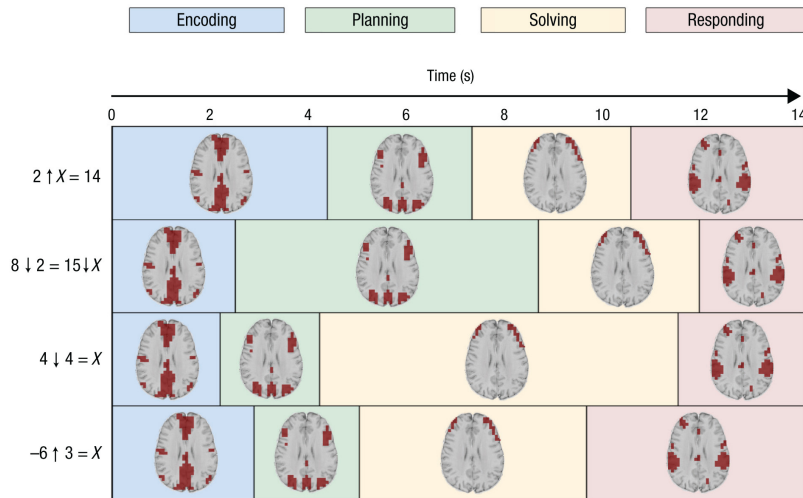


FIGURE 6.1. A three-level control-system model of a person in the tracking situation.

(Powers, 1973)

- What do we want to know?

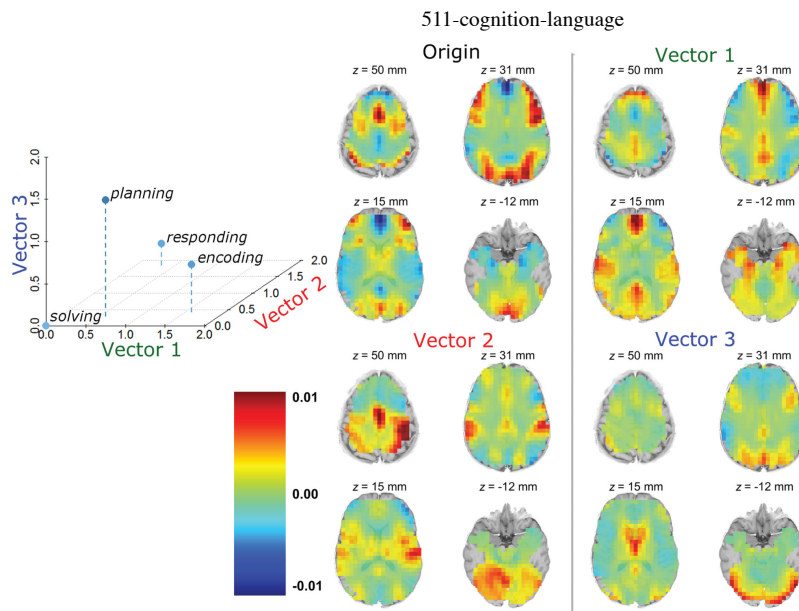
- What parts of the nervous system are evoked by cognitive process X? (localization)
- How does neural data support/undermine theory X of cognition?
- "...our survey nevertheless still makes it clear that very few resources are currently being devoted to using neuroimaging data to test theories about cognition."  
(Tressoldi, Sella, Coltheart, & Umiltà, 2012)  
(<http://dx.doi.org/10.1016/j.cortex.2012.05.024>)
- Also (Coltheart, 2013) (<http://dx.doi.org/10.1177/1745691612469208>)
- Neuroscience can constrain models of cognition (White & Poldrack, 2013)  
(<http://dx.doi.org/10.1177/1745691612469029>)
  - One process or two
  - Serial vs. parallel processing
- Show me your (cognitive) model...



