

Context-dependent neural representation of time

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Outline

- **Introduction**
- **Expt. 1:** Temporal context-dependent perception of single time intervals (fMRI)
- **Expt. 2:** Temporal context-dependent working memory for single time intervals (Behaviour & fMRI)
- **Expt. 3:** Learning the temporal structure of natural sequences (Electrophysiology)
- **Discussion**

Why study timing?

- Important for accurate sensorimotor processing as well as higher cognitive functions.
- Natural sensory signals e.g. speech and music show rich temporal dynamics.
- Timing is integral for planning smooth, coordinated movements e.g. dancing.
- No peripheral receptors for time unlike for sensory signals.
- Timing deficits co-occur with several neurological disorders e.g. Parkinson's.

Models of Timing

Dedicated models:

Timing is mediated by dedicated modules in the brain.

e.g. cerebellum, basal ganglia, supplementary motor areas
visual, auditory and somatosensory cortex
parietal and frontal cortex

Intrinsic models:

Timing is an intrinsic computation that emerges from local network dynamics.

cf. Buonomano group

Context

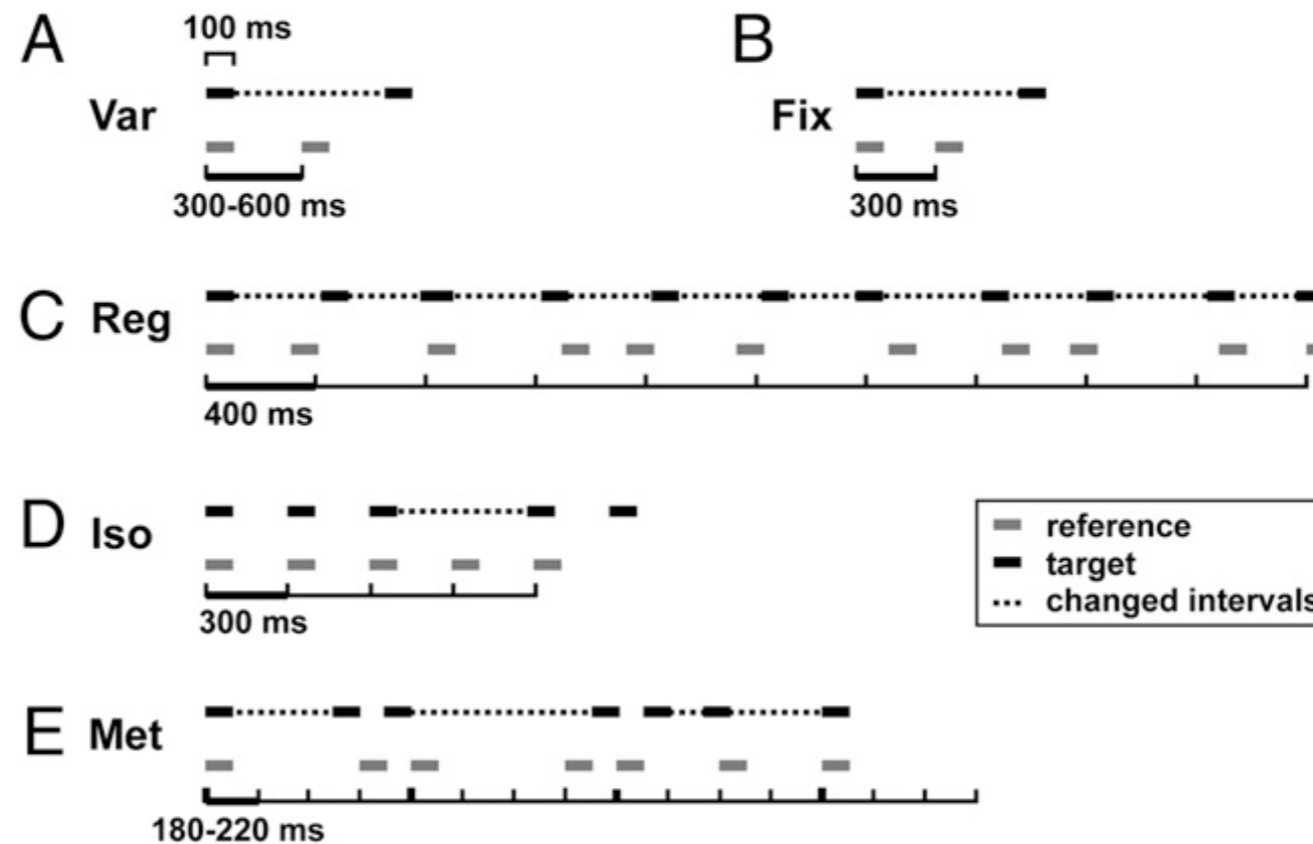
Several factors modulate our perception of time
(different aspects of timing; at different timescales etc.):

- Attention
- Memory
- Reward
- Decisions
- Movement
- Emotion
- Temporal context

1. Temporal context-dependent perception of single time intervals

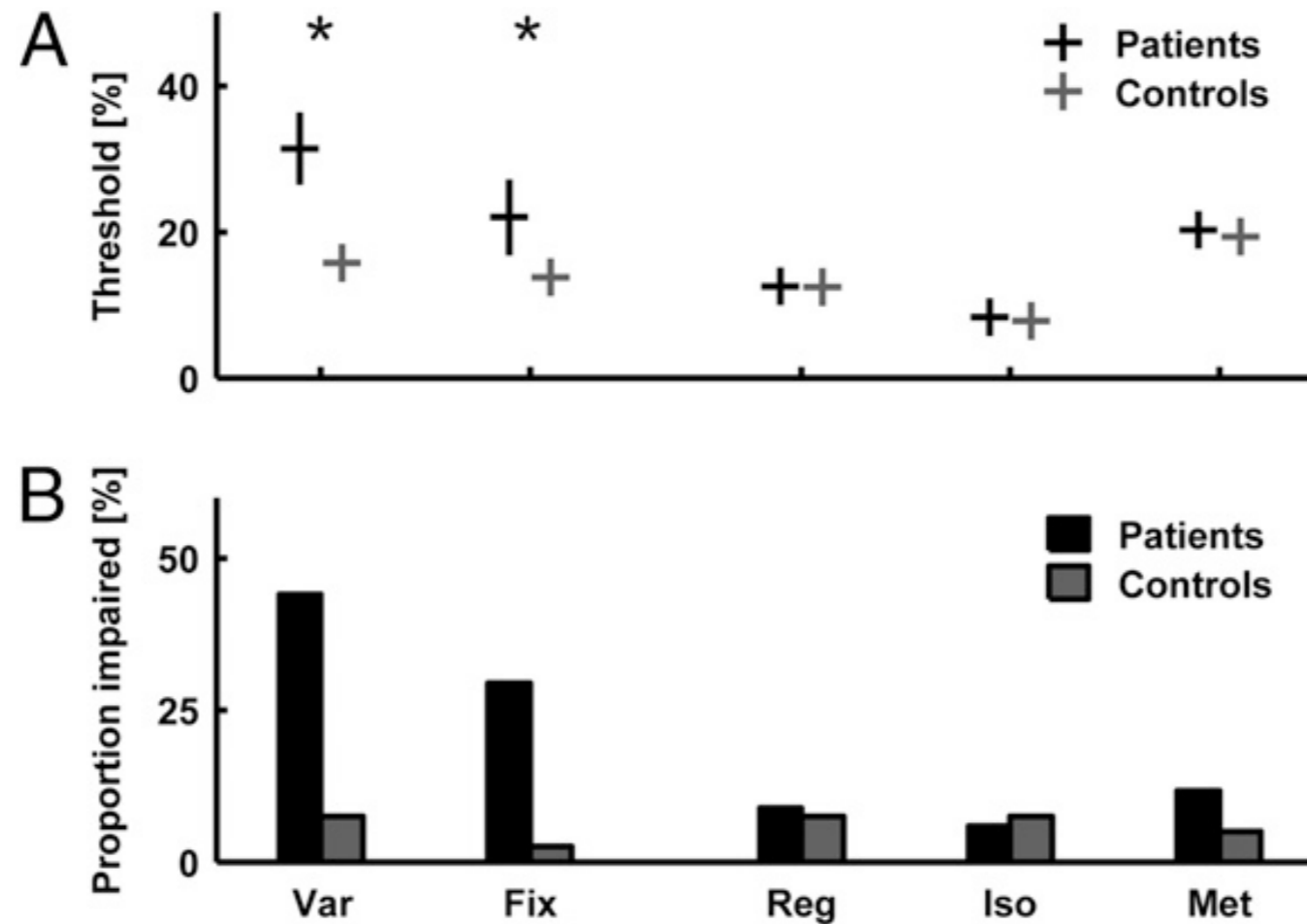
Duration-based timing

Encoding absolute duration of individual time intervals (ΔT_i)



