Context-dependent representation of auditory time intervals

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Outline

- Introduction
- Perception of time (fMRI)
- Working memory for time (behavior & fMRI)
- Rapid learning of temporal sequences (electrophysiology)

Introduction

Why study timing?

Natural auditory signals such as speech and music evolve over time and vary from one instant to another.

Important for accurate sensorimotor processing e.g.
speech production, playing a musical instrument, dancing etc.

Lack of dedicated neural machinery for perceiving time makes it an interesting challenge to uncover the brain's timing code.

Impairment of temporal processing co-occurs with movement related disorders like Parkinson's, Huntington's, Ataxia etc.

Focus is on accurately modeling natural temporal processing using sequences of intervals (as opposed to single intervals).

Brain substrates

Motor structures:

Basal ganglia

Cerebellum

Supplementary motor area

Pre-motor cortex

Inferior Olive

Other areas:

Prefrontal cortex

Parietal cortex

Sensory cortices

Insula

cf. Grahn, Chen, Coull,
Bengtsson,Wiener, Llinas

-> However, it is not clear what specific aspect of timing these areas are involved in.

Models of Timing

Dedicated models:
timing is mediated by dedicated processes and areas in the brain.

cf. Ivry - cerebellum
cf. Meck - striatum

Intrinsic models:
there are no specialized brain areas that encode time and that time is intrinsically processed by neuronal ensembles as part of their specific cortical function.

cf. Buonomano

Classifications of Timing

Sub-second	vs.	Supra-second	(Lewis and Miall)
Automatic	vs.	Cognitive	(Lewis and Miall)
Implicit	vs.	Explicit	(Coull and Nobre)
Event-based	vs.	Emergent	(Ivry et al.)
Duration-based	vs.	Beat-based	(Griffiths et al.)

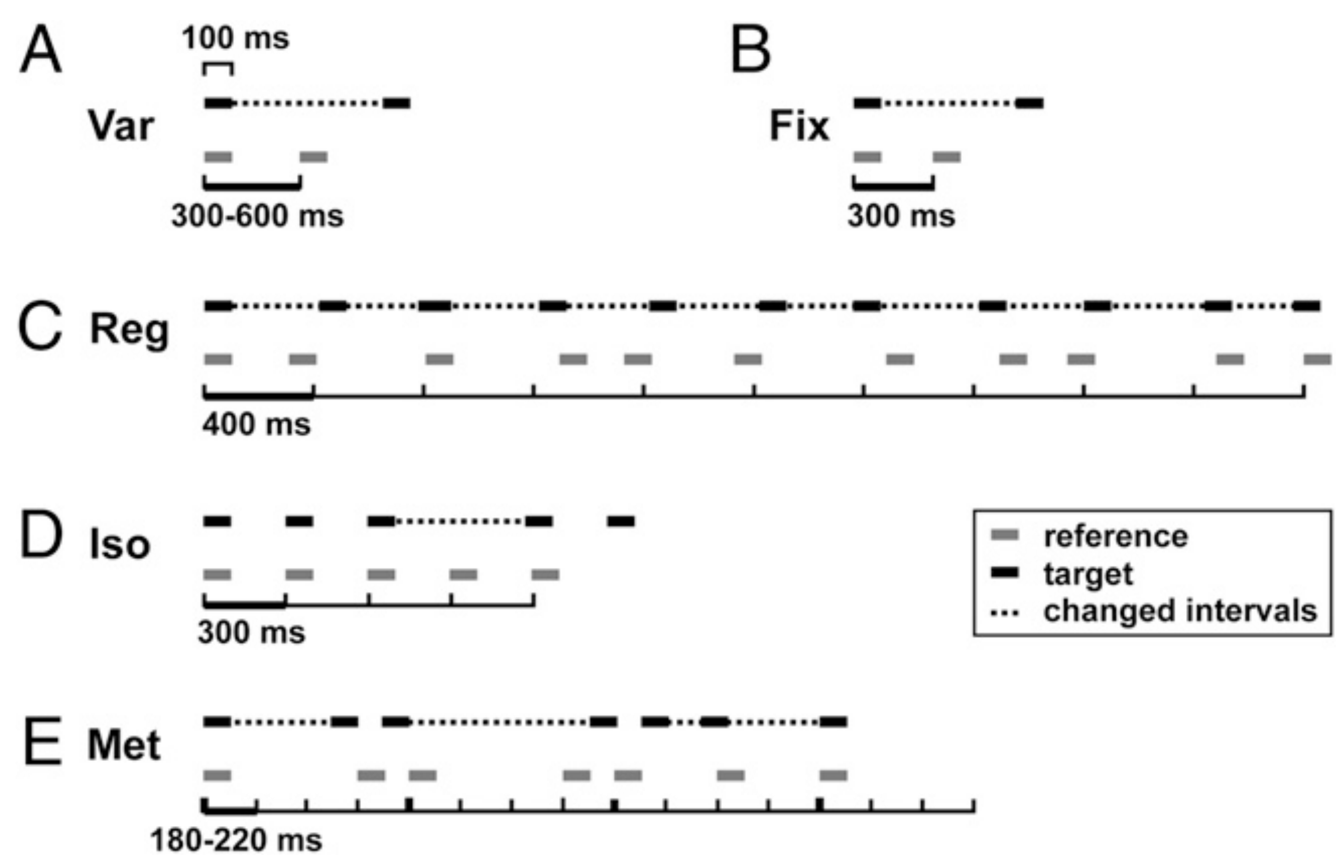
-> Important to clarify the particular kind of timing task/mechanism.

Perception of Time

Teki et al., 2011 *J Neurosci*

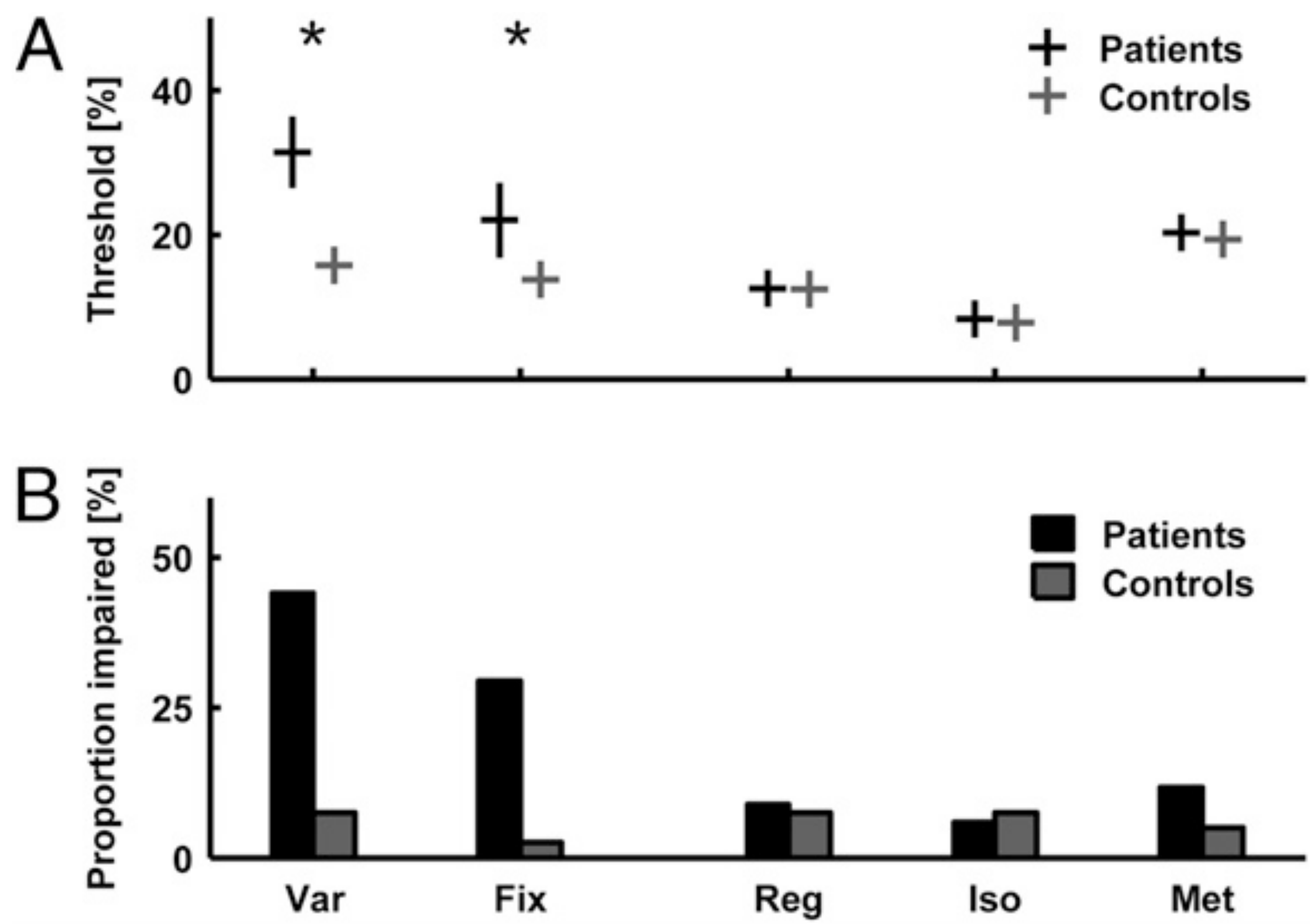
Duration-based timing

Encoding absolute duration of individual time intervals (ΔTi)



