Subcortical Contributions to Language: The Fruit Below the Rind

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Introduction

The Issue

The study of the neurobiology of language has highlighted cerebral cortex while largely overlooking subcortical structures

This proclivity for cortex is found in both basic and translational research on language (as well as on other higher cognitive domains, e.g., reading, music, math)

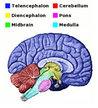
Subcortex has likely been ignored due to:
-methodological factors (fMRI: small nuclei, artifacts, …)
-various biases: small, not on surface. Streetlight Effect

Subcortex likely important in language:
For both anatomical and evolutionary reasons, multiple subcortical structures throughout the brain (well beyond the basal ganglia and cerebellum) likely play substantial roles in language and other domains:
-*Anatomical:* connectivity with cortical areas underlying language/cognition; also, there's lots of subcortex
-*Evolutionary:* animal subcortical precursors; cooptation

Our Solution

A comprehensive review of subcortical cognition

Review covers:
-subcortical (sub)structures throughout the brain (except cerebellum): lower and upper brainstem, diencephalon, telencephalon



-language as well as multiple lower and other higher cognitive functions

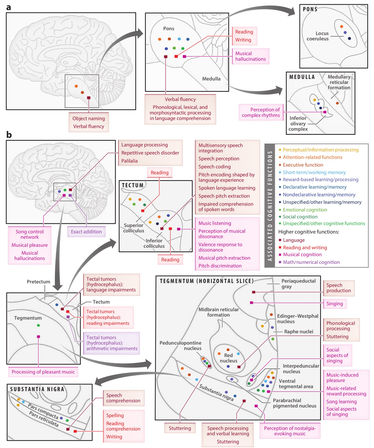
- Perceptual/information processing
- Attention-related functions
- Executive function
- Short-term/working memory
- Reward-based learning/processing
- Declarative learning/memory
- Nondeclarative learning/memory
- Unspecified/other learning/memory
- Emotional cognition
- Social cognition
- Unspecified/other cognitive functions

Higher cognitive functions:
- Language
- Reading and writing
- Musical cognition
- Math/numerical cognition

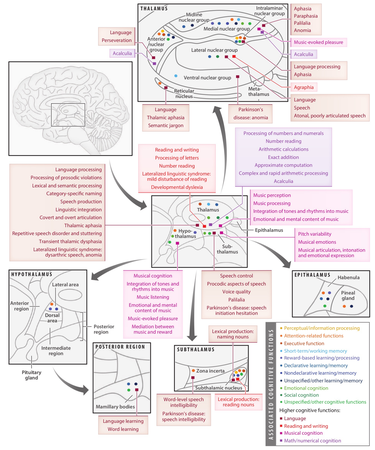
Two goals of the review:
-examine the extent of known subcortical contributions to language and other cognitive domains
-provide structure-function map for guiding future research

A Guide to Terra Cognita: Comprehensive Review of Known Structure-Function Map of Subcortical Cognition

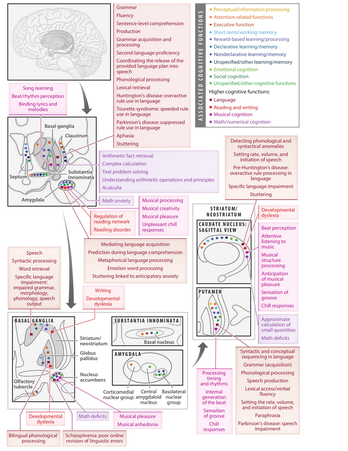
Contributions of multiple subcortical structures to language and other higher (and lower) cognitive domains



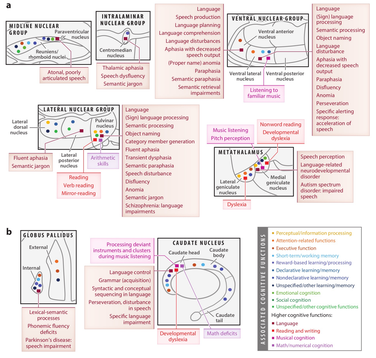
a) Lower brainstem: pons, medulla
b) Upper brainstem (midbrain)



Diencephalon: thalamus, hypothalamus, subthalamus, epithalamus



Telencephalon: basal ganglia, claustrum, amygdala, septal nuclei, substantia innominata



Substructures of thalamus and basal ganglia

A deep dive into lexical functioning

Subcortical structures implicated in lexical functioning:
-*Word learning*: mammillary bodies, lentiform nucleus
-*Lexical retrieval*: pons, many thalamic nuclei, subthalamus, striatum
-*Conceptual processing*: various thalamic and basal ganglia structures
-*Phonological processing*: red nucleus, various basal ganglia structures

How do they contribute to lexical functioning?
-Connectivity and cooptation can inform this

Mammillary bodies:
-*Connectivity*: hippocampus–fornix – mammillary body: declarative memory
-*Cooptation*: declarative memory has been coopted for word learning
Mammillary bodies in fact were predicted to underlie word learning (Ullman, 2004, 2016)

The findings are real and important

The findings are overall real:

Subcortical contributions to language/cognition are *extensive*, with converging evidence

In fact, the review likely *undercounts* these subcortical contributions (due to methodological constraints and biases)

The findings are overall important:

Subcortical contributions to language/cognition are *necessary*: lesion evidence implicates many structure-function mappings

Note that although subcortical lesions could lead to cortical dysfunction (e.g., diaschisis), so could the converse be true

See the four accompanying supplemental tables in the paper for more information and references

The Nature of Subcortical Cognition

A theoretical framework of (sub)cortical language/cognition built on three principles:

1) *One structure to many functions: core computations*
E.g., 'selection' for basal ganglia, based on direct and indirect pathways
Underlies executive function, working memory, procedural memory, grammar

2) *Many structures/circuits to one function*:
-Complementary (e.g., dorsal/ventral streams for vision or language)
-Redundant (e.g., procedural and declarative memory for skills/grammar)

3) *Dynamic*: contributions can vary by time, context, population…
E.g., whether skills/grammar learned in procedural and/or declarative memory

Proposed framework:
The MaMa (many-to-many) dynamic model of (sub)cortical contributions to language /cognition

Exploring Terra Incognita: How to Expand the Structure-Function Map of Subcortical Contributions

Where to look: Leveraging anatomical and evolutionary principles

Subcortical structures that are promising candidates for supporting language/cognition:

Anatomical: Structure is connected to cortical structures underlying language/cognition

Evolutionary:
-Structure underlies same/precursor function in non-human animals
-Cooptation: structure subserves analogous computations or functions in (non-)cognitive domains: Cooptation from non-cognitive to cognitive functions, lower to higher cognitive functions, higher to higher functions

How to look: A guide to methodologies for revealing subcortical cognition

Example: (f)MRI – approach, scanning, processing, analysis:

-Hypothesis-driven focal scanning
-Higher field-strength scanners (7 T, 10.5 T)
-Avoid multi-channel coils
-fMRI sequences with high signal/noise ratios
E.g., three-shot spiral dual-echo out-out sequence
-Anatomic alignment using specialized atlases for subcortical structures
-Controlling for physiological fluctuations

We also present recommendation for tDCS, intracranial brain recording/stimulation, EEG, MEG, TMS

In Closing

Our paper aims to stimulate research on subcortical contributions to language/cognition
This should advance our understanding of the neural bases of language/cognition
The time may be ripe to shine light on the fruit below the rind

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