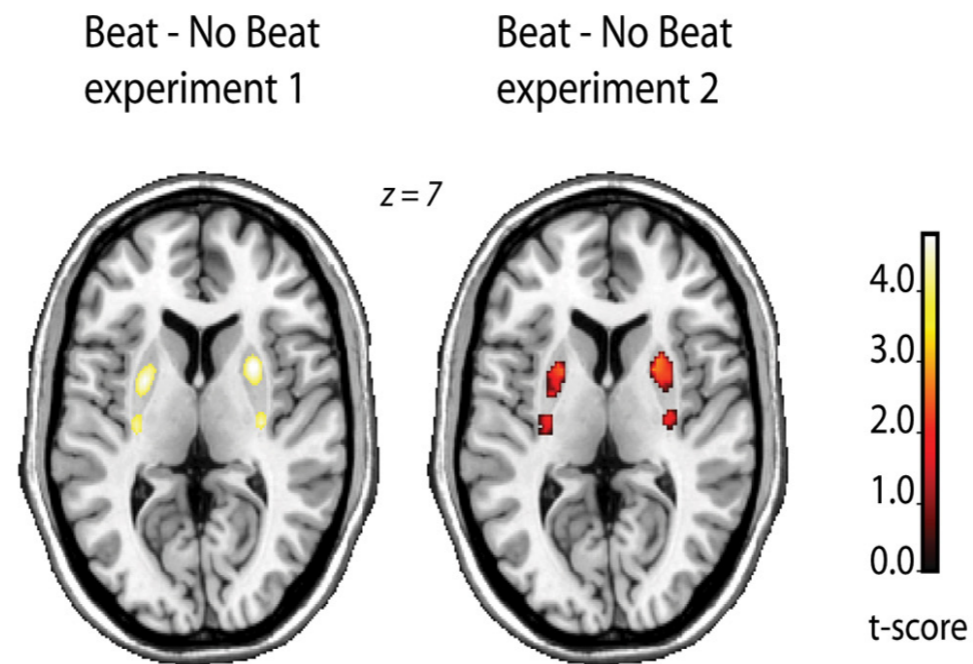
Duration-based timing

Patients with SpinoCerebellar Ataxia Type 6 with lesions to superior cerebellum

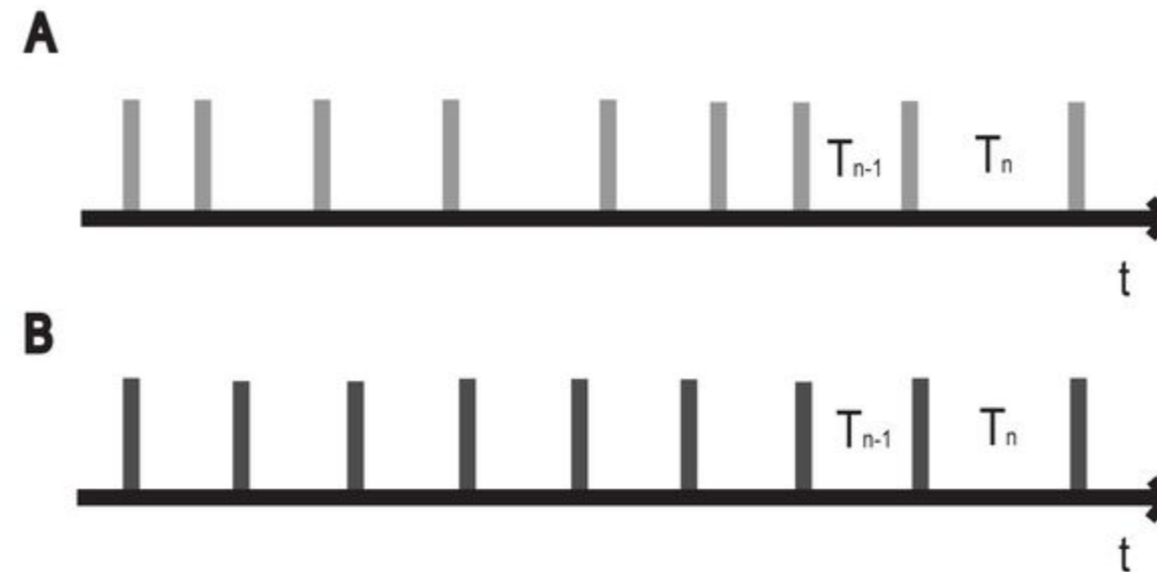


Beat-based timing

Timing of intervals relative to a regular beat ($\Delta T_i / T_{\text{beat}}$)



Paradigm



Task: $T_n > \text{or} < T_{n-1}$

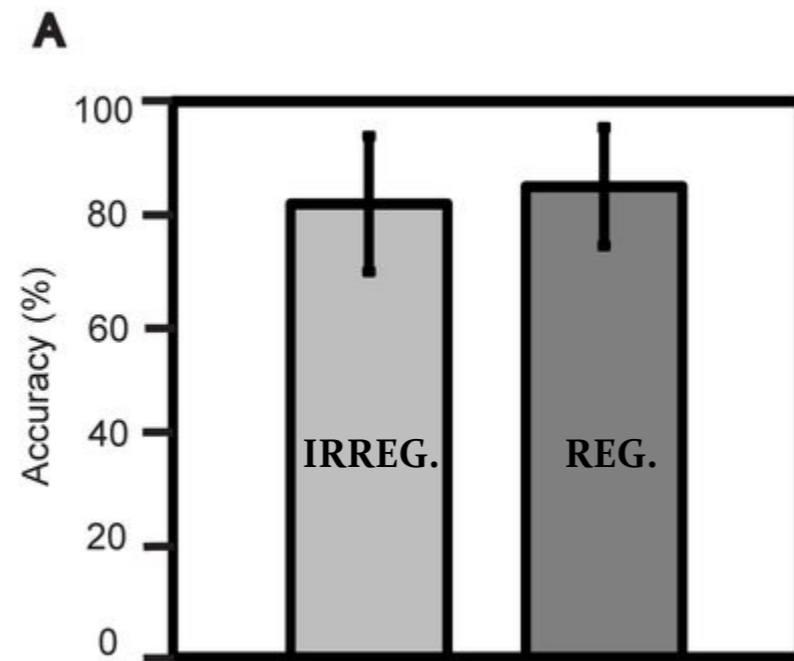
Sequence A: Irregular with 15% average jitter; $\Delta T = 30\%$ of IOI

Sequence B: Regular with an isochronous beat; $\Delta T = 15\%$ of IOI

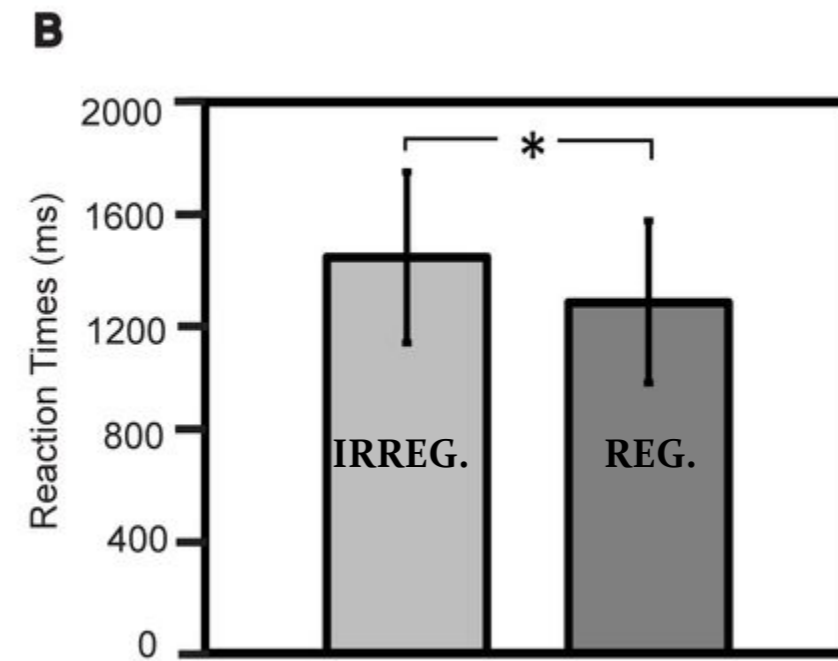
Irregular > Regular (measure of absolute timing)

Regular > Irregular (measure of relative timing)