Duration-based timing

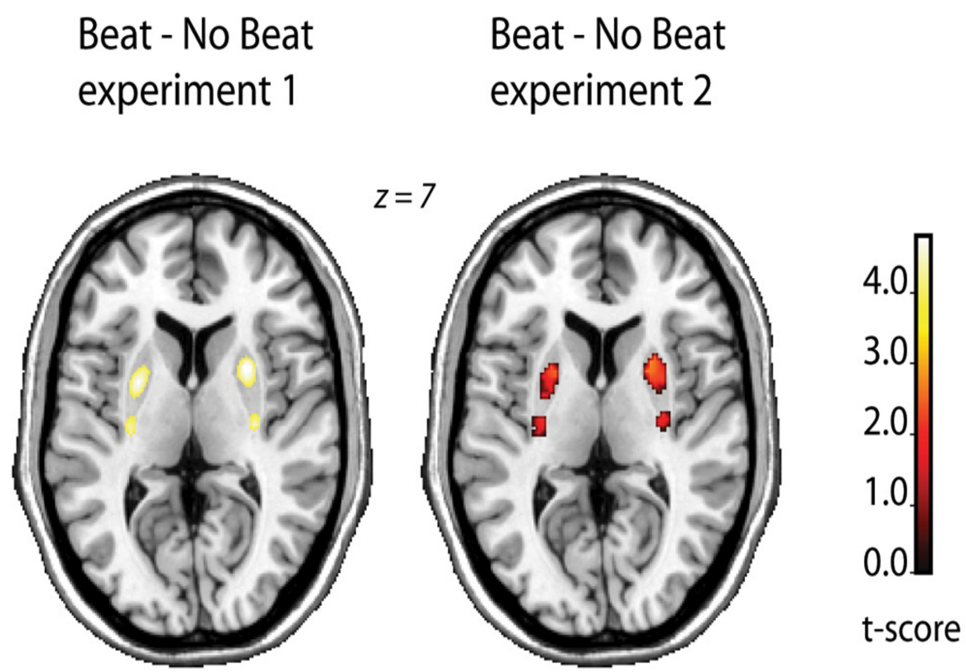
Patients with SpinoCerebellar Ataxia Type 6 with lesions to superior cerebellum



Grube et al., 2010 *PNAS*

Beat-based timing

Timing of intervals relative to a regular beat (ΔTi / Tbeat)



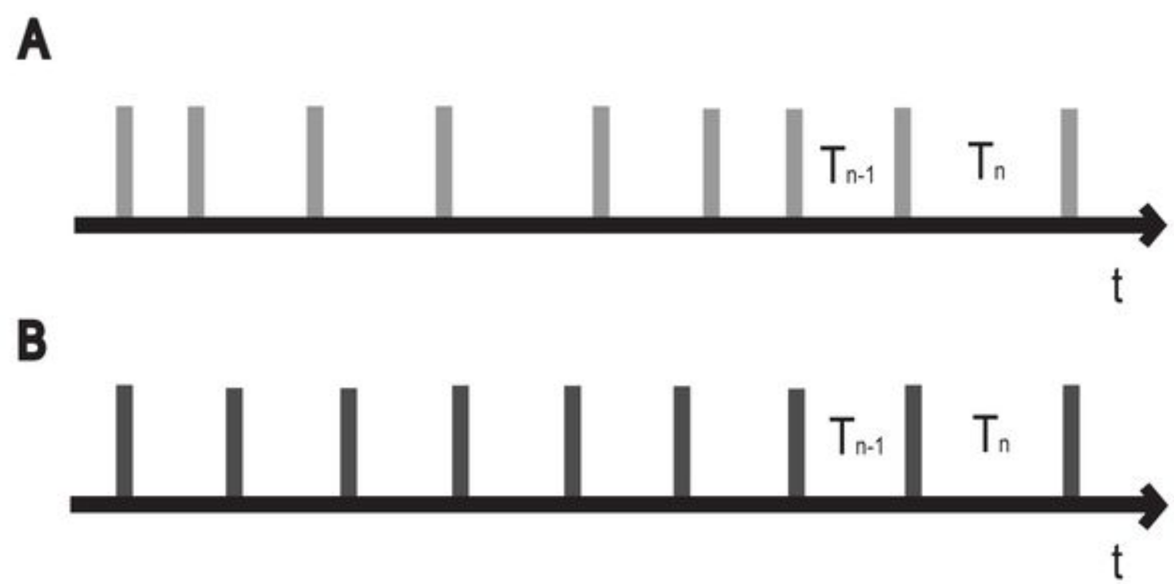
Grahn et al. 2009 *J Neurosci*

Hypotheses for fMRI

H1: Cerebellum more involved in absolute, duration-based timing

H2: Basal ganglia more involved in relative, beat-based timing

Paradigm



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

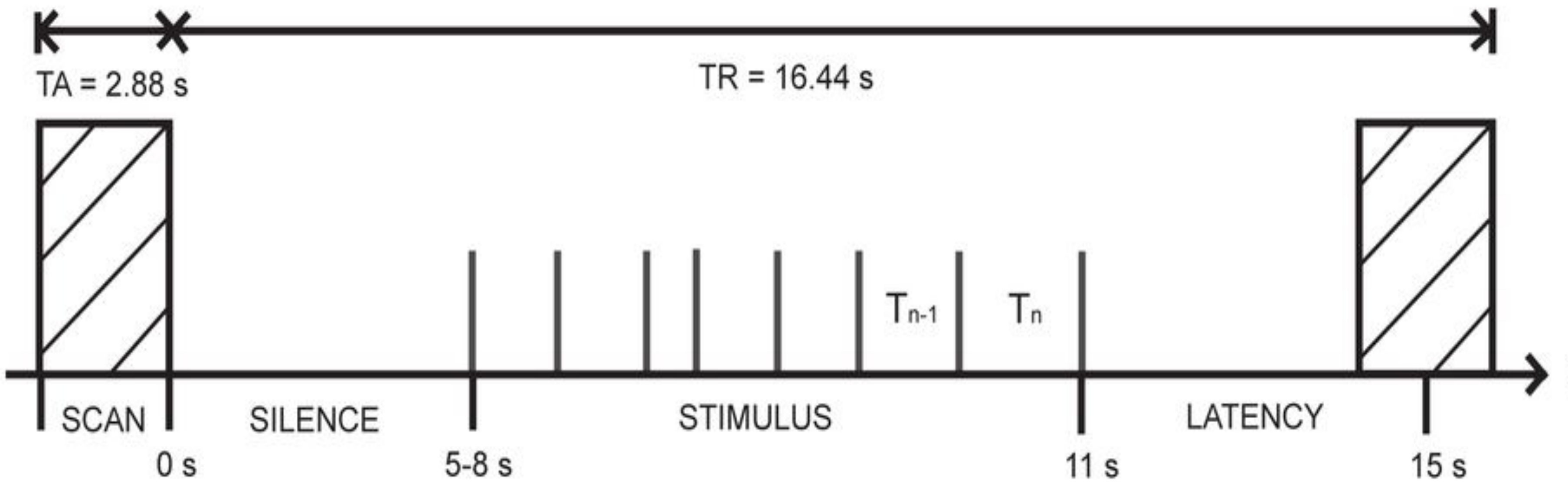
Sequence A: Irregular with 15% average jitter; deltaT = 30% of IOI

Sequence B: Regular with an isochronous beat; deltaT = 15% of IOI

Irregular > Regular (measure of absolute timing)

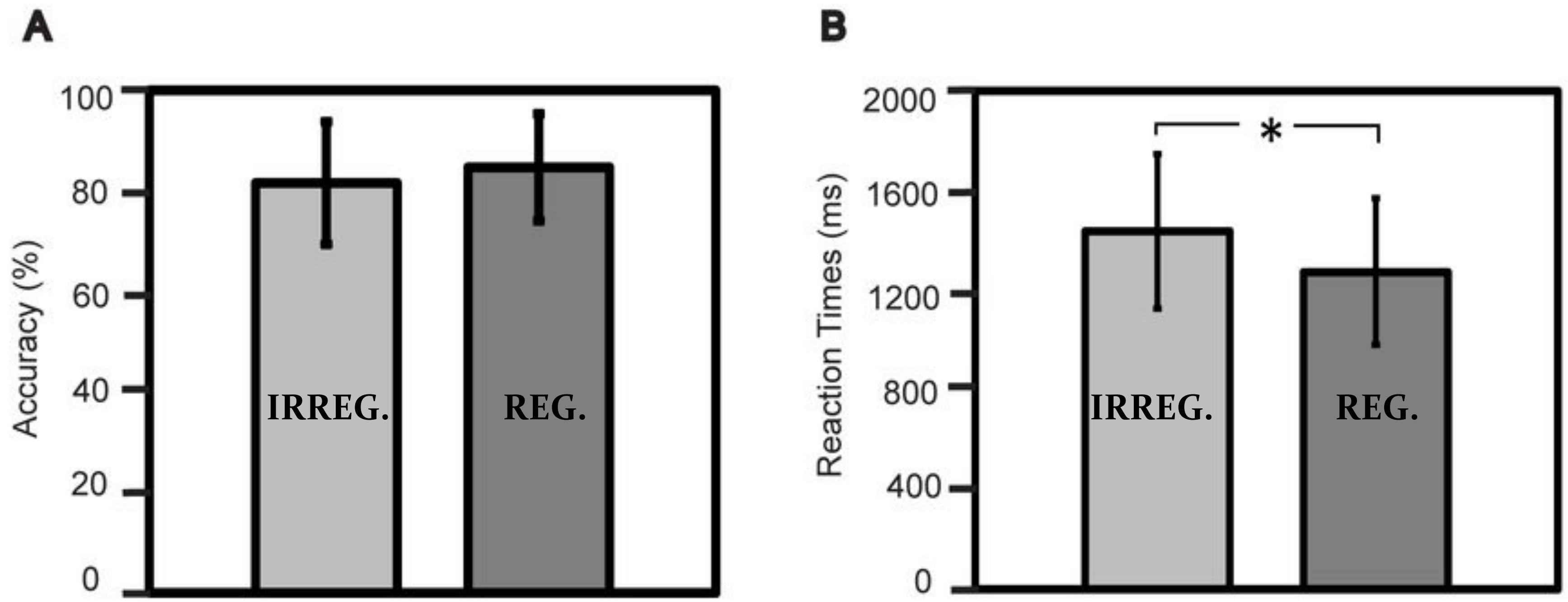
Regular > Irregular (measure of relative timing)