(Anderson, Pyke, & Fincham, 2016) (<http://dx.doi.org/10.1177/0956797616654912>)

Fig. 1. Illustration showing the durations of the four stages associated with problem solving. In the four example problems, the arrows denote new mathematical operators that participants had learned. In each stage, the axial slice ( $x = 0$  mm,  $y = 0$  mm,  $z = 28$  mm in Talairach space) highlights brain regions in which activation in that stage was significantly greater than the average activation during problem solving. Brain images are displayed with the left hemisphere on the right-hand side.

(Anderson, Pyke, & Fincham, 2016) (<http://dx.doi.org/10.1177/0956797616654912>)



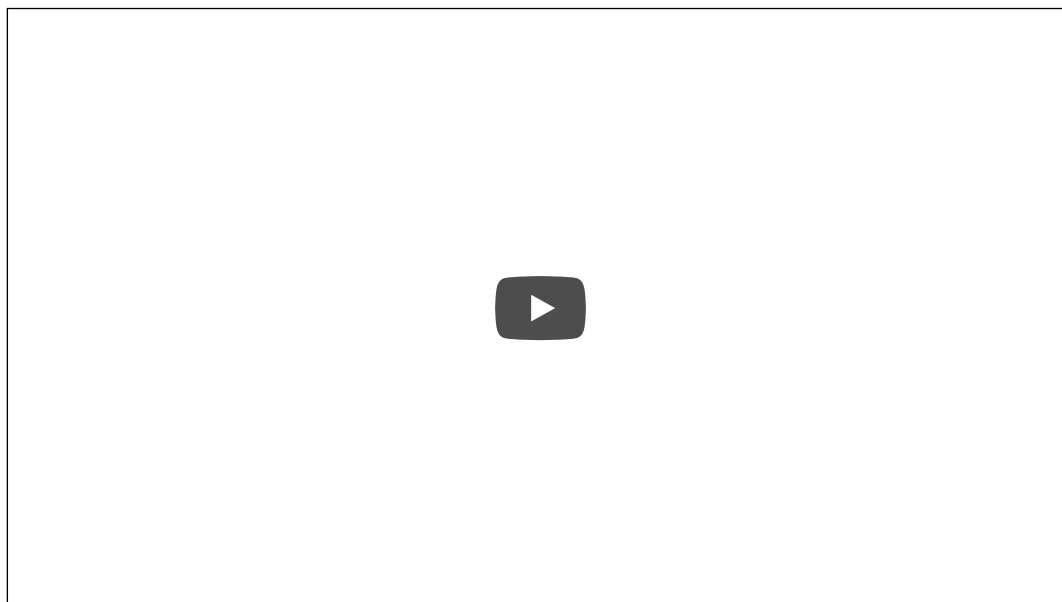
(Anderson, Pyke, & Fincham, 2016) (<http://dx.doi.org/10.1177/0956797616654912>)

Fig. 4. The four brain signatures placed in a 3-D space where the activity of a stage is a sum of the activity of the signature in the solving stage plus a sum of the three vectors weighted by their coordinates in the space. The heat maps illustrate the proportion of change in activation relative to baseline. The coordinates of the stages are as follows (in Talairach space)—encoding:  $x = 1.61$ ,  $y = 0.37$ ,  $z = 0.58$ ; planning:  $x = 0.58$ ,  $y = 0.28$ ,  $z = 1.38$ ; solving:  $x = 0$ ,  $y = 0$ ,  $z = 0$ ; and responding:  $x = 0.37$ ,  $y = 1.78$ ,  $z = 0.28$ . Brain images are displayed with the left hemisphere on the right-hand side.

(Anderson, Pyke, & Fincham, 2016) (<http://dx.doi.org/10.1177/0956797616654912>)

## Language and the brain

### Language behavior



- Productive
  - Speaking (2-5 words/s), modulate prosody, often combined with gesture
  - Writing, typing (.5-1.5 words/s)
- Receptive
  - Listening, responding (facial expressions, gestures, laughter, etc.)
  - Reading (3-5 words/s)
- How so fast? Time for feedback?

