Neurophysiology of speech perception

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Goal

• Understand the brain mechanisms underlying how speech signals are encoded and transformed into behaviorally relevant constructs.

Learner Outcomes

• Discuss the acoustical properties of the speech signals and talk about how these properties are encoded by the brain.
• Describe the latest neuroscience methods used to study speech perception.
• Discuss the impact of language, music and training experiences on the neurophysiology of speech perception.
• Understand how the brain processes speech signals in challenging listening environments.

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ROADMAP

I. Introduction: Speech signal, computational challenges for the brain
II. Neural (subcortical) reconstruction of the speech signal
III. Neural (cortical) representation of the speech signal
IV. Learning and neuro-plasticity

The speech signal: acoustics

Figure 1.1. Source-filter characterization of speech production with cross-section of vocal tract. Fant, 1960

McGettigan and Scott, 2012
**Phonetic quality.** The essential material from which we derive linguistic meaning (Linguistic)

**Affective (or emotional) quality.** Accompanies the linguistic message of speech and may contribute to the meaning of speech (Paralinguistic)

**Personal quality.** Outside the ordinary linguistic aspect of speech. Provides personal information about the talker. (Extralinguistic)

**Transmittal quality.** Provides perspectival information: talkers location, distance, presence of background noise, influence of environmental acoustics etc. (Perspective information)

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**Acoustic cues**

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**Speech signals are highly variable**

1. **Between talkers**
   - short vocal tracts: higher formant values; larger vowel space
   - the same formant frequencies will correspond to different vowels for different talkers

2. **Within talker**
   - connected speech vs. clear speech

3. **Environment**
   - various acoustic conditions

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**Speech is highly context-dependent (examples)**

- production of phonemes interacts with production of neighboring phonemes (co-articulation)
- acoustic cues broadly distributed in time
- no clear point at which cues for one phoneme start and the next begins
- acoustically different utterances must be mapped onto single phoneme

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**Speech signal is hard to segment**

- “phonemes are not like beads on a string” Hocket

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**Simple model of speech recognition**

- perception areas of the brain process the cues to help later stages of speech recognition

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**The speech signal: Information**

- phonemes are not like beads on a string

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**Broadbent and Ladefogt**
Things we do: use multiple cues

- Listeners pay attention to multiple cues rather than relying on a single cue => some information is redundant (several cues mean the same thing)
  - E.g., stop gap, voice bar, burst, VOT, F1 formant transition
- advantage: if we can’t hear all the cues, we may be able to recognize speech based on what we can hear
  - cues can be masked by noise or due to hearing impairment
  - talkers do not produce all of the cues clearly
  - talkers with different accents may produce a different set of cues than you expect

Things we do: use other senses

- Despite all this variability...
  - High speed of processing
  - Ability to “normalize” across speakers

Things we do: use temporal cues


**Figure 1:** Top panel shows the percentage of correctly identified words (% correct) depending on the SNR for the auditory-alone (A: dashed line) and the AV (solid line) conditions. Significant differences between both conditions are indexed with stars. (Ross et al., 2016)

**Figure 2:** Examples of spectral reduction for the speech token “kind of.” The original spectrum is shown with squares, “kind” with circles, and “of” with triangles. Other bands are reduced progressively by 3 dB at each level from top to bottom. The effect is most apparent in the low-frequency region, with the first two bands showing the most reduction. (Ross et al., 2016)

Things we do: categorical perception

- Categorize variable input
- Give greater perceptual weight to some acoustic differences than others
- Result: equal physical steps perceived as unequal
Stimuli

- When testing for categorical perception of VOT, simple CV syllables are made which differ equally in the timing of VOT.
- Example
  - Synthetic stimuli on the ba-pa continuum
  - From 0-40ms VOT
  - 5 ms increments

Categorical Perception

Identification: label the sound as b or p (or b, d or g).
This method = forced-choice identification

Discrimination: are two sounds same or different?
ABX method = listen to sound A, then sound B, then sound X. Is X the same as A or B?