fMRI design



- Fixed 4s latency from stimulus offset to mid-slice acquisition to capture timing decision
- 48 contiguous slices per volume
- TR: 16.44 s; TA: 2.88 s; flip angle α: 90°
- Slice thickness: 2 mm with 1 mm gap between slices
- In-plane resolution: 3.0 x 3.0 mm^2
- Slices were tilted by - 7° (T>C) to obtain full coverage from the cerebellum

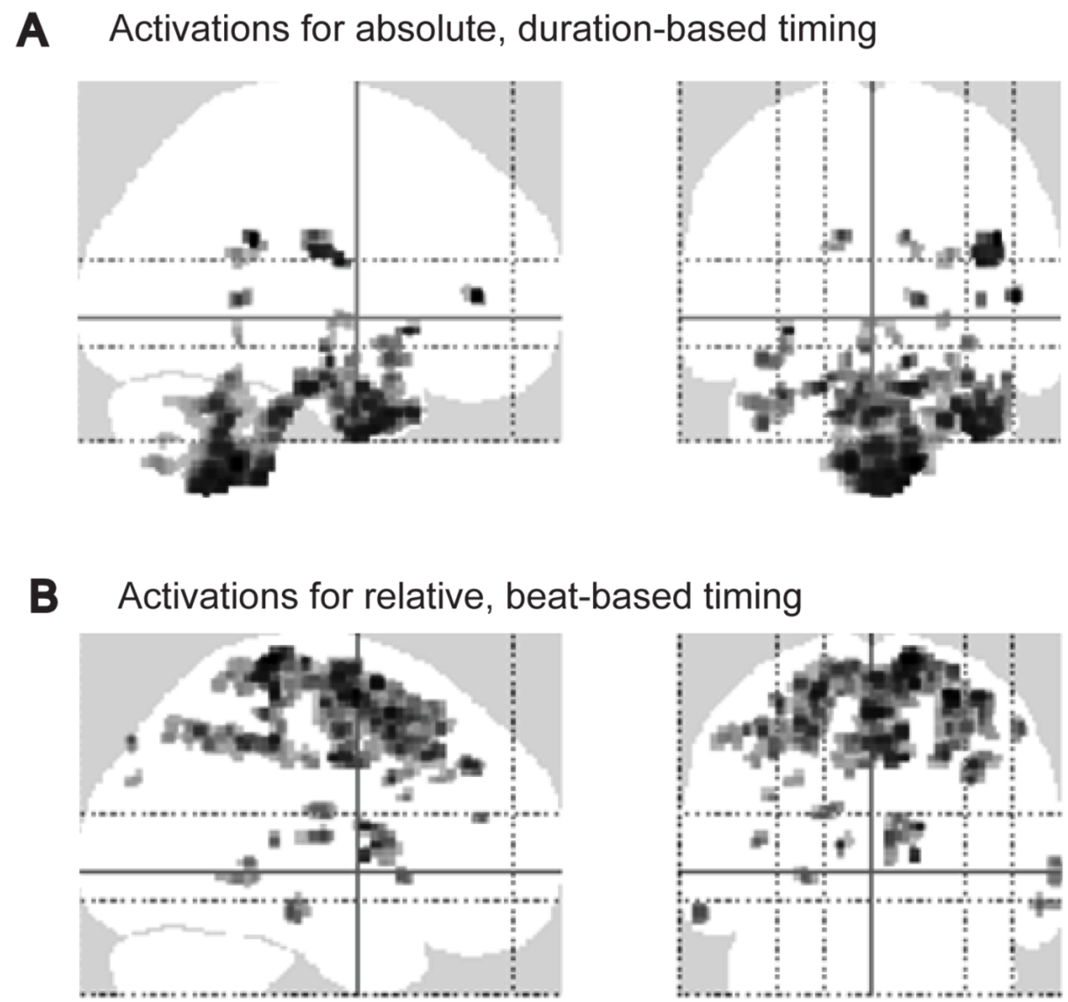
Behavior in scanner



Mean	**81.53%**	**84.72%**	**1438**	**1275**
SEM	± 12.28%	±10.64%	± 297 ms	± 312 ms

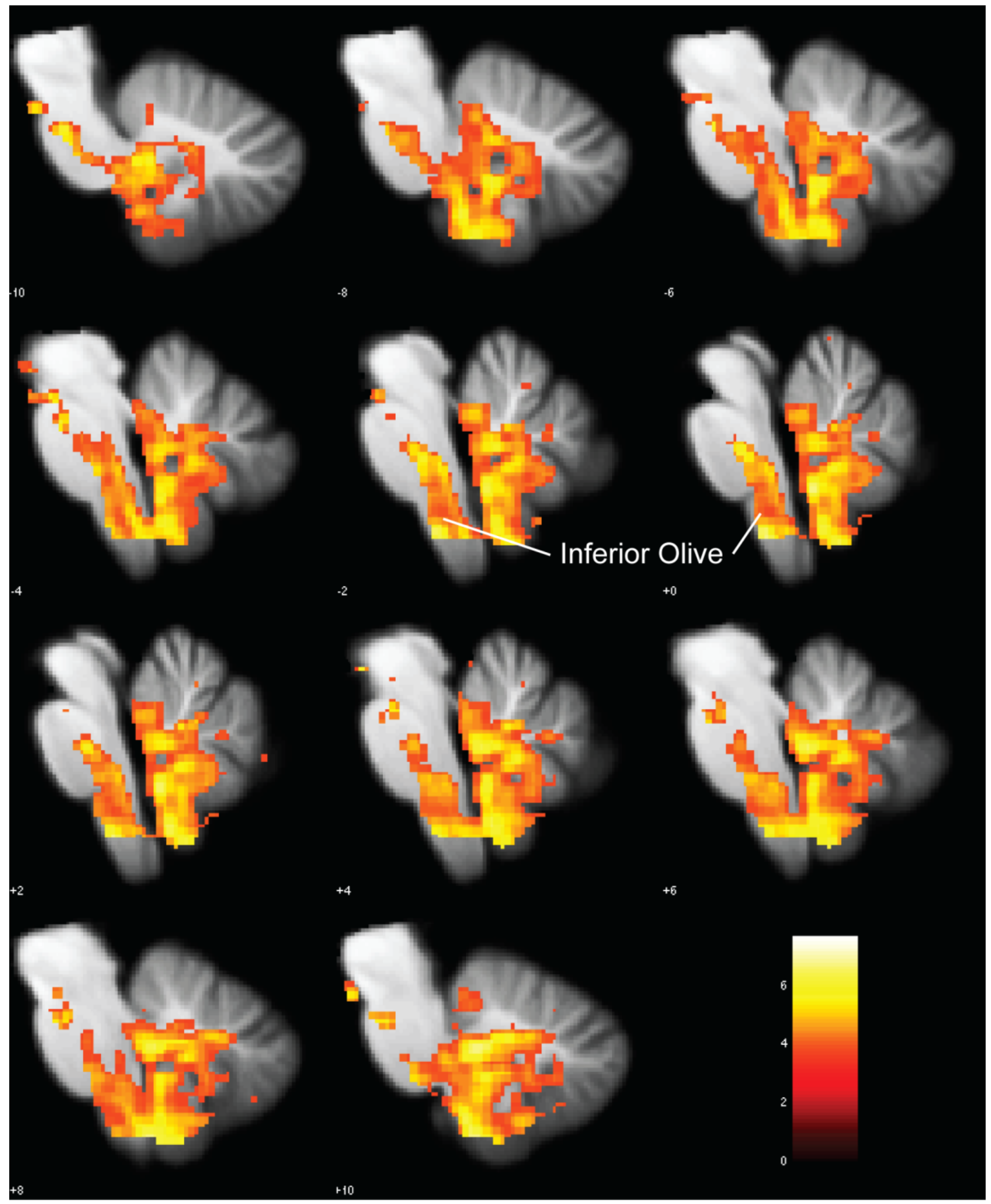
(N = 18)