## Hierarchical structure of language information

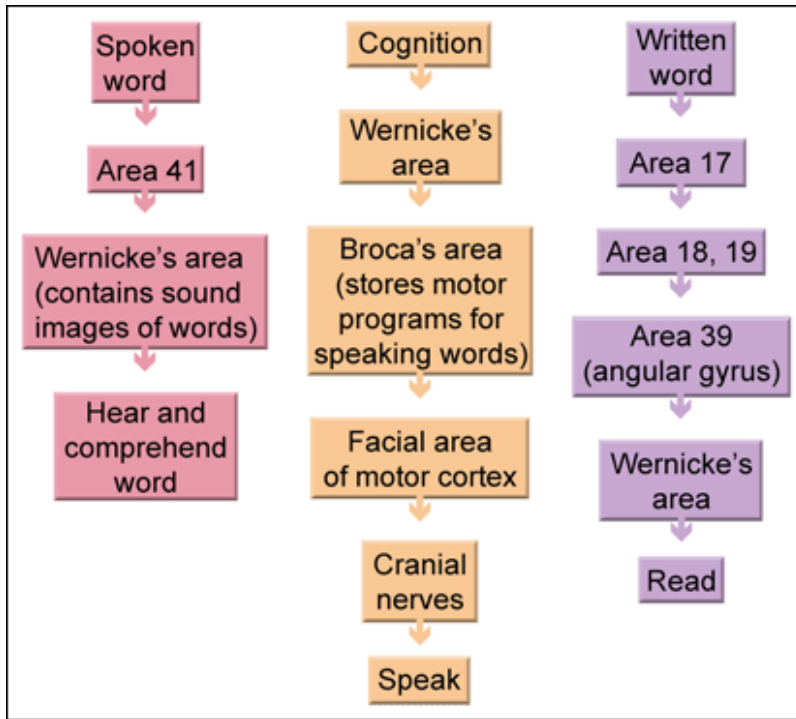
- Phonetic
  - |Ber| |wiTH| |mē|
- Syntactic
- Semantic



- Pragmatic

## Wernicke-Geschwind (WG) model

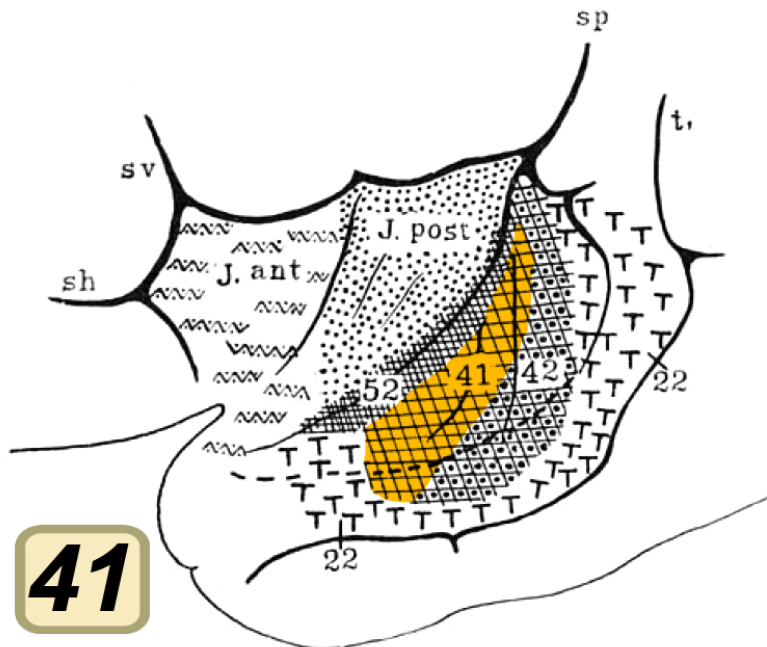
- Carl Wernicke ([https://en.wikipedia.org/wiki/Carl\\_Wernicke](https://en.wikipedia.org/wiki/Carl_Wernicke))
- Norman Geschwind ([https://en.wikipedia.org/wiki/Norman\\_Geschwind](https://en.wikipedia.org/wiki/Norman_Geschwind))
- Perception ≠ production