Behavior



Mean **81.53%** **84.72%**
SEM ± 12.28% ± 10.64%

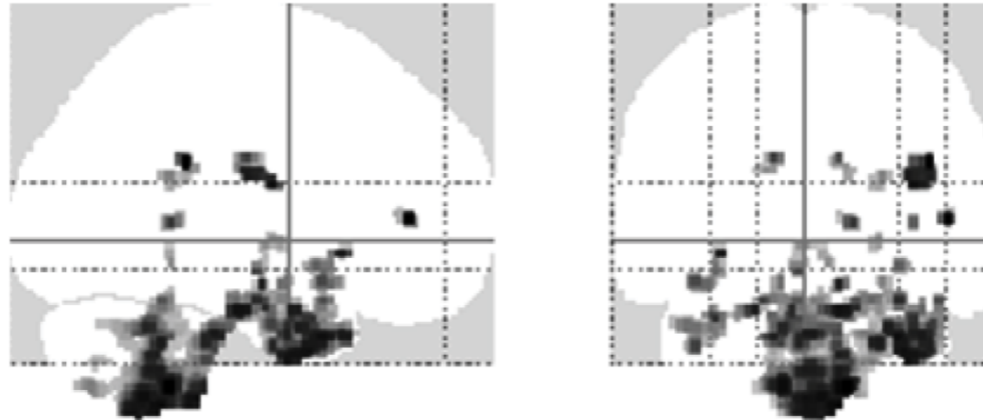


1438 **1275**
± 297 ms ± 312 ms

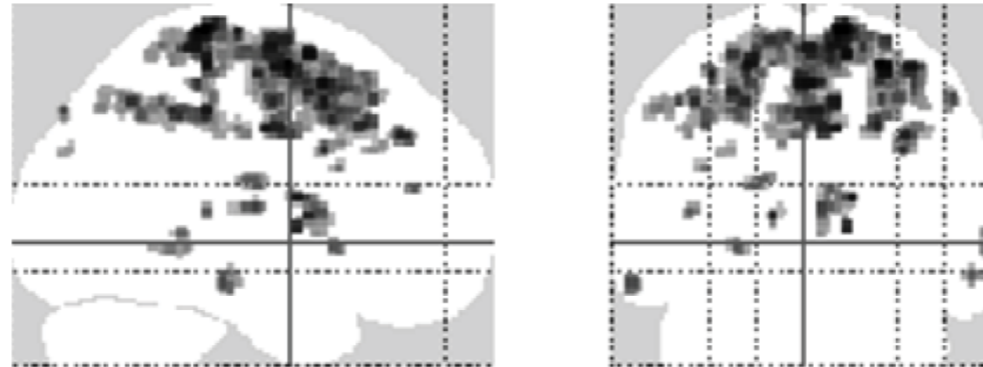
(N = 18)