fMRI results

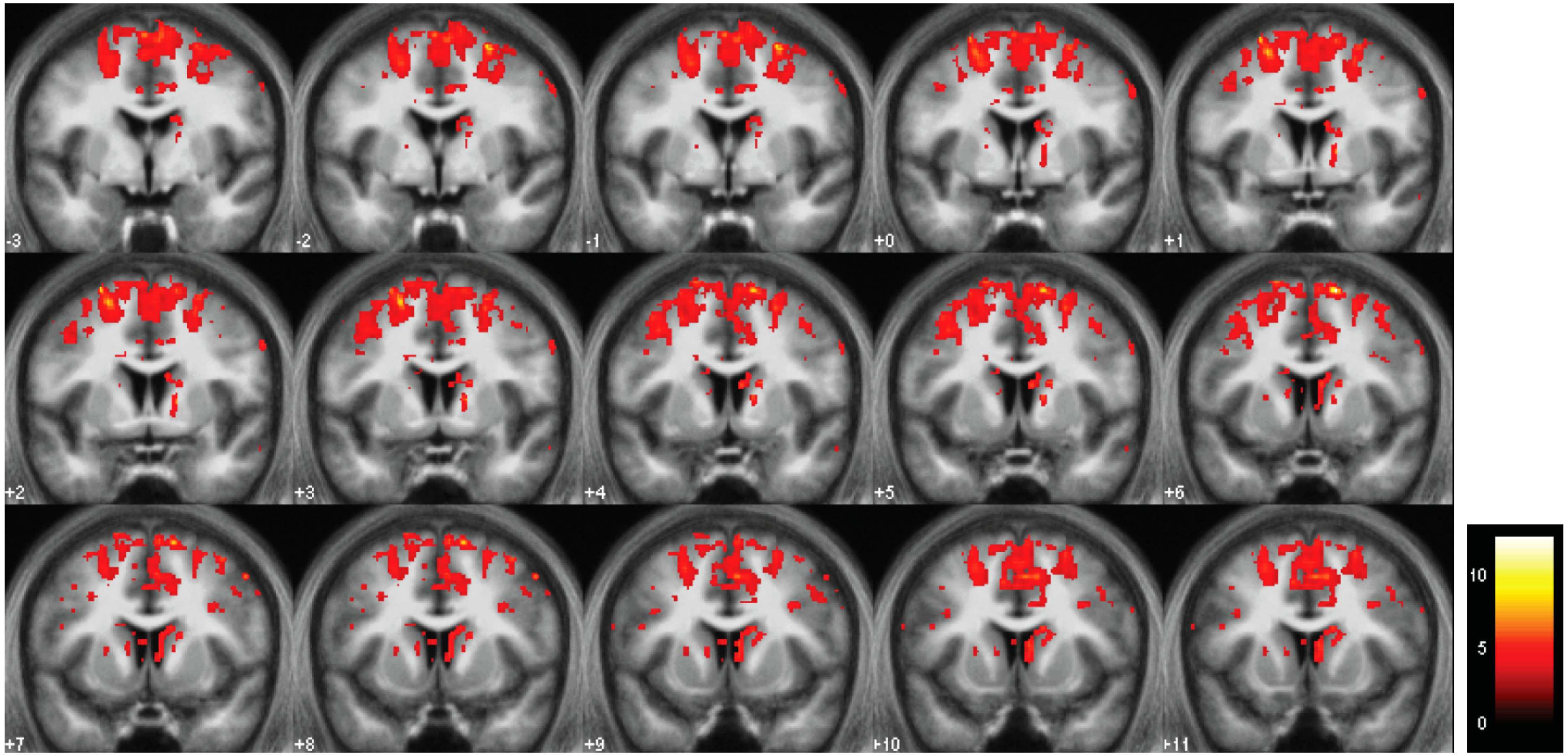


Duration-based timing

x = -10 to 10 mm

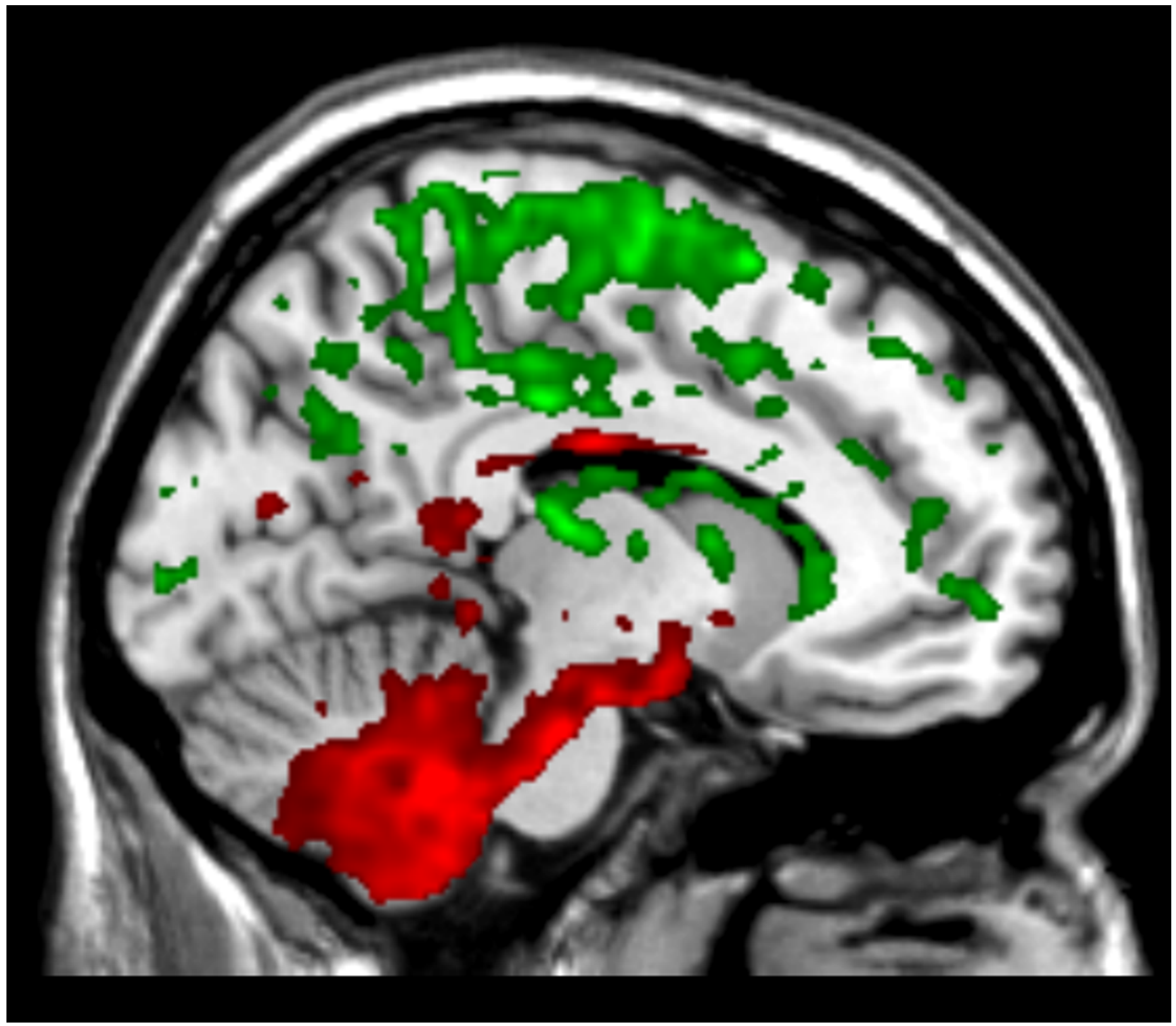


Beat-based timing

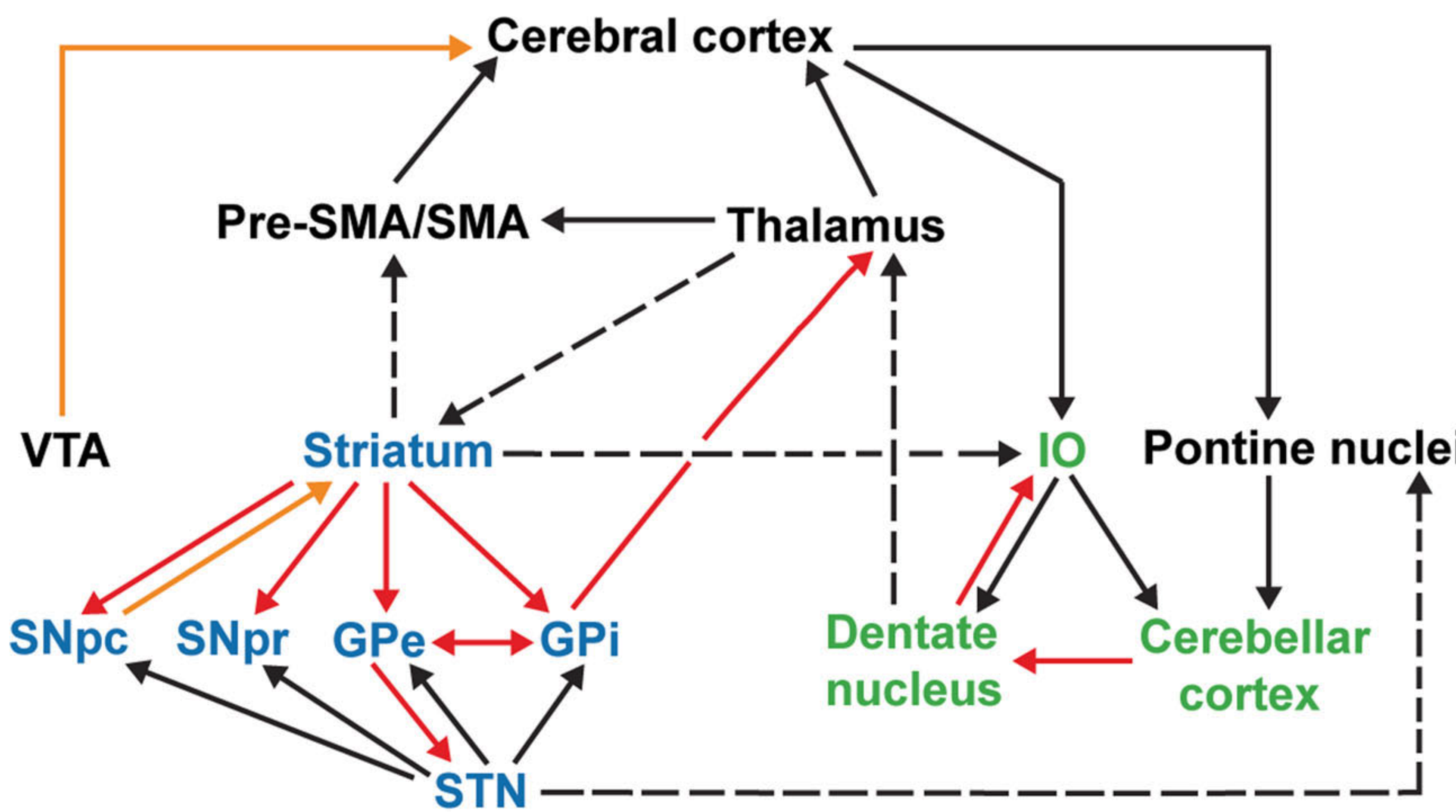


x = -3 to 11 mm

Functional dissociation



Unified model



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

Summary