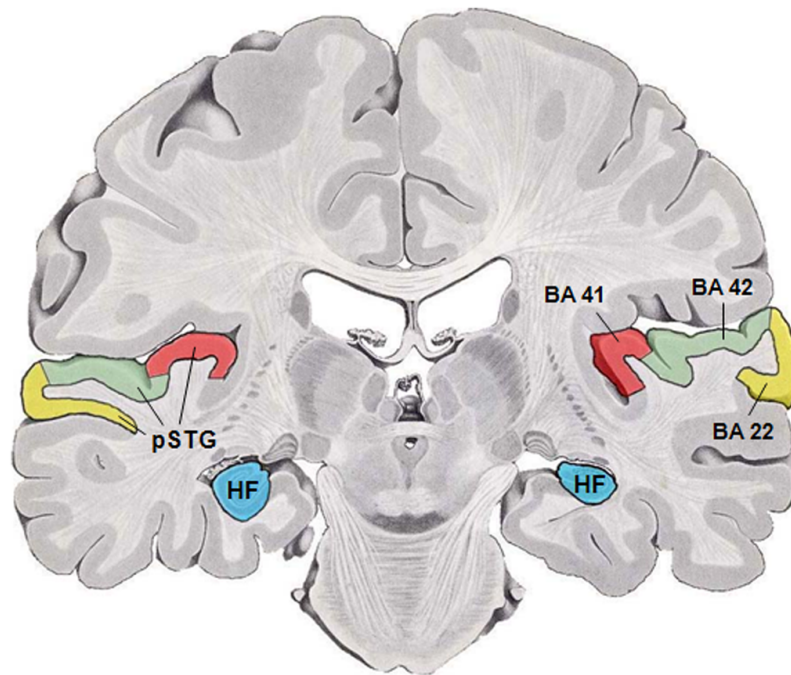
Wikipedia

### Wernicke's area (Brodmann Area or BA 42)

- Adjacent to primary auditory cortex (A1; Heschl's gyrus; BA 41)
- Perception
- Receptive or 'fluent' aphasia



Wikipedia



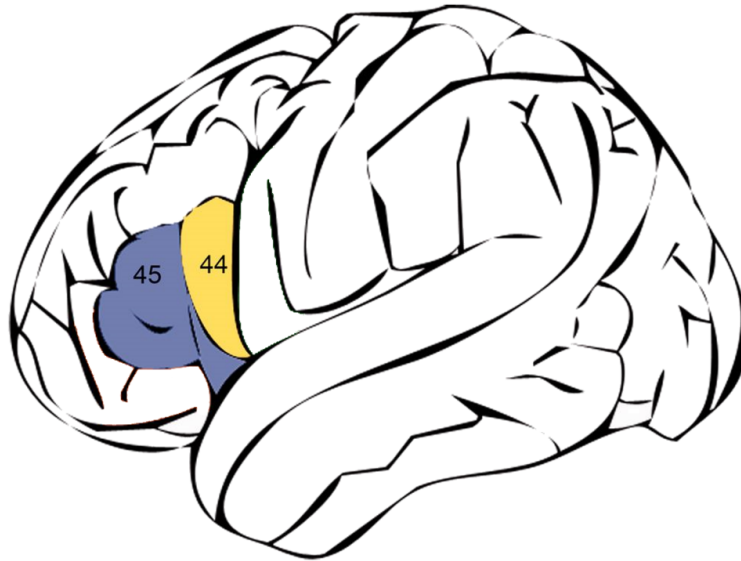
Wikipedia

Wernicke's aphasia



## Broca's area

- Inferior frontal gyrus, pars opercularis (BA 44) & pars angularis (BA 45)
- Production
- Expressive aphasia