fMRI results

A Activations for absolute, duration-based timing

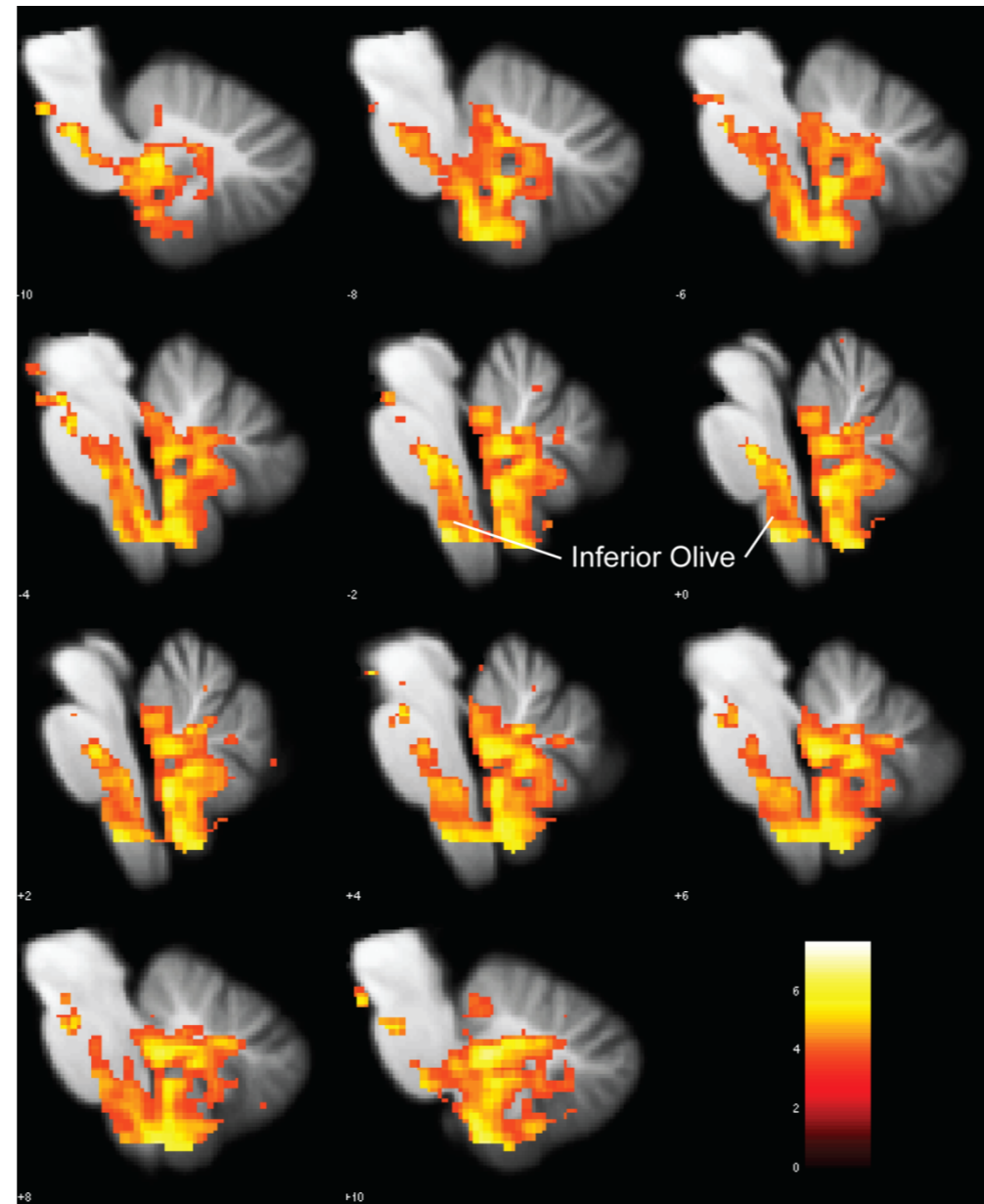


B Activations for relative, beat-based timing

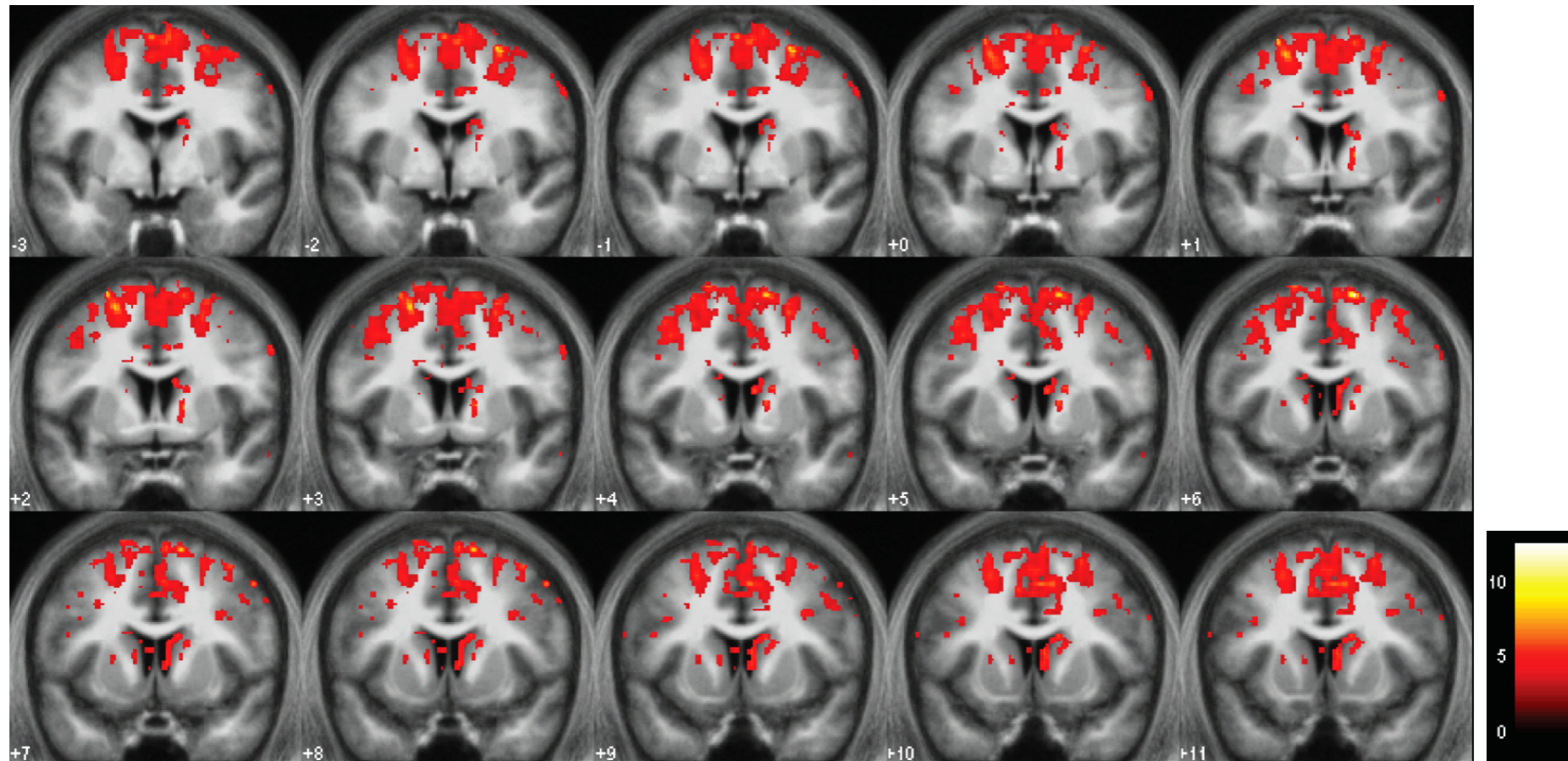


Duration-based timing

x = -10 to 10 mm

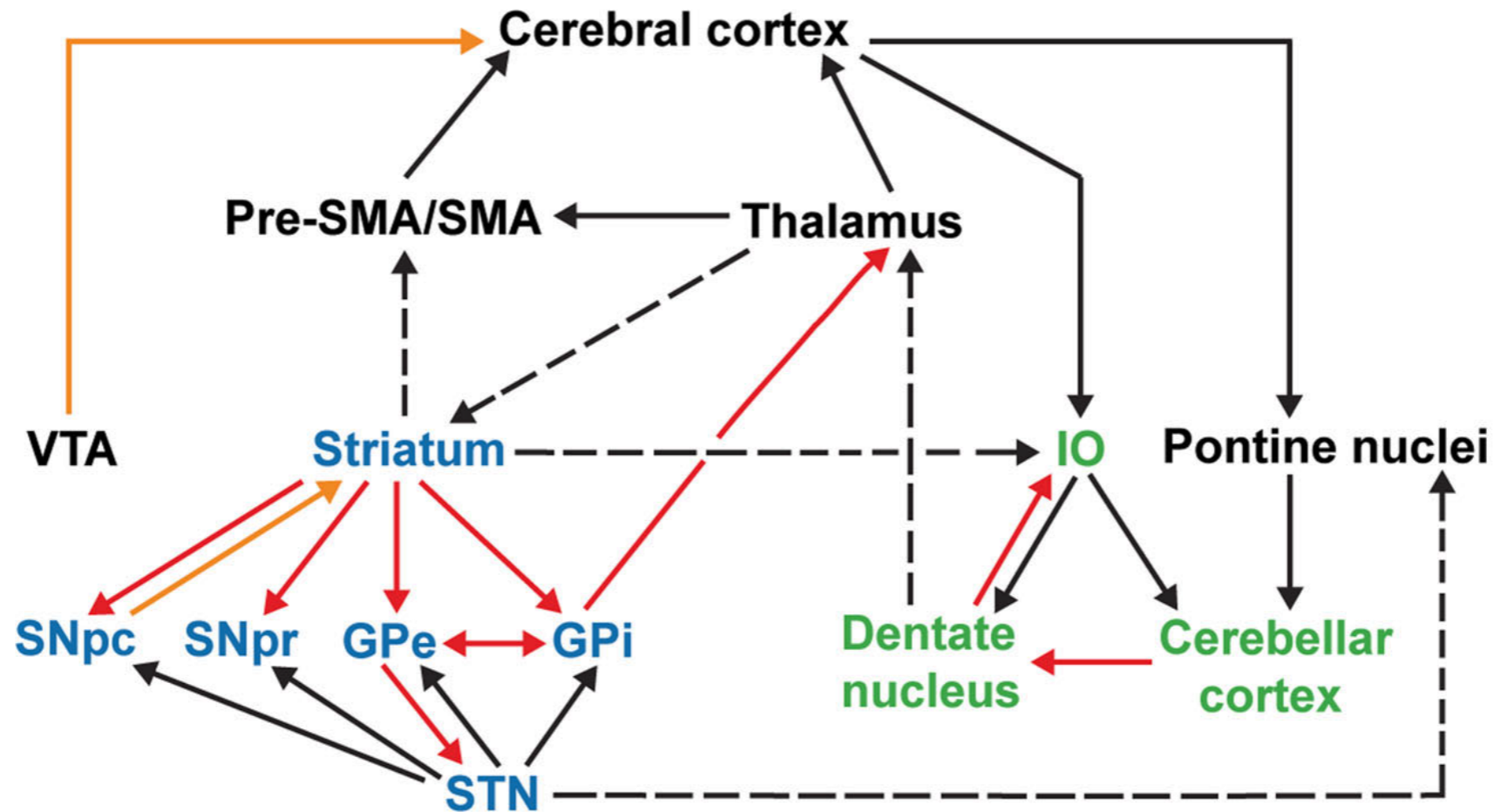


Beat-based timing



x = -3 to 11 mm

Network architecture



Teki et al., 2012 Frontiers

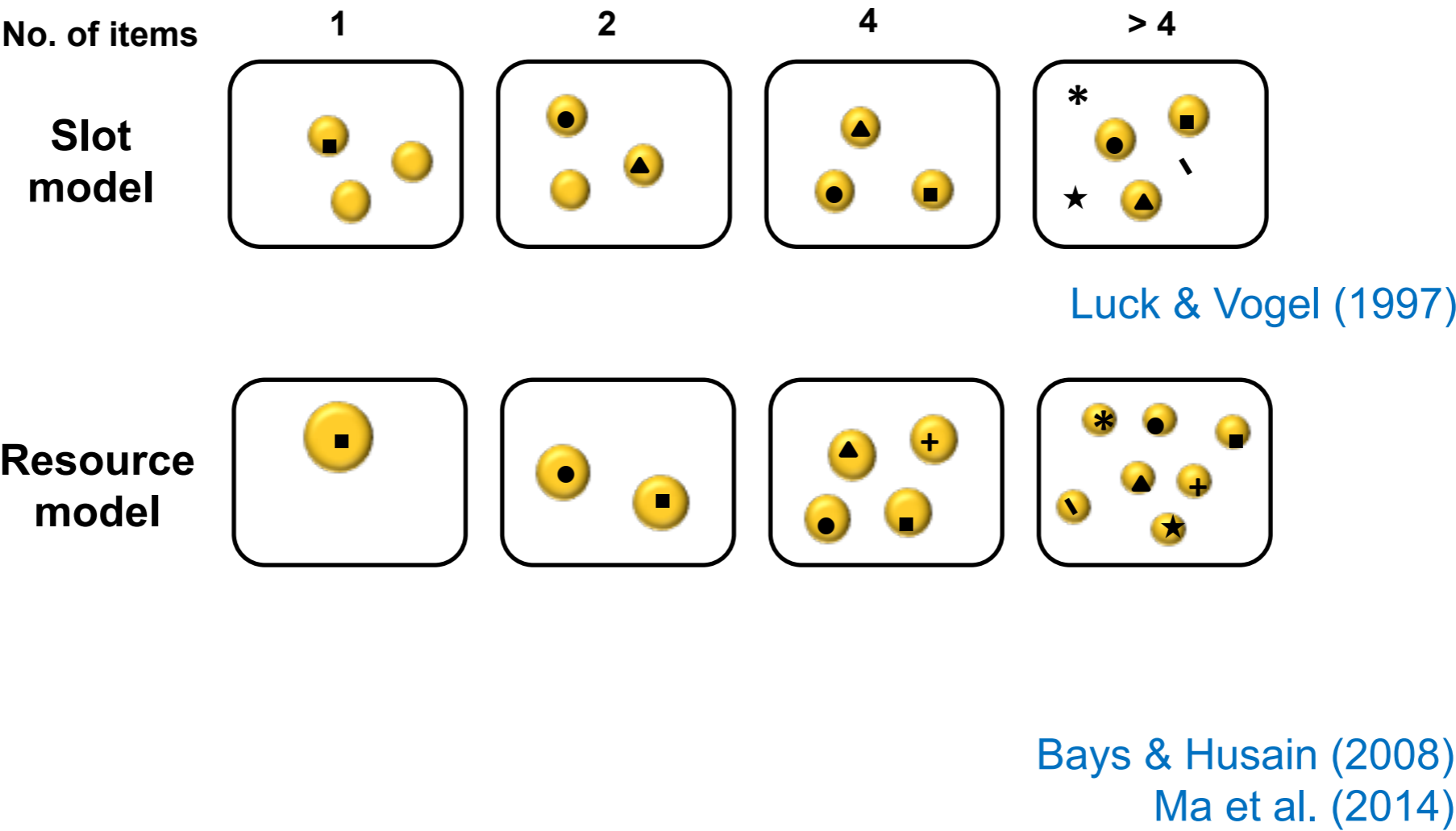
Allman, Teki et al., 2014 Ann Rev Psychol