Perception of time intervals depends on the temporal context of the sequences containing those intervals.

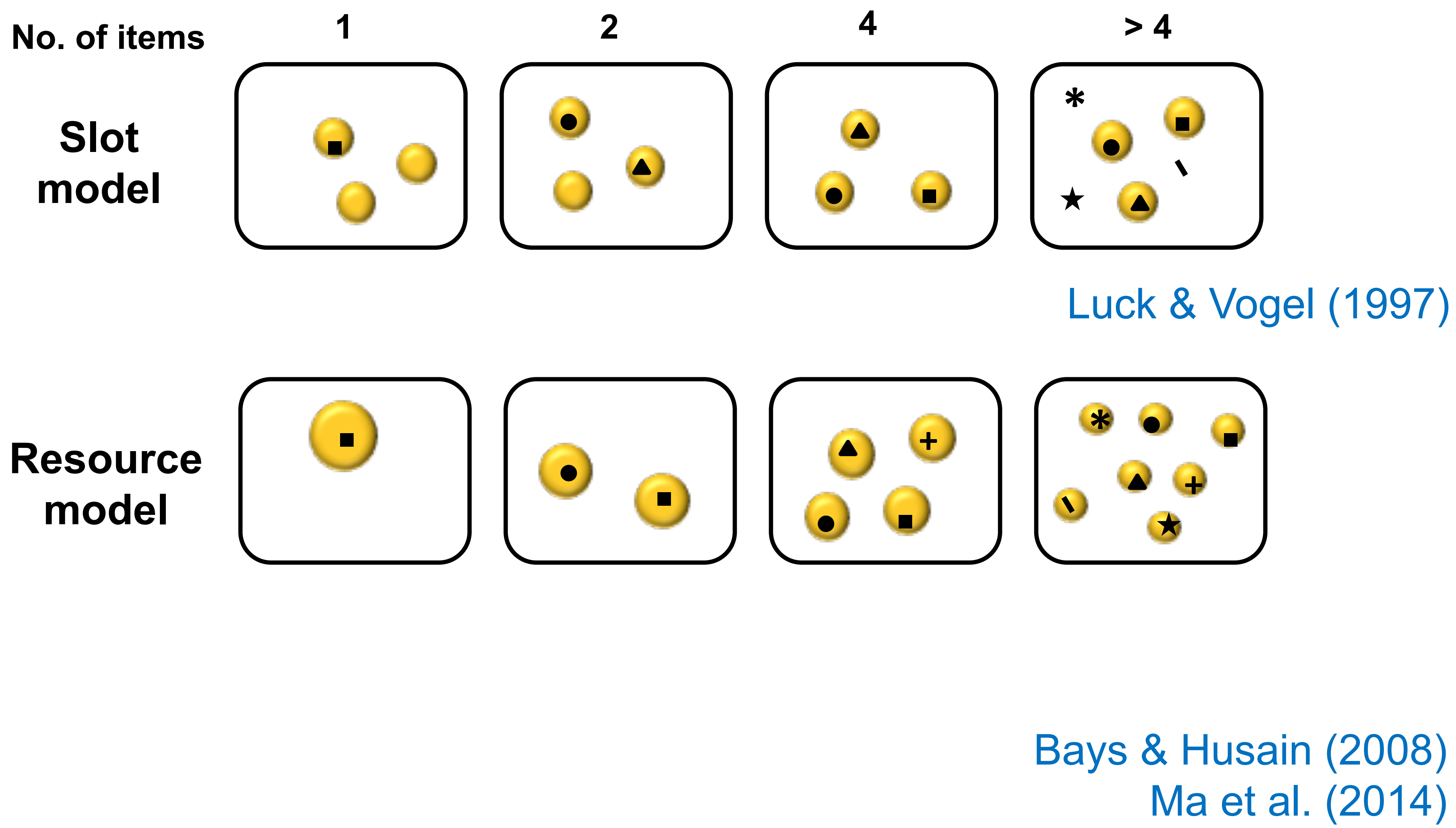
Olivocerebellar network involved in duration-based timing in irregular, unpredictable temporal context.

Striato-thalamo-cortical network involved in beat-based timing in regular, predictable temporal context.

Working memory for time (behavior)