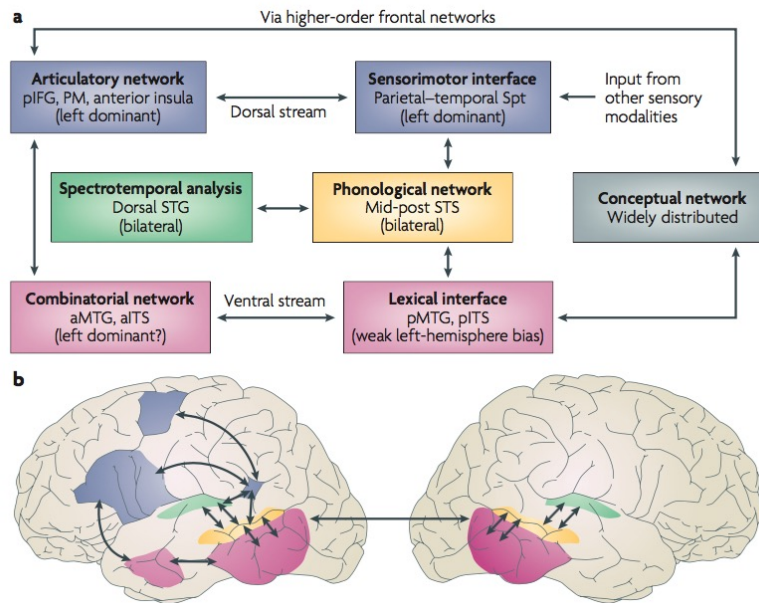


Wikipedia



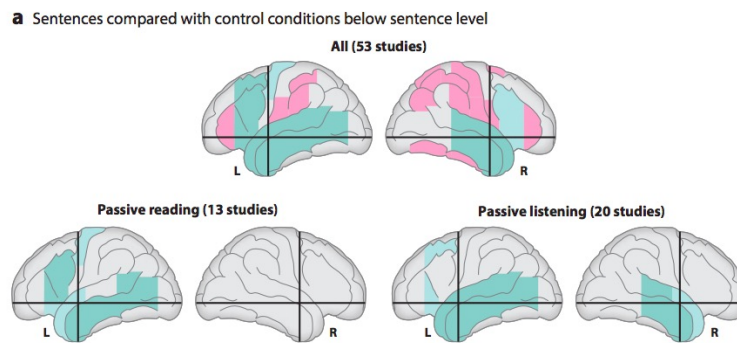
## Dual streams (Hickok & Poeppel, 2007) (<http://doi.org/10.1038/nrn2113>)

- Ventral (speech signals -> semantics)
- Dorsal (speech signal acoustics -> articulatory networks in frontal lobe)

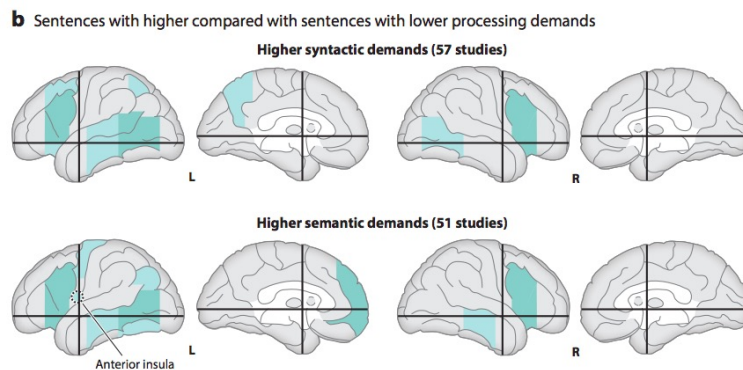


(Hickok & Poeppel, 2007) (<http://doi.org/10.1038/nrn2113>)