cf. Peter Strick for cerebellum-striatum connections

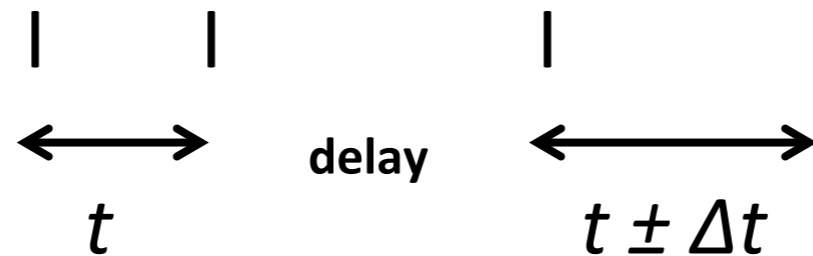
cf. Chen et al., 2014 *Nat. Neurosci.* for CB-BG physiology

2. Temporal context-dependent working memory for single time intervals

Models of working memory

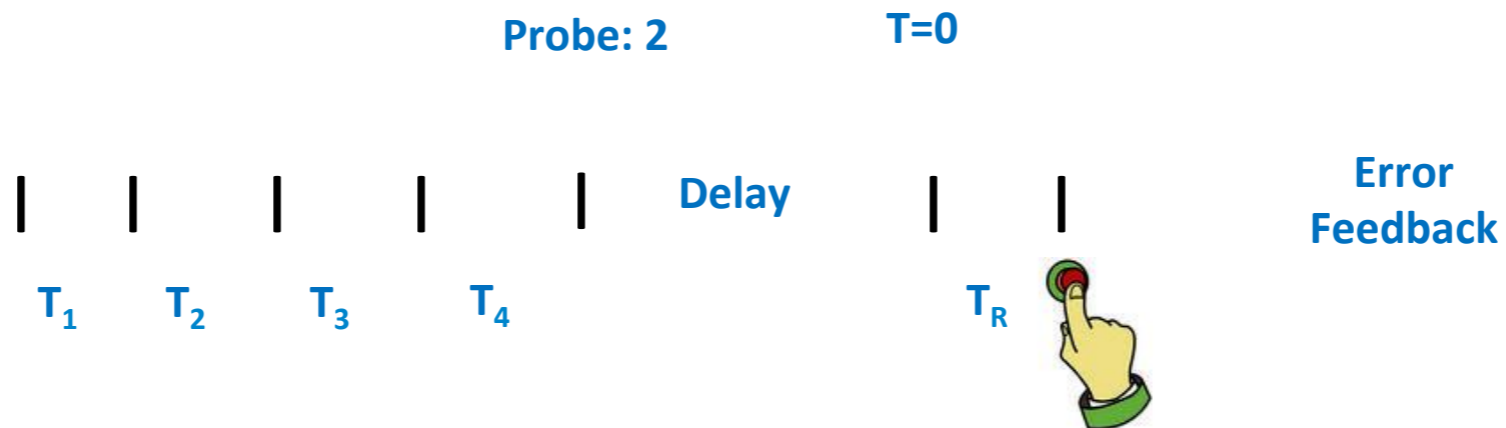


From single intervals to sequences



- discrimination task
- binary/categorical measure
- no variation of memory load
- isolated intervals; no variation of rhythmic structure

Paradigm



Perceptual time matching response = T_R (adjusted for reaction time)

Timing error response = $T_R - T_{\text{probe}}$

Precision of WM for time = $1/\text{STD} (T_R - T_{\text{probe}})$

Conditions

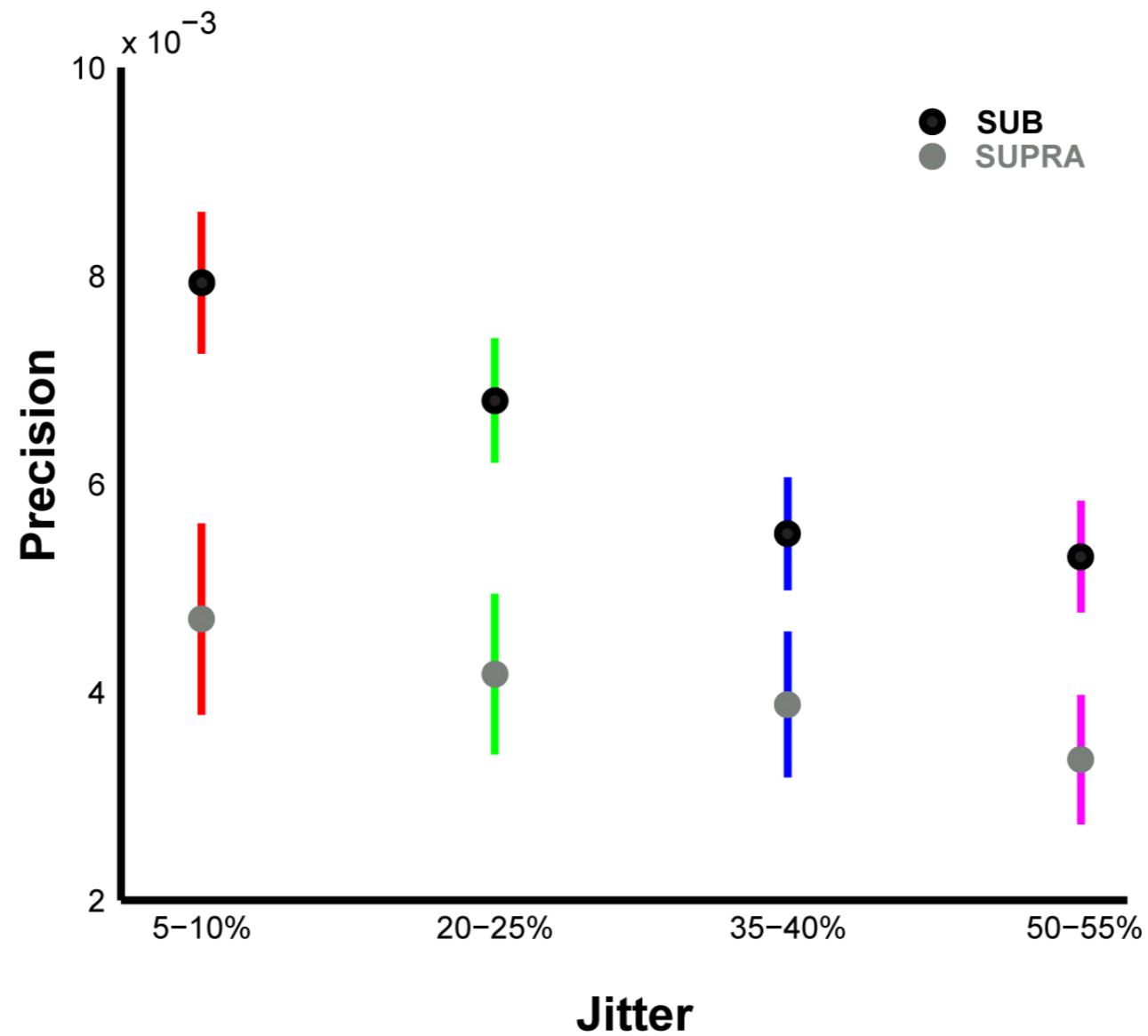
1: 'SUB'

- No. of intervals: 4
- IOI: 500-600 ms
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

2: 'SUPRA'

- No. of intervals: 4
- IOI: 1.0 - 1.2 s
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

Precision vs. Jitter



Significant effect of jitter for SUB ($p=0.01$) but not SUPRA ($p=0.65$)

N = 10 each

Conditions

1: 'SUB'

- No. of intervals: 4
- IOI: 500-600 ms
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