Categorical vs. Continuous Perception

Continuous Perception
Linear relation between variation in VOT and perceptual identification

Categorical Perception
Non-linear relation between variation in VOT and perceptual identification

Identification experiments

- Discrimination task:
  - Are the two stimuli same or different?
  - ABX experiment: Does stimulus X match stimulus A or B?
  - 0 and 20 ms VOT; 20 and 40 ms VOT; 10 and 30 ms VOT, etc.
  - Pairs presented in random order
- Predictions:
  - if the pairs are easy to distinguish, accuracy 100%
  - if pairs are difficult to distinguish, accuracy 50% (guessing)
Discrimination experiments

- One pair that is easy to distinguish
- 20 and 40 ms VOT pair
- For all other pairs, discrimination at chance level
- Half of the time "same", half of the time "different"
- Failure to discriminate within a sound class.

The computational challenge of speech perception

- Deceptively automatic and effortless
- Computations involved is huge!
- For example: Speech produced involves vocalization (source), which passes through resonant oral and nasal cavities (filter)
  - Source carries information about 'who'
  - Filter carries information about 'what'
  - Numerous other information
- Continuous speech needs to be broken down (analog (acoustic) to digital (neural) code) by our ear!
- Needs to be reconstructed by the nervous system
- Reconstruction needs to be mapped to stored representations
- For example:
  - Sound to meaning mapping (what is being said)
  - Sound to articulation mapping (how is it being said)
  - Sound to ideosynaptic mapping (who is speaking)

Speech perception: From sound to sense

- Disturbance: Any disturbance (e.g. vocal fold vibration, tuning fork being struck) causes a change in pressure of a medium (could be gas, liquid, or a solid medium)
- Transmission: Pressure change transmitted through a medium to the listener’s ear (in the form of a mechanical vibration)
- Transduction process: Cochlea (end sensory organ) converts mechanical vibration to a neural code
- Deconstruction: Auditory periphery (cochlea) does a form of Fourier analysis (complex sound wave broken to constituent components)
- Reconstruction: Central auditory structures reconstruct the complex sound
- Perception: The complex sound is analyzed (what/who/where)

The computational challenge of speech perception

- Rapidly unfolding dynamics
- Phoneme processing is incredibly fast and flexible: 10-15 phonemes per second in typical speech
- as many as 40-50 in artificially accelerated speech (Liberman et al., 1967; Cole & Jakimilt, 1980)
- Speech needs to be mapped onto semantic and syntactic systems
- But also has a motor mapping
  - We often repeat to remember/comprehend speech
  - We can instantly learn new words with novel combination of speech sounds
Auditory physiology primer

Widely-accepted view
Subcortical auditory levels, primarily the inferior colliculus (IC); **New view:**
Also contributions from the auditory cortex (AC)

Spontaneous firing
Neural variability
Stochastic process

The auditory pathway

Basilar membrane is flexible and responds to sound energy
Introduction

- Human sub-cortical function thought to be hard-wired. Represents incoming signals with unwavering precision.
- Plethora of recent studies suggest that the auditory midbrain is plastic even in adulthood
- How the mature human auditory subcortical system solves the stability-plasticity conundrum is unclear.

Definition: Frequency-Following Response (FFR)

Scalp-recorded FFR reflects sustained, phase-locked activity in neural ensembles within the auditory subcortical system (Chandrasekaran & Kraus, 2010, Psychophysiology).

Stimulus

FFR


Neural reconstruction of the speech signal: the FFR

A metric by another name: cABR Speech-ABR Envelope Following Response (EFR)

Filtered to isolate brainstem contribution

80–1000 Hz filter

The frequency-following response (FFR: A neurophonic).

(Weiss et al. 1975, Science; Smith et al. 1975, Electroencephalogr Clin Neurophysiol)
The origins of the scalp-recorded FFR

Widely-accepted view
Subcortical auditory levels, primarily the inferior colliculus (IC)

New view:
Also contributions from the auditory cortex (AC)

Evidence for subcortical origins of the scalp-recorded FFR

(Chandrasekaran & Kraus, 2010, Psychophysiology)

<table>
<thead>
<tr>
<th>Evidence for cortical contributions to the scalp-recorded FFR</th>
</tr>
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<tbody>
<tr>
<td>(Coffey et al., 2016, Nature communications)</td>
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</table>