Metaanalytic evidence (Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)

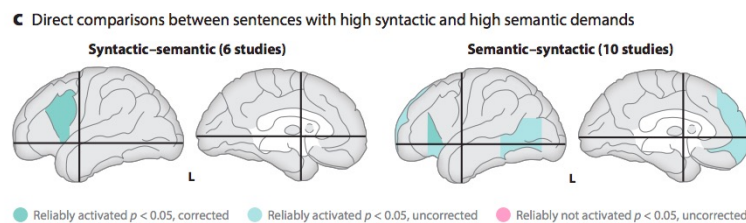


(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)



(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)

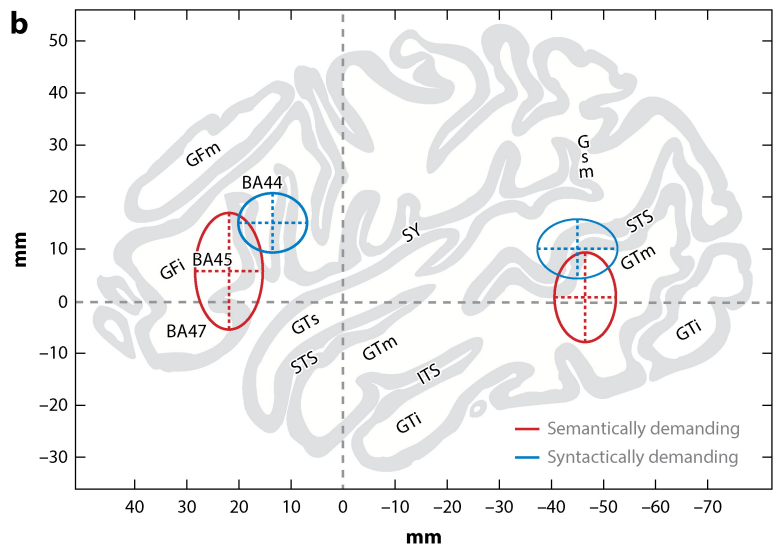
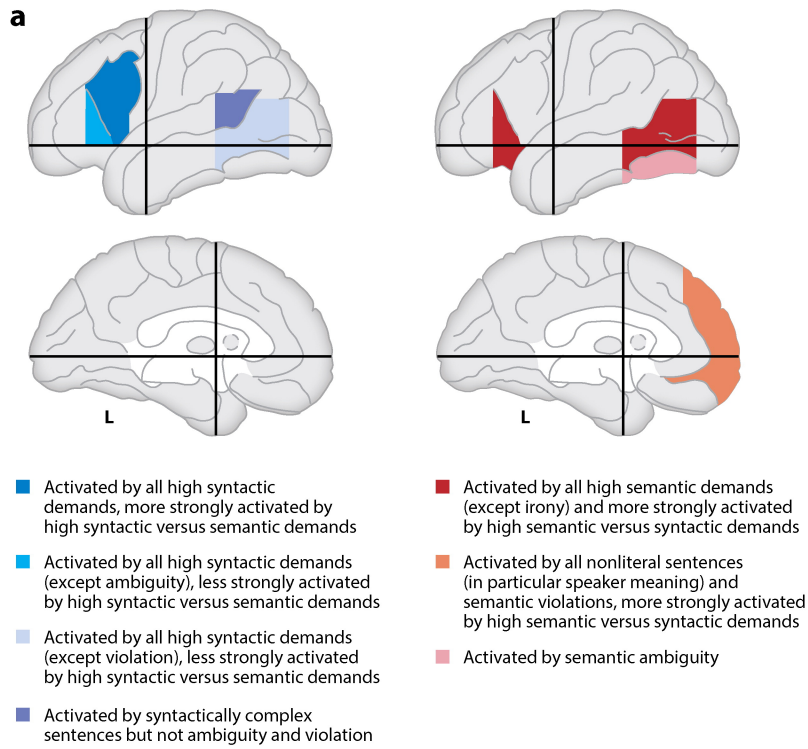