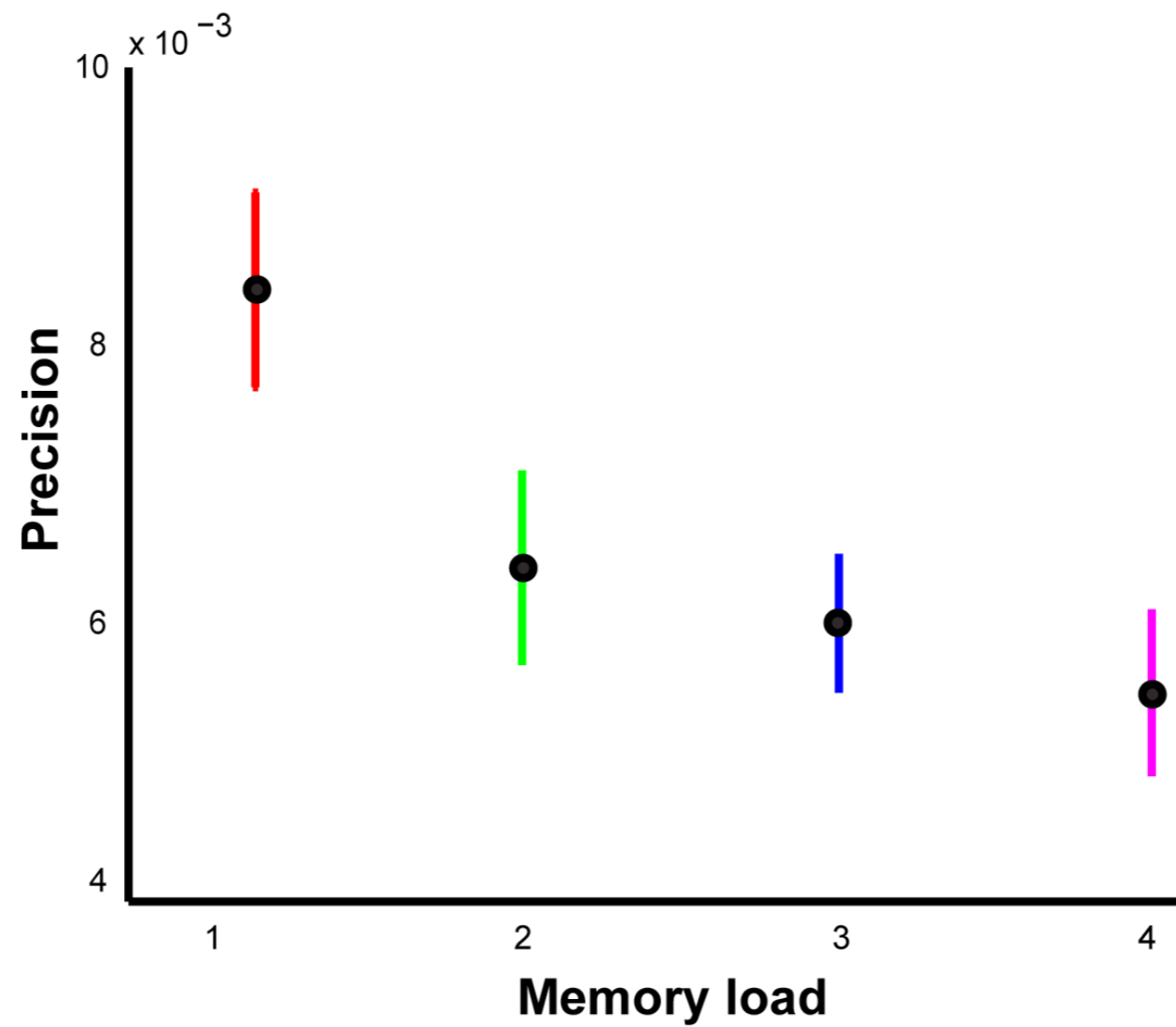
2: 'SUPRA'

- No. of intervals: 4
- IOI: 1.0 - 1.2 s
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

3: 'Memory load'

- No. of intervals: 1 - 4
- IOI: 500-600 ms
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

Precision vs. Load



Significant effect of WM load ($p=0.01$)

$N = 8$

fMRI

To examine brain areas that encode WM for time as a function of:

Temporal regularity

Memory load

(fixed WM load)

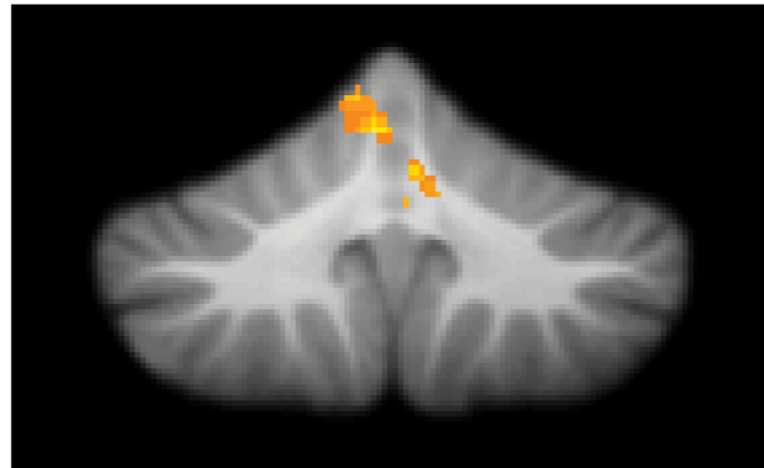
(fixed regularity)

WM load (# intervals)	Temporal regularity (% jitter)
4	5-10%, 20-25%, 35-40%, 50-55%
3	20-25%
2	20-25%
1	20-25%

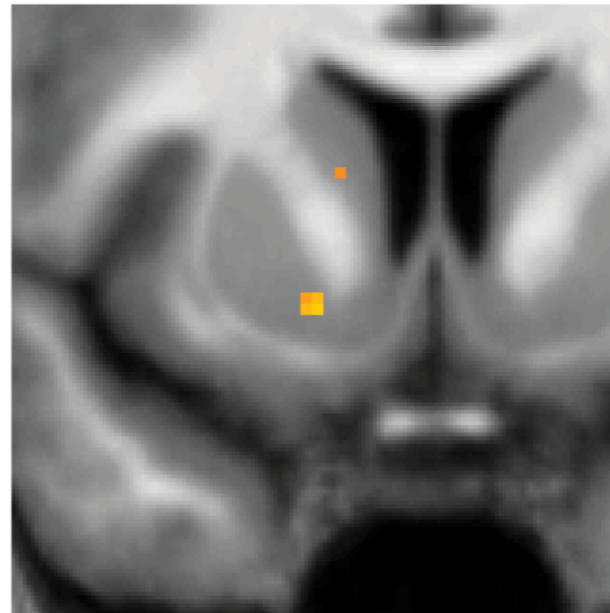
Effect of temporal regularity

A)

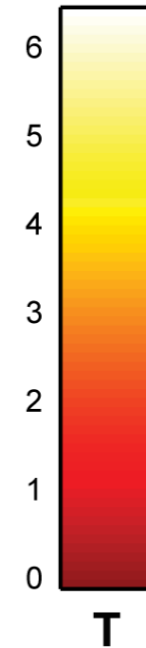
Increasing jitter



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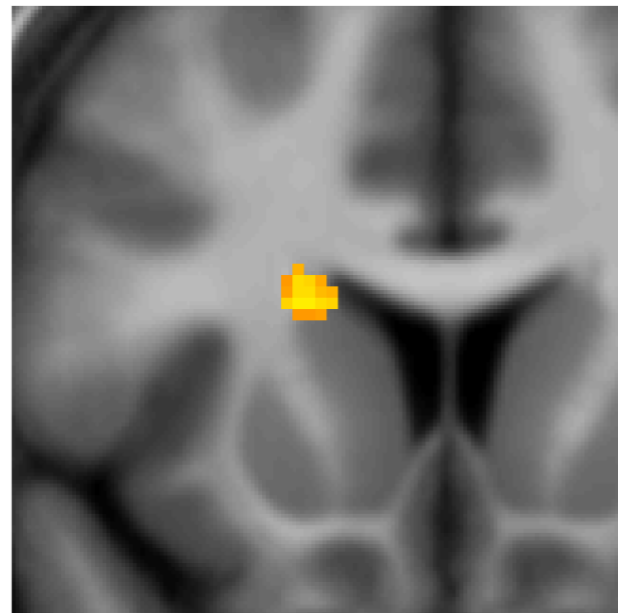