**Table 2.** Directions among Covariable Microphysioco (CM), Auditory Brainstem Responses, and Cortical Evoked Potentials

<table>
<thead>
<tr>
<th>CM</th>
<th>ABR/FFR</th>
<th>Cortical EPs</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Origin</strong></td>
<td><strong>Recording characteristics</strong></td>
<td><strong>CM, LL, IC</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Imicula</strong></td>
<td><strong>Responses present to alternating</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Stimulus level</strong></td>
<td><strong>P100</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Recording montage</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Response characteristic</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Fidelily</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Onset latency</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Latency variability</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
<tr>
<td><strong>Subject characteristics</strong></td>
<td><strong>Materiality</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
<tr>
<td><strong>Anodal</strong></td>
<td><strong>Unaffected by stimulus</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
<tr>
<td><strong>Anterior</strong></td>
<td><strong>Unaffected by attention</strong></td>
<td><strong>Latency shifts with stimulus</strong></td>
</tr>
</tbody>
</table>

CN: cochlear nucleus, LL: lateral lemniscus, IC: inferior colliculus, MGB: medial geniculate body (see Figure 2).
Evidence for cortical contributions to the scalp-recorded FFR
(Coffey et al., 2016, Nature communications)

Utility of the FFR

- Can be recorded regardless of age, language, motivation, or attention level
- Captures acoustic details of speech sounds with high fidelity
- Experience-dependent and reliable across individuals

The human FFR reflects time-invariant frequency information
(Greenberg et al., 1987, Hearing research)

The human FFR reflects (linguistic) time-variant pitch-relevant information
(Krishnan et al., 2004, Hearing research)

Test-retest Consistency

Xie, Reetzke, Chandrasekaran, 2017, Journal of Neurophysiology

Signal averaging

How many trials must be averaged to obtain a robust and reliable response?
Developmental Trajectory

Skoe et al., 2015, Cerebral Cortex

Human auditory function thought to be hard-wired. Represents incoming signals with unwavering precision.

Plethora of recent studies suggest that the auditory processing is plastic even in adulthood

Timescale, mechanisms underlying plasticity is unclear in humans.

Introduction

From Chandrasekaran and Kraus, 2010, Psychophysiology

Mechanisms underlying auditory subcortical processing from animal models

- Corticofugal (top-down) modulation from auditory cortex via extensive corticofugal (descending) pathways
  - Responsible for egocentric selection of auditory signals
  - Egocentric selection: Fine-tune representation of signals that are frequent-occurring and behavioral relevant to the organism
    (Yan and Suga, 1996; Suga et al., 1997; Suga, 2009; Bajo and King, 2015; Malmierca et al., 2015)

- Stimulus-specific adaptation (SSA) in auditory subcortical nuclei (e.g. inferior colliculus)
  - SSA refers to decreased responsiveness to frequent occurring sounds relative to a novel sound (Malmierca et al., 2014)
  - Preserved SSA even after the disruption of corticofugal modulation from the auditory cortex (Anderson, & Malmierca, 2015)

Long-term Auditory Experience (Lexical Tones)

Language experience

(Krishnan et al., 2005, Cognitive Brain Research; Xie et al., 2017, Journal of Neurophysiology)

Specificity of experience-dependent plasticity

Specificity of experience-dependent plasticity

(Non)Specificity of experience-dependent plasticity

Bilingual experience
(Krumen et al., 2012, *PNAS*)

Musical experience
(Wong et al., 2007, *Nature neuroscience*)

Online Stimulus Context (Lexical Tones)
(Lau, Wong, Chandrasekaran, 2017, *Journal of Neurophysiology*)

Online Stimulus Context (Lexical Tones)
(Lau, Wong, Chandrasekaran, 2017, *Journal of Neurophysiology*)

Online Stimulus Context (Lexical Tones)
(Lau, Wong, Chandrasekaran, 2017, *Journal of Neurophysiology*)

Language experience & Development (Jeng et al. 2011b)
The promise of FFR as a biomarker of auditory processing

FFR reflects fidelity, experience, decline, depredation, and disorder

The Test That Can Look Into A Child's (Reading) Future: a half-hour test — to predict kids' literacy skill before they're old enough to begin reading. ....if this isn't an honest-to-goodness crystal ball, it's close. (NPR, 2015)


Summary

- Human sub-cortical function reconstructs the speech signal with unwavering precision
- Subcortical processing of speech signals is also malleable to experiences across different time scales.
- FFR is a promising biomarker that provides insights into the process of signal reconstruction in the human auditory system.