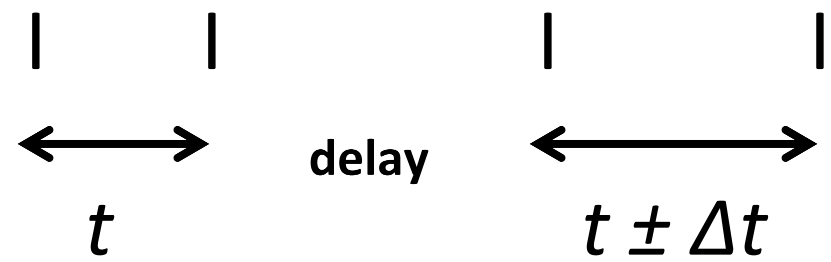
Teki & Griffiths (2014) *Frontiers*

Models of working memory



Joseph, Teki et al. (2015) *Brain Res. in progress*

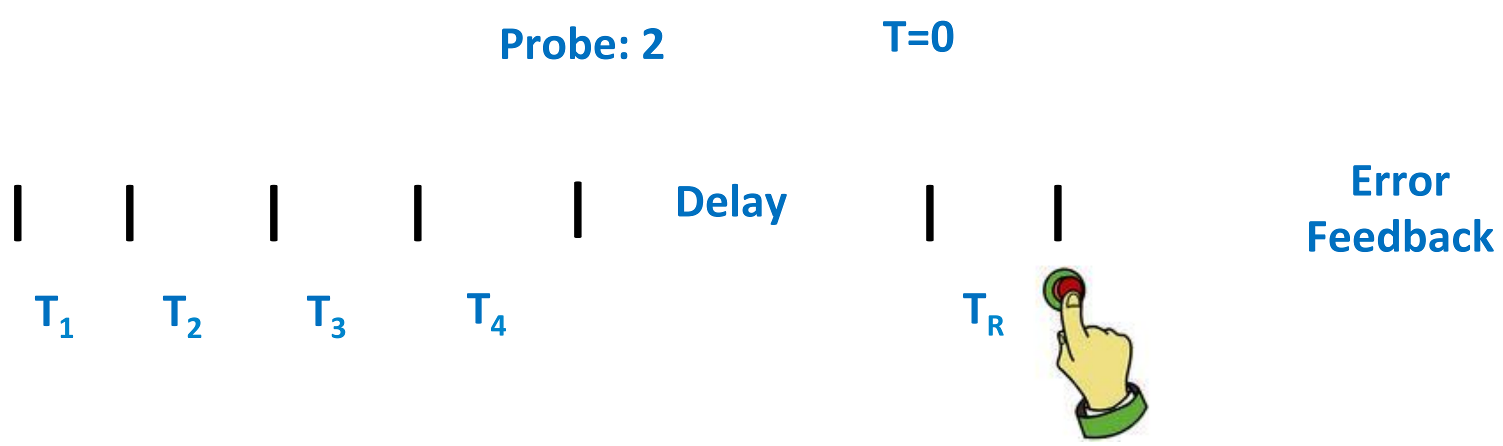
Previous paradigms



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

Rao et al. 2001; Coull et al., 2008

Behavioral paradigm



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

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

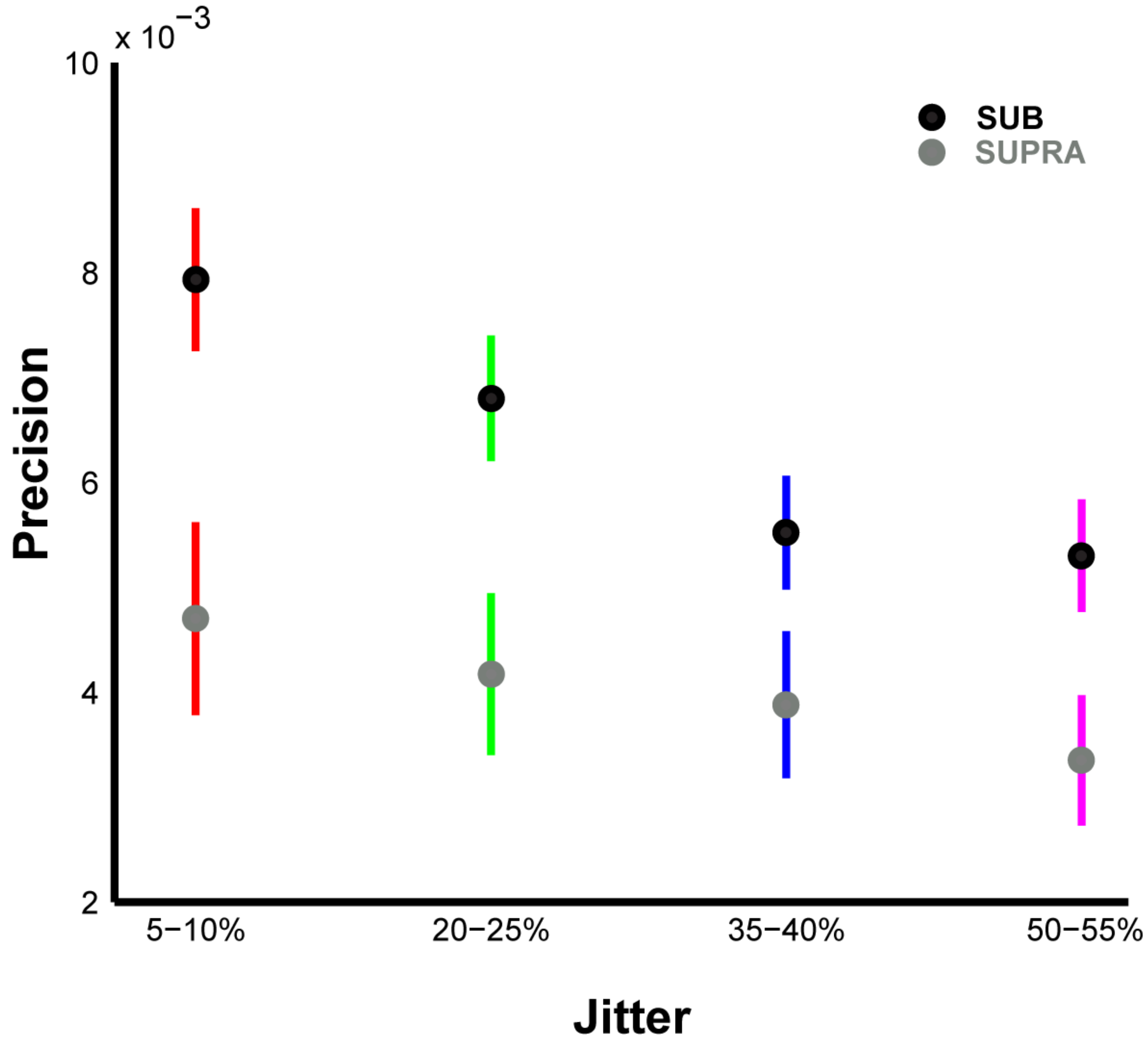
Precision of WM for time = $1/STD(T_R - T_{probe})$

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%

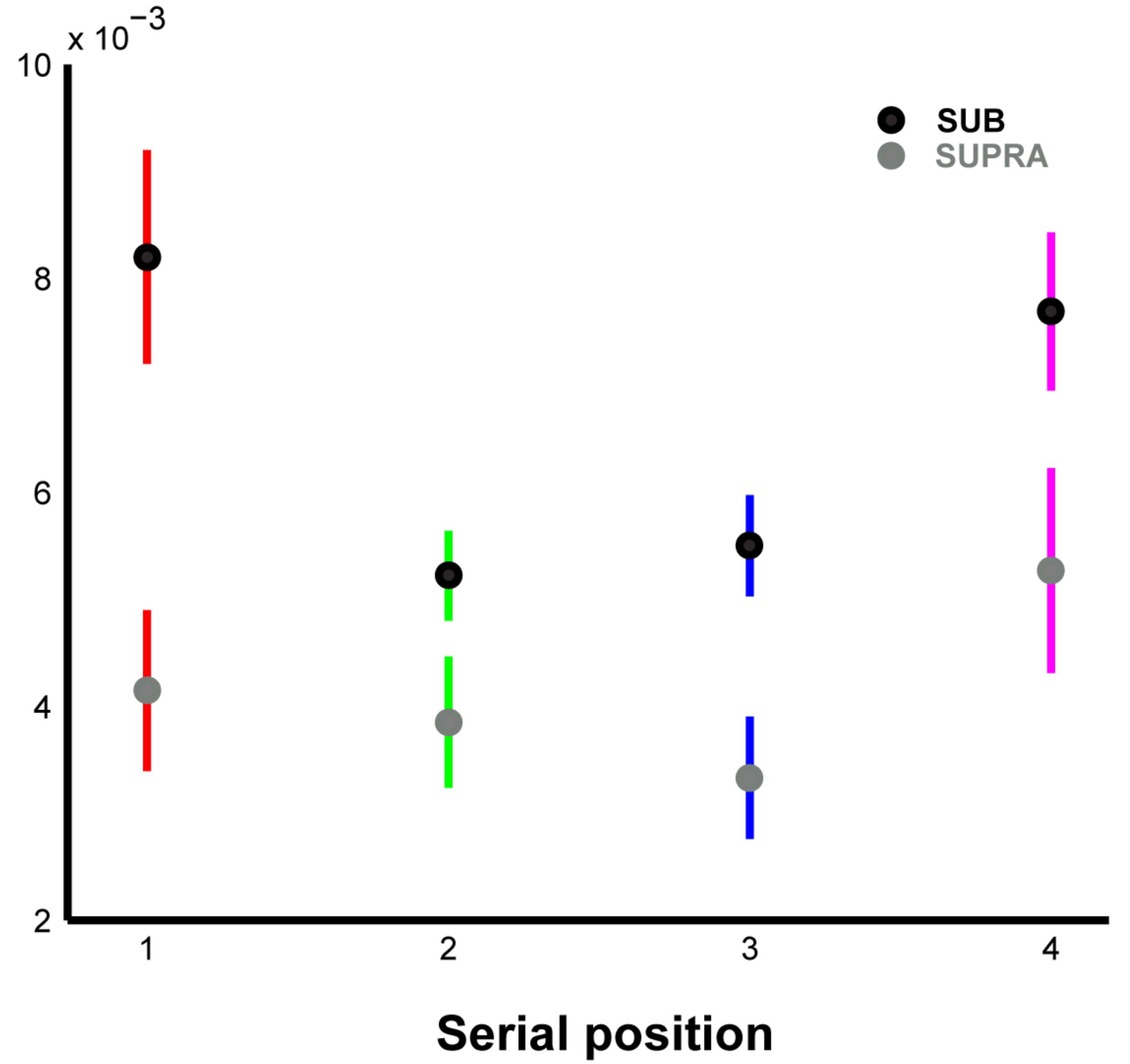
Precision vs. Jitter



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

N = 10 each

Precision vs. Position



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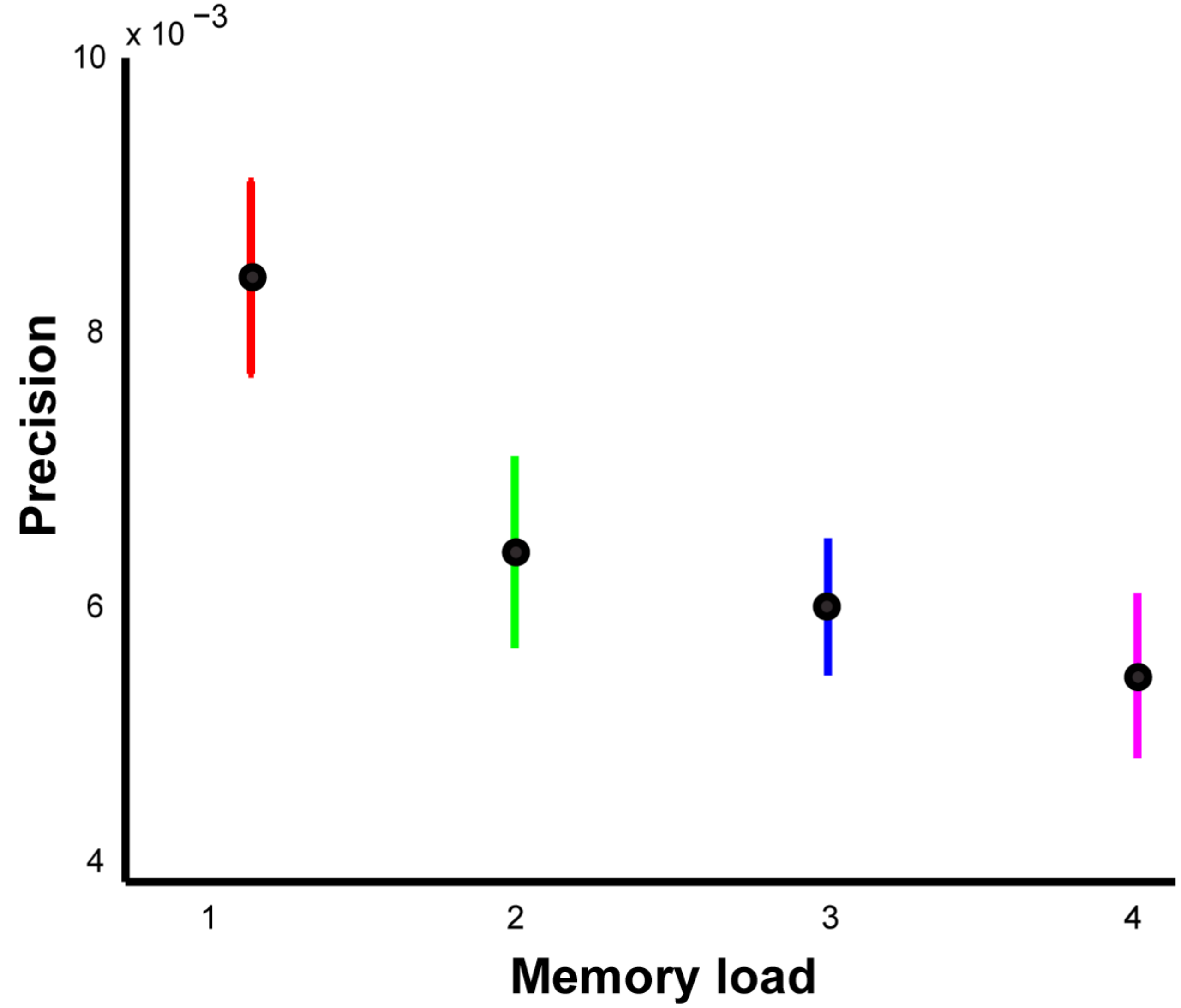
- IOI: 1.0 - 1.2 s
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