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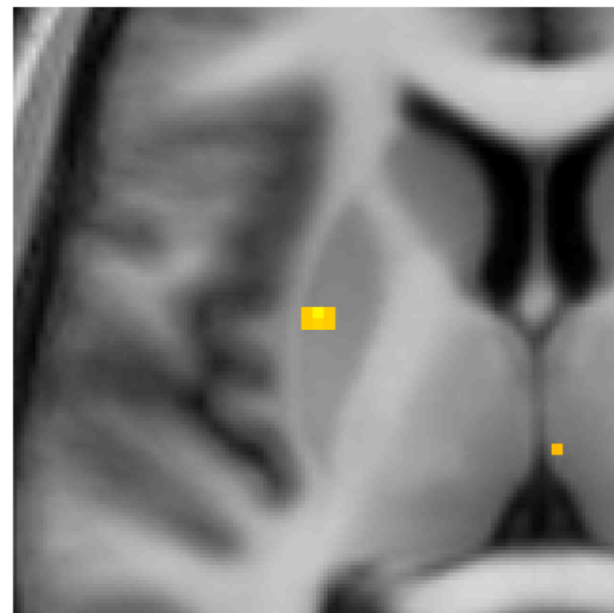


B)

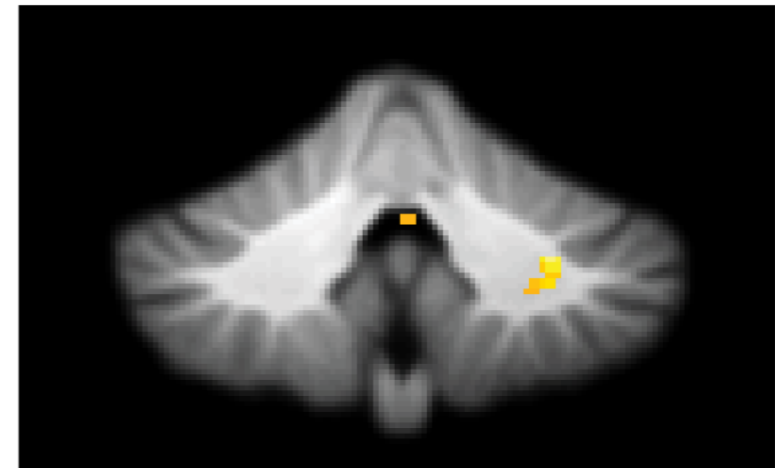
Decreasing jitter



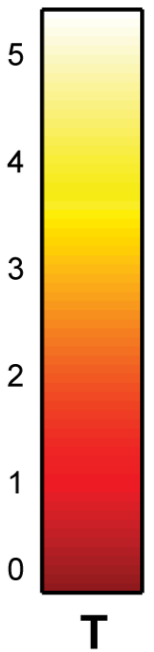
CAUDATE NUCLEUS



PUTAMEN



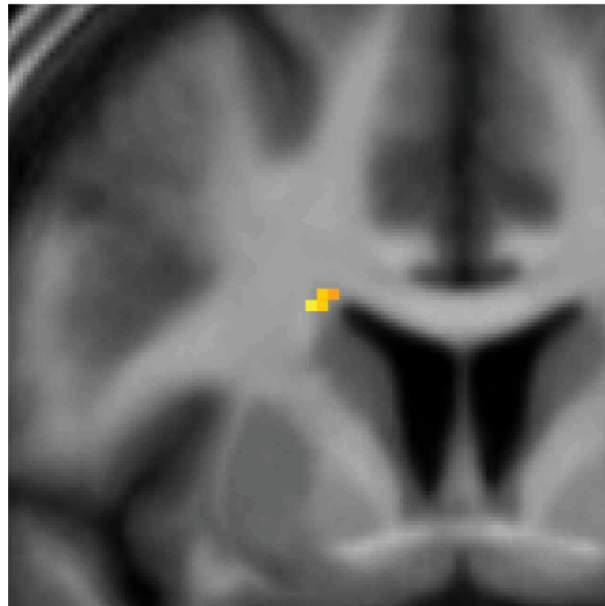
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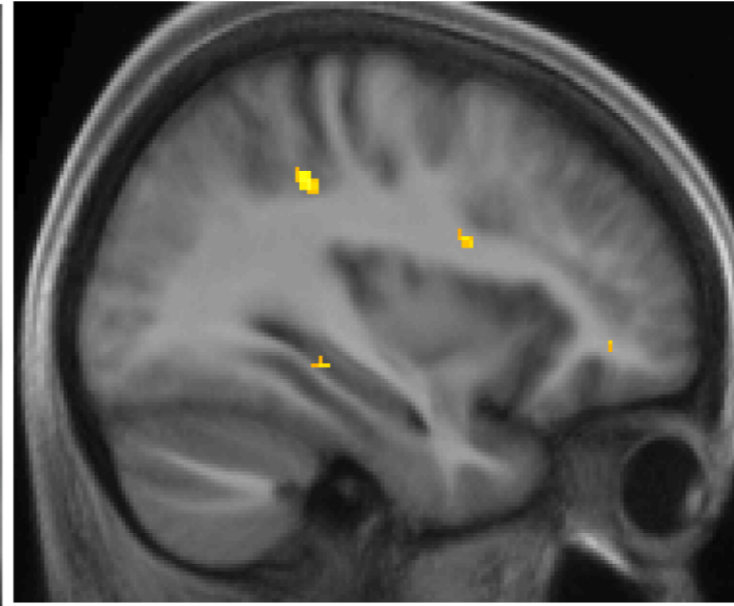
Effect of working memory load

A)

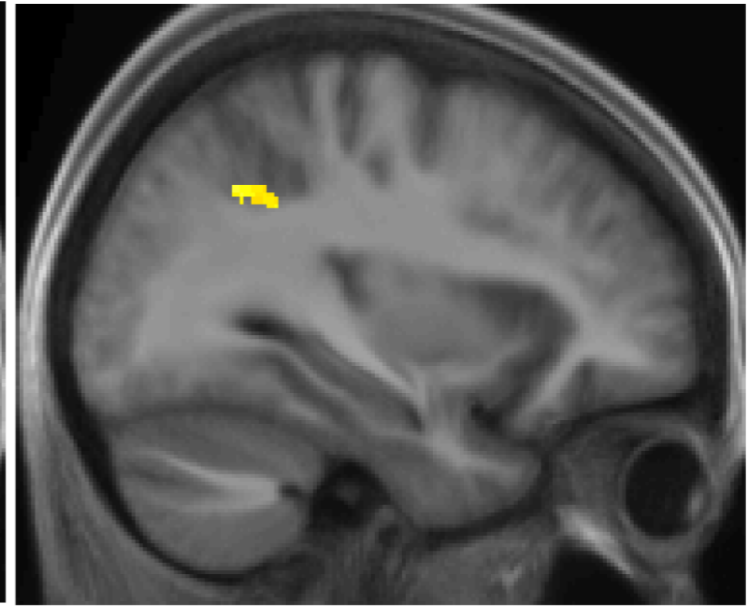
Increasing load



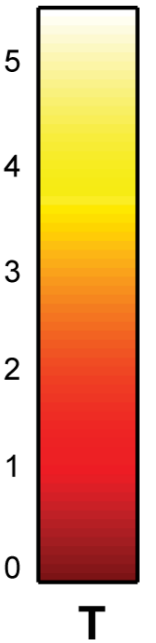
CAUDATE NUCLEUS



RIGHT PARIETAL CORTEX

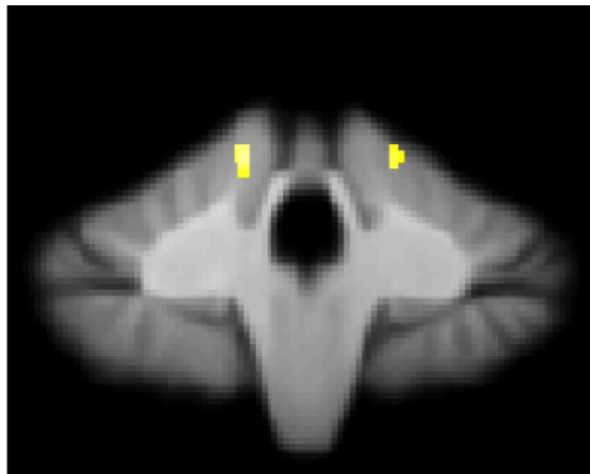


LEFT PARIETAL CORTEX

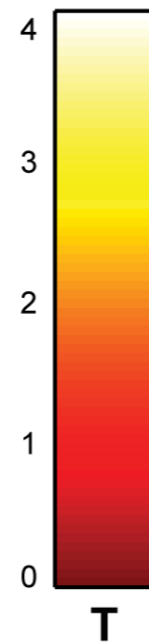


B)

Decreasing load



CEREBELLUM



3. Learning the temporal structure of natural sequences

Paradigm

Training phase:

Expose ferrets to a sequence of artificial vowels with different frequencies, ABCD and record from auditory cortex using multi-channel electrodes ($n = 32$).

Test phase:

Examine whether neural responses show evidence of generalization when ABCD is later presented with different acoustic manipulations e.g.

- timbre,

- timing (absolute or relative),


- predictability,

- background noise.