ROADMAP

I. Introduction: Speech signal, computational challenges for the brain

II. Neural reconstruction of the speech signal

III. Neural representation of the speech signal

IV. Learning and plasticity
Both hemispheres can perceive speech

“Word deafness”: speech perception is impaired, despite intact hearing and sometimes even intact recognition of nonspeech sounds.

Crucially, it usually requires bilateral lesions to the middle and posterior portions of the STG and underlying white matter, while often sparing Broca’s gyrus.

<table>
<thead>
<tr>
<th>Description</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>“a noise”</td>
<td>Codier et al. (1984), Buchman et al.</td>
</tr>
<tr>
<td>“a bat or buzzing”</td>
<td>Mendez &amp; Godman (1980)</td>
</tr>
<tr>
<td>“like wind in the trees”</td>
<td>Ziegler (1952)</td>
</tr>
<tr>
<td>“like the rustling of leaves”</td>
<td>Luna (1986)</td>
</tr>
<tr>
<td>“like jabbering or a foreign language”</td>
<td>Deno &amp; Senetta (1975), Auerbach et</td>
</tr>
<tr>
<td>speech simply does not “register”</td>
<td>(1982), Buchman et al. (1986), Mendez &amp;</td>
</tr>
<tr>
<td>“words just run together”</td>
<td>Godman (1982)</td>
</tr>
<tr>
<td>“words come too quickly”</td>
<td>Saffran et al. (1976)</td>
</tr>
<tr>
<td></td>
<td>Klass &amp; Harper (1956)</td>
</tr>
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<td></td>
<td>Albert &amp; Bower (1974)</td>
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</table>

Hemispheric temporal specialization
“asymmetric sampling in time” hypothesis

- Some phonemic distinctions rapid others slower
  - Cat/Got (20ms)
  - CONTENT/conTENT (180-300ms)
- LH specialized for rapid phonemic transitions
- RH specialized for larger “chunks” such as syllables

Asymmetric sampling in time hypothesis (Poeppel, 2003)

- Primary auditory cortex carves incoming sound stimuli into large or small temporal windows
  - Slow vs Fast sampling
- LH samples much faster than RH as indexed by its oscillatory activity
  - See next

Asymmetric sampling in time hypothesis (Poeppel, 2003)

- LH dominance for rapid changes of ~20-80 ms, which is the range of phonemic contrasts (e.g., /k/ vs. /g/, or pets vs. pet)
- RH dominance for slower changes of ~150-300 ms, which is the range of syllabic contrasts (e.g., stress)

Specialization of the RH for slow acoustic distinctions

- Speech envelope: slow changes in speech that mark prosody

EEG Study: High Temporal Resolution
Theories of speech perception

- Speech perception involves matching highly variable acoustic signal to finite stored representation in the brain
  - What are the nature of the stored representation?
    - Phonemes are recognized on the basis of acoustic landmarks
    - Phonemes are recognized on the basis of articulatory gestures
      - Motor theory of speech perception

Theories have different neural predictions

Support for acoustic-based theories

"Who" Is Saying "What"? Brain-Based Decoding of Human Voice and Speech

Is there enough information in the auditory regions to classify vowels and speakers?


Conclusion

- Information within auditory regions to discriminate 'who' and 'what' information
- What does this mean
  - Auditory regions may be enough for speech perception, still does not prove acoustic landmark theory of speech perception (relatively low classification accuracies)
Support for motor-based theories

Motor-based theories

Motor cortex essential for Perception

The Essential Role of Premotor Cortex in Speech Perception (Meister et al. 2006)

- TMS video

fMRI data from 2 participants - regions that activated both during production as well as perception (target sites for repetitive TMS)

Results

Phonemes & Distinctive Features

- Phonemes can be characterized by a binary distinctive feature matrix
  - E.g., +/- Nasal, +/- Lip Rounding, etc

- What happens when everything +nasal?
  - “Mama is going to Nancy’s home.”
  - When might this happen?