(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)

Figure 1. Schematic representation of the brain showing regions with reliably reported activations for sentences compared with nonsentential stimuli (a) and sentences with high syntactic or semantic processing demands compared with simpler sentences (b,c). The left posterior inferior frontal gyrus is further subdivided into Brodmann areas (BA) 44 (above black line), BA 45 (below black line, above AC-PC line) and BA 47 (below AC-PC line). Green regions indicate a reliable number of reports. Pink regions indicate no reports in 53 studies. For details, see Supplemental Tables 2, 3, and 4. Abbreviations: AC, anterior commissure; PC, posterior commissure).

(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)



**AR** Hagoort P, Indefrey P. 2014. Annu. Rev. Neurosci. 37:347–62

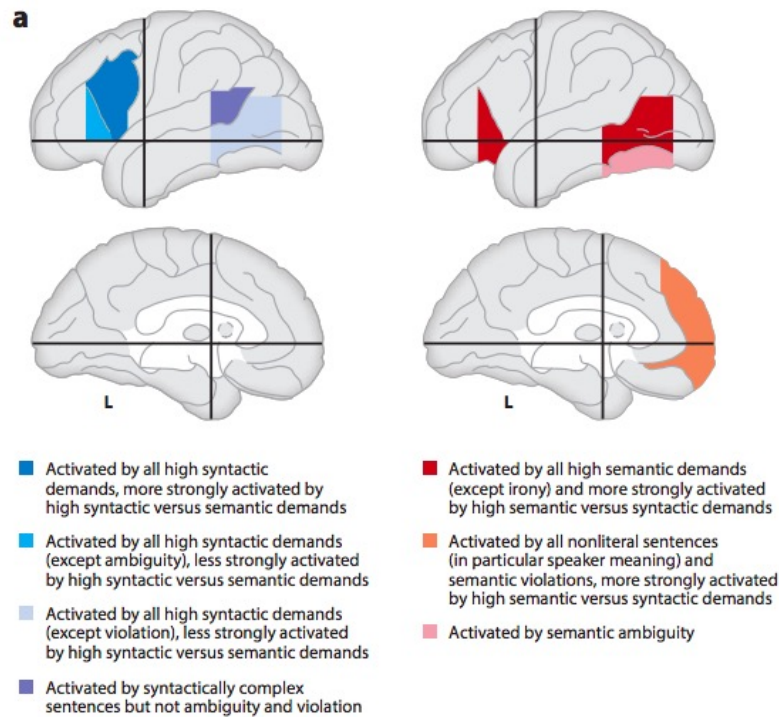
(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)

*“A meta-analysis of numerous neuroimaging studies reveals a clear dorsal/ventral gradient in both left inferior frontal cortex and left posterior temporal cortex, with dorsal foci for syntactic processing and ventral foci for semantic processing. In addition... further networks need to be recruited to realize language-driven communication to its full extent.”*

(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)

## Summing up

- WG model incomplete, simplistic
  - Broca's not just production; Wernicke's not just perception
  - Beyond single words...
- Rapid, fluent comprehension and production of language relies on
  - Distributed temporal/frontal networks
  - Efficient bottom-up and top-down processing
  - Syntactic vs. semantic/articulatory processing



(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)

Figure 2. (a) Summary of activation patterns for sentences with high syntactic or semantic processing demands compared with simpler sentences. (b) Syntactic/semantic gradients in left inferior frontal and posterior temporal cortex based on 28 studies reporting posterior temporal cortex activation for syntactically demanding or semantically demanding sentences compared with less demanding sentences (see Supplemental Figure 13 for details). The centers represent the mean coordinates of the local maxima, and the radii represent the standard deviations of the distance between the local maxima and their means. Abbreviations: GFm, GFi, middle and inferior frontal gyri; BA, Brodmann area; GTs, GTm, GTi, superior, middle, and inferior temporal gyri; STS, ITS, superior and inferior temporal sulci; Gsm, supramarginal gyrus.