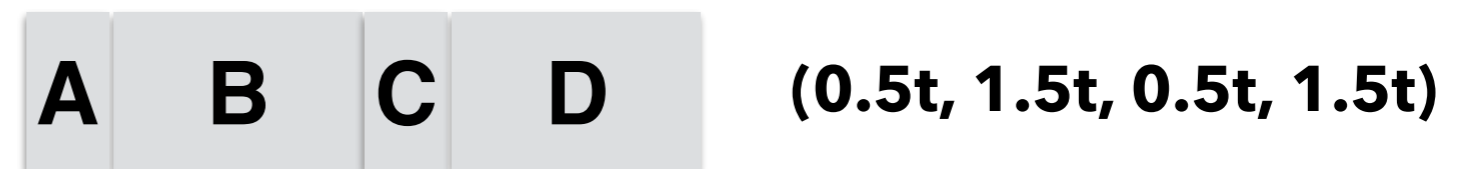
Paradigm

Training phase

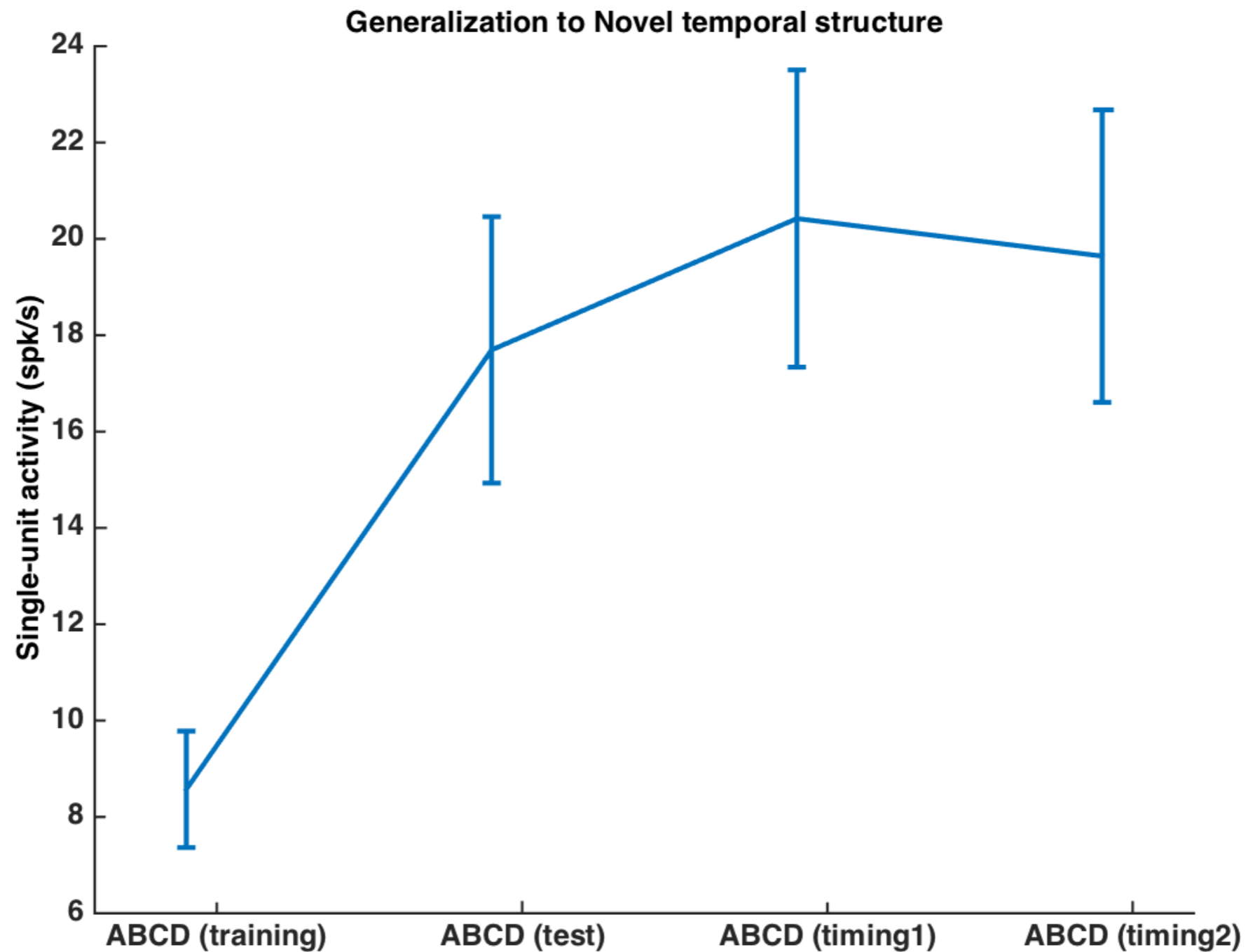



t

Test phase



Generalization to novel timing structure



(n = 58 neurons in primary auditory cortex)

General conclusions

- Neural representation of time is context-dependent.
- Temporal context modulates perception and working memory for time.
- Basal ganglia and cerebellum are specialized for temporal context-dependent perception and memory for time.
- Focus on representation of time at the level of sequences vs. intervals.
- Insights from neural population recordings in candidate timing areas
e.g. sensory cortex, basal ganglia, cerebellum etc.

Discussion

Highlight the context

that modulates timing in your study design

Duration of time intervals

Focus on time intervals observed in natural sensory environment, motion patterns etc.

Neural code for a single time interval vs. sequence of temporal patterns

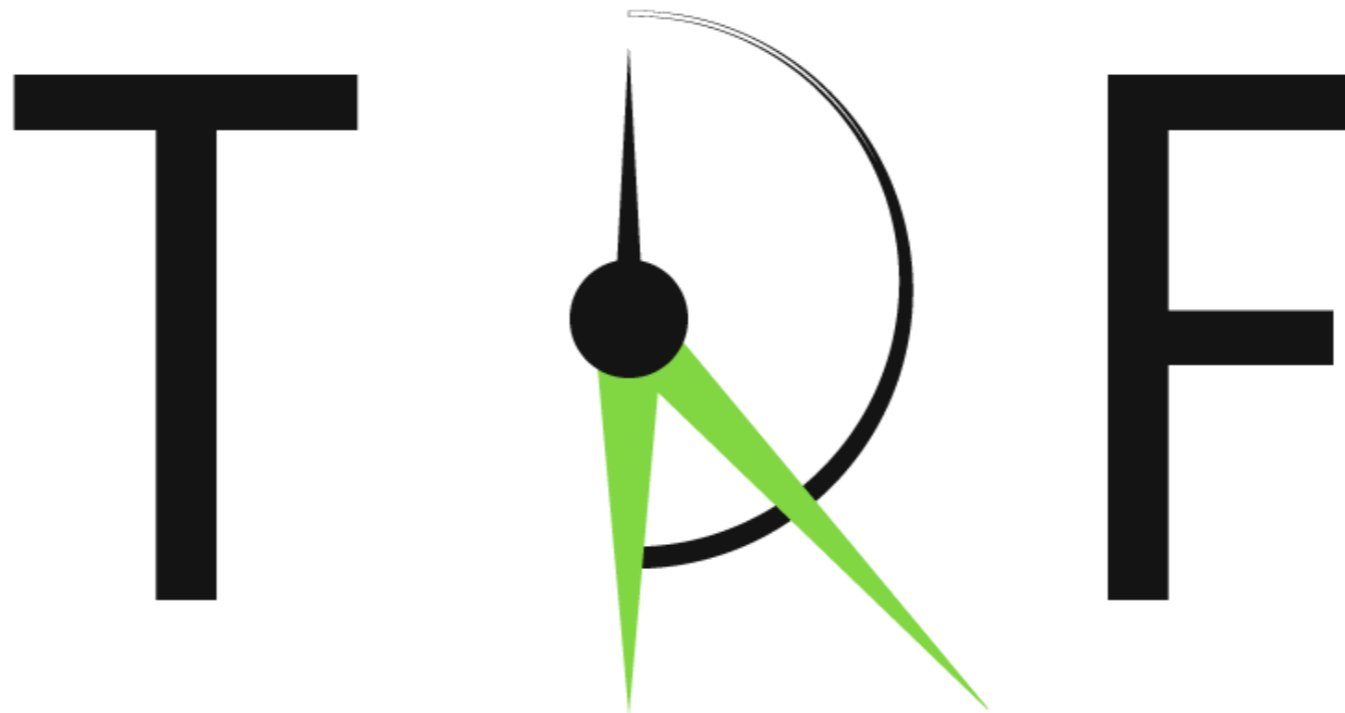
Examine representation of time at the single interval level as well as at the level of sequences (both within and across sequences).

Dedicated vs. intrinsic models

Timing maybe an intrinsic network computation but certain brain areas may be specialized for representing time in specific *contexts*.

Thank you!

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