3: 'WM'
- 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

Conditions

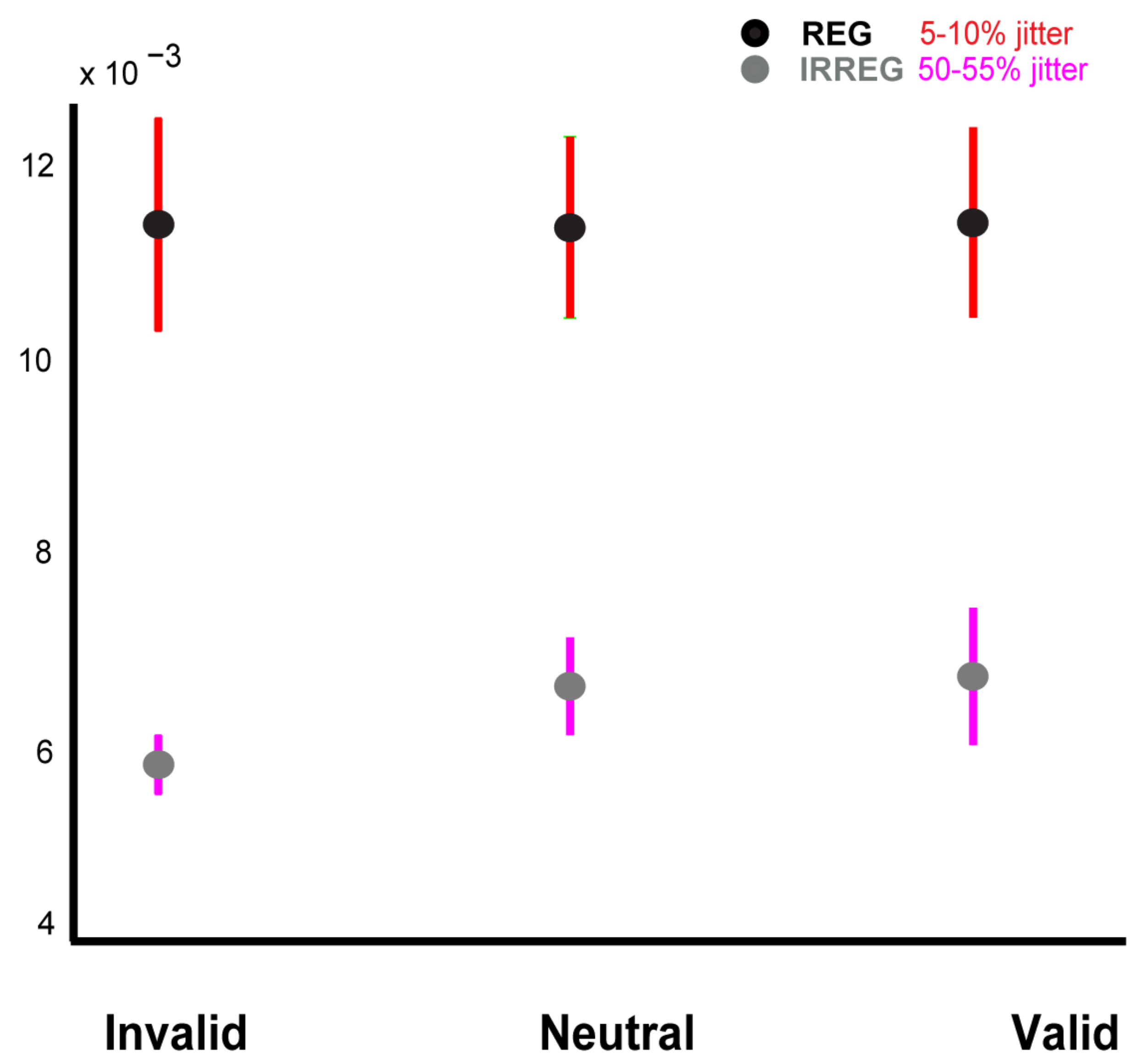
1: 'SUB'
- No. of intervals: 4
- IOI: 500-600 ms
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

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

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

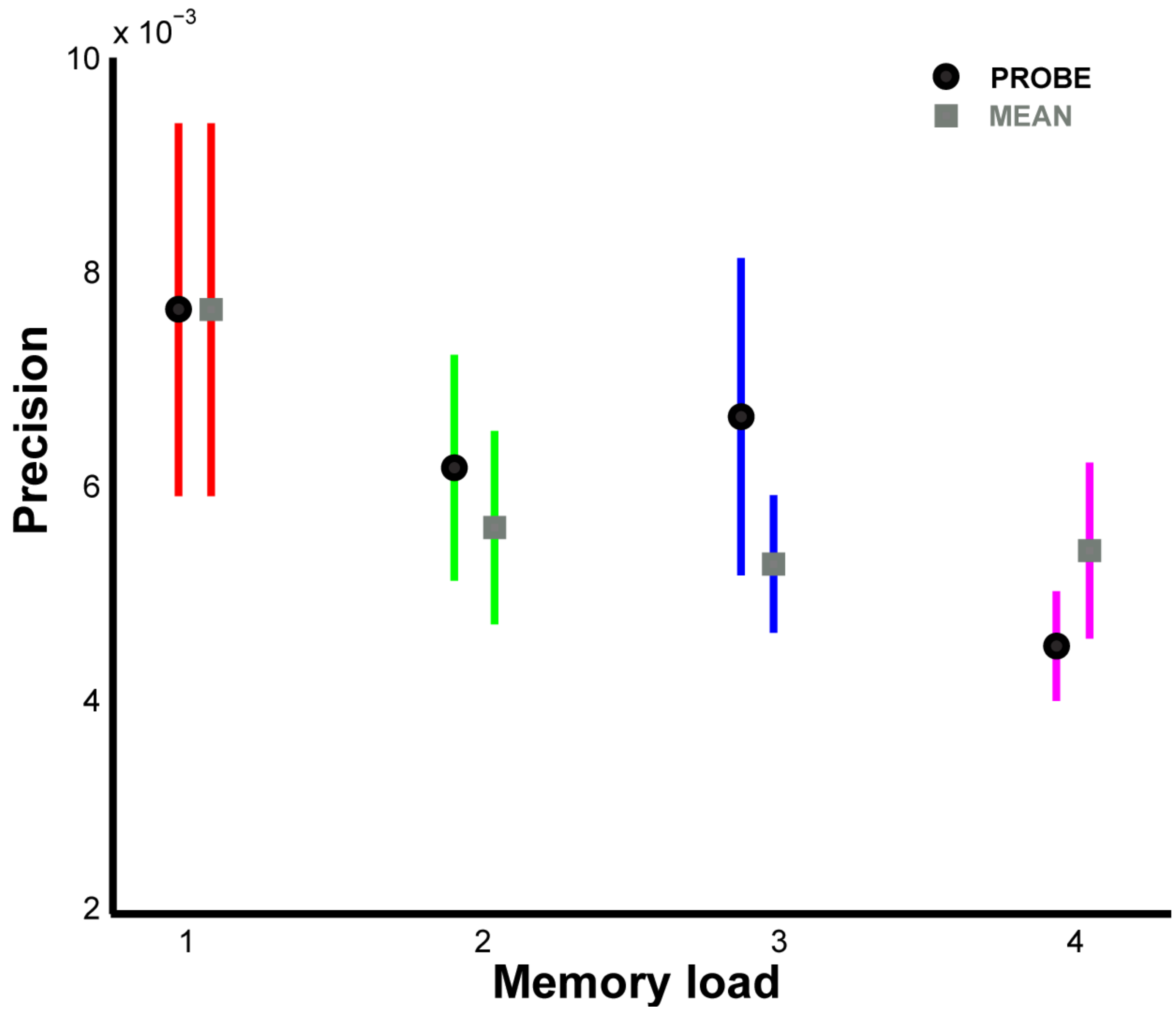
4: 'CUED'
- No. of intervals: 4
- IOI: 500-600 ms
- Jitter levels: 5-10%
- Cue: Valid (56.2%), Invalid (18.8%), Neutral (25%)

Precision vs. Cue



No significant effect of cueing in either context (N = 10 each)

Control analysis



Summary

Memory for a single time interval depends on:

a) the temporal context of the sequence

b) the size of the interval

c) the number of intervals in the sequence

d) but not on the attentional cue (may work for longer supra-second intervals).