(Hagoort & Indefrey, 2014) (<http://doi.org/10.1146/annurev-neuro-071013-013847>)

## References

- Anderson, J. R., Pyke, A. A., & Fincham, J. M. (2016). Hidden stages of cognition revealed in patterns of brain activation. *Psychological Science*, 27(9), 1215–1226. <https://doi.org/10.1177/0956797616654912> (<https://doi.org/10.1177/0956797616654912>)

- Bressler, S. L., & Menon, V. (2010). Large-scale brain networks in cognition: Emerging methods and principles. *Trends in Cognitive Sciences*, 14(6), 277–290. <https://doi.org/10.1016/j.tics.2010.04.004> (<https://doi.org/10.1016/j.tics.2010.04.004>)
- Coltheart, M. (2013). How can functional neuroimaging inform cognitive theories? *Perspectives on Psychological Science: A Journal of the Association for Psychological Science*, 8(1), 98–103. <https://doi.org/10.1177/1745691612469208> (<https://doi.org/10.1177/1745691612469208>)
- Fox, D. (2016). What sparked the Cambrian explosion? *Nature*, 530(7590), 268–270. <https://doi.org/10.1038/530268a> (<https://doi.org/10.1038/530268a>)
- Hagoort, P., & Indefrey, P. (2014). The neurobiology of language beyond single words. *Annu. Rev. Neurosci.*, 37, 347–362. <https://doi.org/10.1146/annurev-neuro-071013-013847> (<https://doi.org/10.1146/annurev-neuro-071013-013847>)
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nat. Rev. Neurosci.*, 8(5), 393–402. <https://doi.org/10.1038/nrn2113> (<https://doi.org/10.1038/nrn2113>)
- Powers, W. T. (1973). *Behavior: The control of perception*. Aldine Chicago. Retrieved from [http://www.pctresources.com/Other/Reviews/BCP\\_book.pdf](http://www.pctresources.com/Other/Reviews/BCP_book.pdf) ([http://www.pctresources.com/Other/Reviews/BCP\\_book.pdf](http://www.pctresources.com/Other/Reviews/BCP_book.pdf))
- Shine, J. M., Breakspear, M., Bell, P. T., Ehgoetz Martens, K. A., Shine, R., Koyejo, O., ... Poldrack, R. A. (2019). Human cognition involves the dynamic integration of neural activity and neuromodulatory systems. *Nature Neuroscience*, 22(2), 289–296. <https://doi.org/10.1038/s41593-018-0312-0> (<https://doi.org/10.1038/s41593-018-0312-0>)
- Swanson, L. W. (2005). Anatomy of the soul as reflected in the cerebral hemispheres: Neural circuits underlying voluntary control of basic motivated behaviors. *Journal of Comparative Neurology*, 493(1), 122–131. <https://doi.org/10.1002/cne.20733> (<https://doi.org/10.1002/cne.20733>)
- Swanson, L. W. (2012). *Brain architecture: Understanding the basic plan*. Oxford University Press.
- Tressoldi, P. E., Sella, F., Coltheart, M., & Umiltà, C. (2012). Using functional neuroimaging to test theories of cognition: A selective survey of studies from 2007 to 2011 as a contribution to the decade of the mind initiative. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, 48(9), 1247–1250. <https://doi.org/10.1016/j.cortex.2012.05.024> (<https://doi.org/10.1016/j.cortex.2012.05.024>)
- White, C. N., & Poldrack, R. A. (2013). Using fMRI to constrain theories of cognition. *Perspectives on Psychological Science: A Journal of the Association for Psychological Science*, 8(1), 79–83. <https://doi.org/10.1177/1745691612469029> (<https://doi.org/10.1177/1745691612469029>)