- Co-articulation violates a fixed taxonomy
  - Why computers have great difficulty with speech recognition

Conclusion

- TMS on motor regions impairs speech perception but not STG
- What does this mean
  - Motor regions may be necessary for speech perception, still does not prove motor theory of speech perception
- Jury is still out

Phonemes & Distinctive Features

- STG populations tuned to features rather than phonemes

Mesgarani et al. 2014
ATLs play a key role in combinatorial semantics, integrating the relations between words and phrases.

red apple vs. fast apple

Left ATL activates for:
Intelligible > Unintelligible Speech
Semantically coherent utterances > Word lists

SPEECH PERCEPTION: THEORY AND CLINICAL ASPECTS

The elephant in the (Lab) room
I. Introduction: Speech signal, computational challenges for the brain

II. Neural reconstruction of the speech signal

III. Neural representation of the speech signal

IV. Learning and plasticity

Language-specific perception of speech sound categories is shaped early in life...

- results in “neural commitment” to native language speech sound inventory
- At the cost of the ability to learn speech sounds of a non-native language
- a striking lack of behavioral plasticity: even extensive (passive) exposure to a second language (post-sensitivitiy period) is not sufficient to attain native-like competence

Kuhl. 2010. Neuron
Werker & Hensch. 2015. Annu. Rev. Psychol
Yeung et al. 2013. J. Mem. Lang
Parker et al., Cognition
Laboratory training approaches yield significant and generalizable learning

- High-variability training
- Trial-by-trial corrective feedback
- Natural speech

Lively et al. (1994)
Lively et al. (1995)
Bradlow et al. (1997)
Bradlow et al. (1998)
Vroomen et al. (2003)

Cortical-subcortical interactions in (adult) speech learning: Premise 1

- Native acquisition of speech categories in infancy via cortical processes involving (largely) unsupervised Hebbian learning.
- In adults, unsupervised learning processes (cortex) are less plastic. Instead, highly plastic, feedback-driven cortico-striatal loops (reflective, reflexive) act as crucial intermediaries in training the less labile temporal lobe circuitry to represent novel speech categories.
- Individual differences in speech learning: (Sub-optimal) novice learning: reflective; experienced (optimal) learning: reflexive

Auditory cortex (A1); posterior superior temporal gyrus (pSTG), prefrontal cortex (PFC), hippocampus (Hipp), thalamus (Thal), caudate (Caud); globus pallidus (GP), putamen (Put); ventral tegmental area (VTA), nucleus accumbens (NAC), substantia nigra (SN). (b) Proposed distinctions in circuitry as a function of expertise.

Cortical-subcortical interactions in (adult) speech learning: Premise 2

Once categorical representations emerge and become stable, corticofugal system modulates early sensory processing of key features in a top-down ‘reverse hierarchical’ manner.

Tone languages: a window into examining experience-dependent plasticity to pitch

...in English, this change in syllable-level F0 does not convey word meaning differences

Gandour. 1983. J. Phonetics

Speech training paradigm...


Behavior

Talk roadmap

- **MRI**: Representation in native listeners
- **MRI**: Emerging category representations
- **EEG**: Emerging sensory plasticity
- **Behavior**: Individual differences

**Feng et al. 2018**
Cerebral Cortex

**Feng et al. in prep**

**Feng et al. in press**
Cerebral Cortex

**Reetzke et al. (2018)**
Current Biology

**Chandrasekaran et al. (2016)**
Journal of Neuroscience

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**Neural representation of tone categories in native listeners (Task effects)**

- **Multivariate pattern classification (MPC)**: Representational similarity analysis (RSA)

**Tone 1**
**Tone 2**
**Tone 3**
**Tone 4**

**Task-General and Acoustic-Invariant Neural Representation of (native) Speech Categories in the bilateral superior temporal gyrus (STG)**

**Category Representation**

- **LSTG**: Low-stimulus tone group
- **HSSTG**: High-stimulus tone group
- **LIPL**: Low-intensity pleasant language

**Feng et al. (2018)**
Cereb. Cortex

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**Neural representation of tone categories in native listeners (Feng et al., in prep)**

- **Iterative Ripple Noise (IRN)**

- **Tone categorization performance**

- **Tone category classification**

- **A**: Tone category classification
- **B**: Cross-stimulus type
- **C**: Cross-stimulus type

**Feedback [correct-incorrect] activates an extensive network**

- Prefrontal cortex: Reflective processing (‘thinking’)
- Dorsal striatum: Reflexive processing, reward value
- Anterior cingulate: Error monitoring/guiding behavioral choices (history of action/outcomes)

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**Emerging category representations in learners**

**Feedback [correct-incorrect]**

- Prefrontal cortex: Reflective processing (‘thinking’)
- Dorsal striatum: Reflexive processing, reward value
- Anterior cingulate: Error monitoring/guiding behavioral choices (history of action/outcomes)

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**Feedback [correct-incorrect]** activates an extensive network
Learning strategies across blocks

- Use quantitative decision-bound models to gain insights into locus of performance deficits/enhancements
- Computational models that make differing assumptions about the categorization strategy used by the observer
- Reflexive models (Striatal Pattern Classifier, SPC), based on the known neurobiology of striatal medium spiny neurons
- Reflective models (Unidimensional rules (UDX), conjunction rules (CJ))
- Identify the "best fitting" model (BIC) on a block-by-block basis

Representational plasticity with sound-to-category training

Feng, Yi, & Chandrasekaran. In press, Cerebral Cortex

Tracing the Trajectory of Sensory Plasticity across Different Stages of Speech Learning in Adulthood

A metric of sensory encoding: the frequency-following response (FFR)

Tracing the trajectory of emerging sensory plasticity

Hypotheses

A. Sensory enhancement is critical for initial stages of learning
B. Changes emerge at later stages of speech learning expertise

Signal Enhancement Theory

Reverse Hierarchy Theory

Cortical-subcortical interactions in (adult) speech learning: Towards a mechanism

1. Within a few hundred trials, behaviorally-relevant, abstract representations emerge in the (bilateral) superior temporal gyrus (STG)
2. Auditory cortico-striatal connectivity, functional coupling relate to individual differences in learning performance
3. The striatum is a key intermediary for speech learning in adulthood when unsupervised learning mechanisms are less labile, but reinforcement learning mechanisms are still active.
4. Sensory plasticity to non-native speech sound patterns not critical for early stages of speech sound learning
5. In line with the reverse hierarchy theory, training-related sensory enhancements may be an outcome of perceptual expertise

Behavior: sources of individual differences

Dual-learning systems (DLS) model

- At least two, competing, feedback-dependent neural circuits mediate speech learning
  - Reflective (negative-to-positive): Explicit, working memory-dependent, hypothesis-testing system mediates learning of simple rules.
  - Reflective (negative-to-negative): Implicit, procedural-learning system mediates schema-based learning of multidimensional-category structures that are not easily decodable by rules.
- Systems COMPLETE on all trials
  - Humans show an initial bias towards reflective processing
  - Successful learners switch to reflexive processing if the reflexive system is more accurate

80% acc
(last training block)
Sources
- Musicianship (Smayda et al. 2017, Frontiers in Psychology)
- Aging (Maddox et al. 2013, Psychology of Aging)
- Genetics (FOXP2). Chandrasekaran et al. 2015, J Neuroscience

Training paradigm
- Talker variability (Chandrasekaran et al. 2014, PBR)
- Information content in feedback (Chandrasekaran et al. 2014, PBR)
- Timing of feedback (Chandrasekaran et al. 2014, PBR)
- Performance Pressure (Maddox et al. 2016, Applied Psycholing)
- Instructions (Chandrasekaran et al. 2016, AP&P)
- Reward structure (Han et al. in prep)

Towards neurobiologically-inspired training approaches: information content
- Training paradigm

Towards neurobiologically-inspired training approaches: timing of feedback
- Training paradigm

Towards neurobiologically-inspired training approaches: performance pressure
- Training paradigm

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