Working memory for time (fMRI)

Teki et al., *under submission*

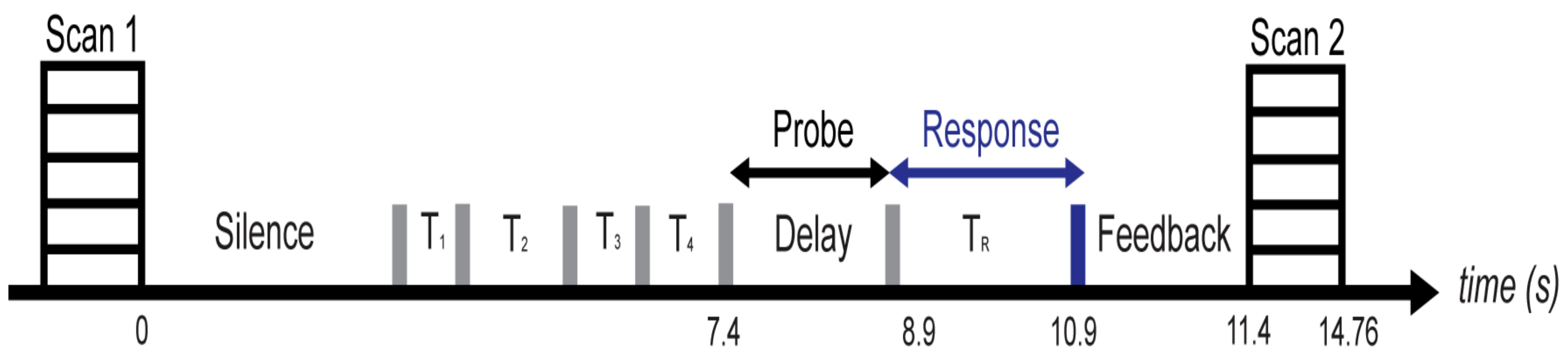
Aims

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

Temporal regularity (fixed WM load)
Memory 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%

fMRI design



TR = 14.76s
Response window = 2.5s
Latency to scan = 4.0s
2 rhythm followed by 2 WM blocks (32 trials per block)

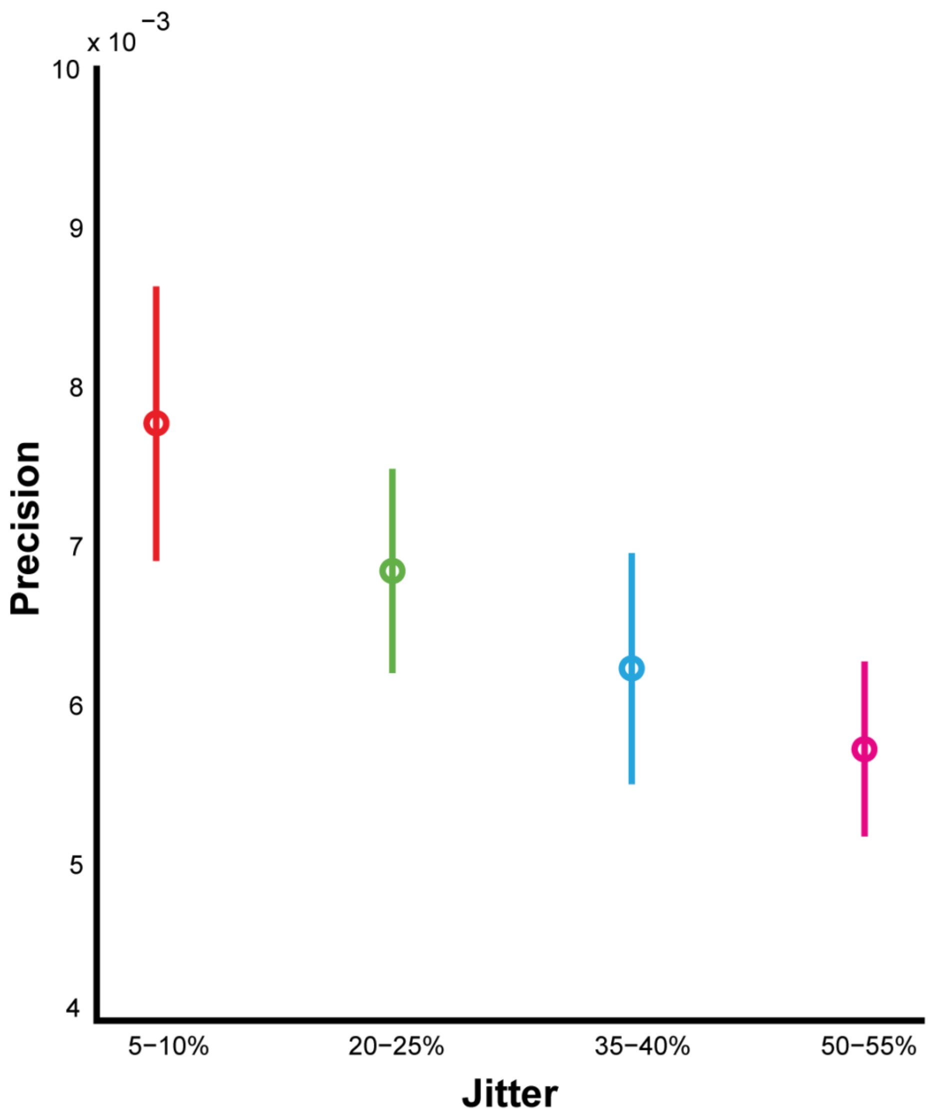
Analyses

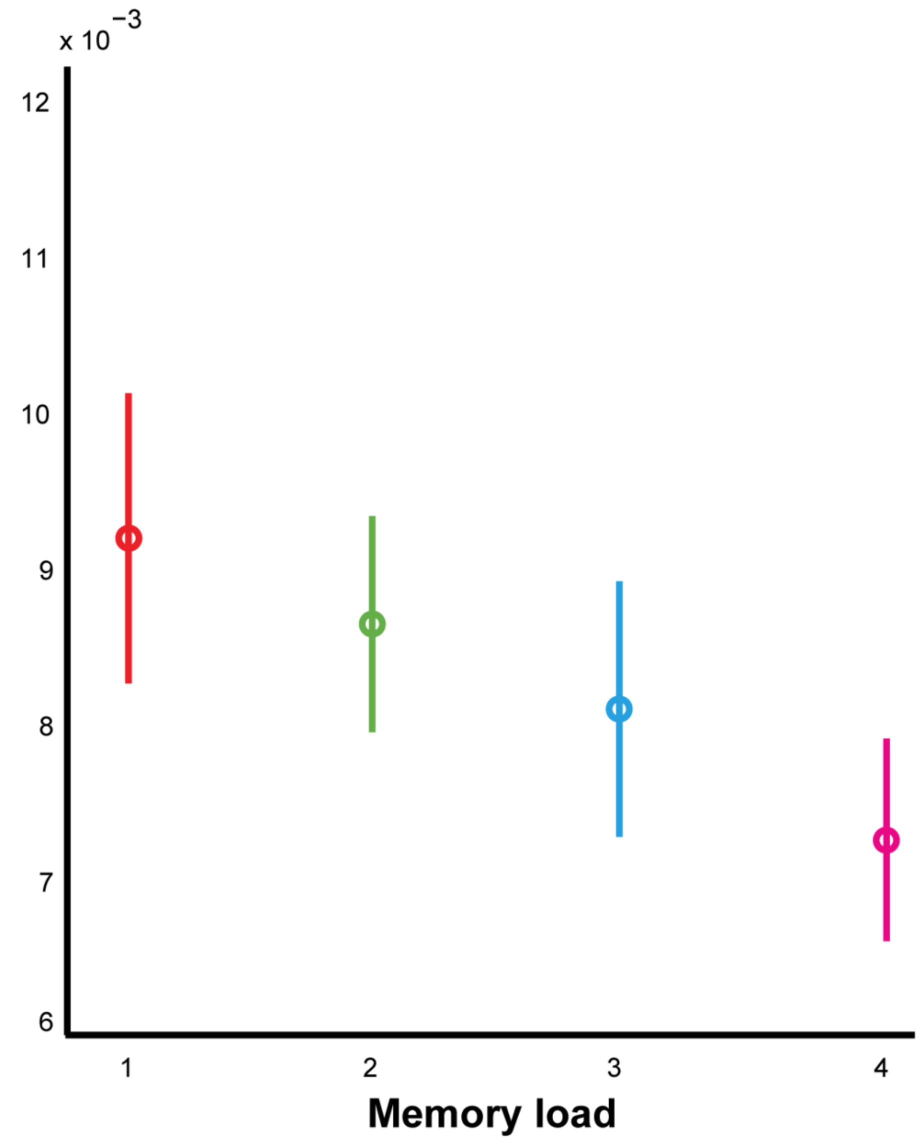
A. Effect of varying regularity (for fixed no. of intervals)

B. Effect of varying number of intervals (for fixed temporal regularity)

C. VBM analysis: GM volume correlation with behavior

Behavior in scanner

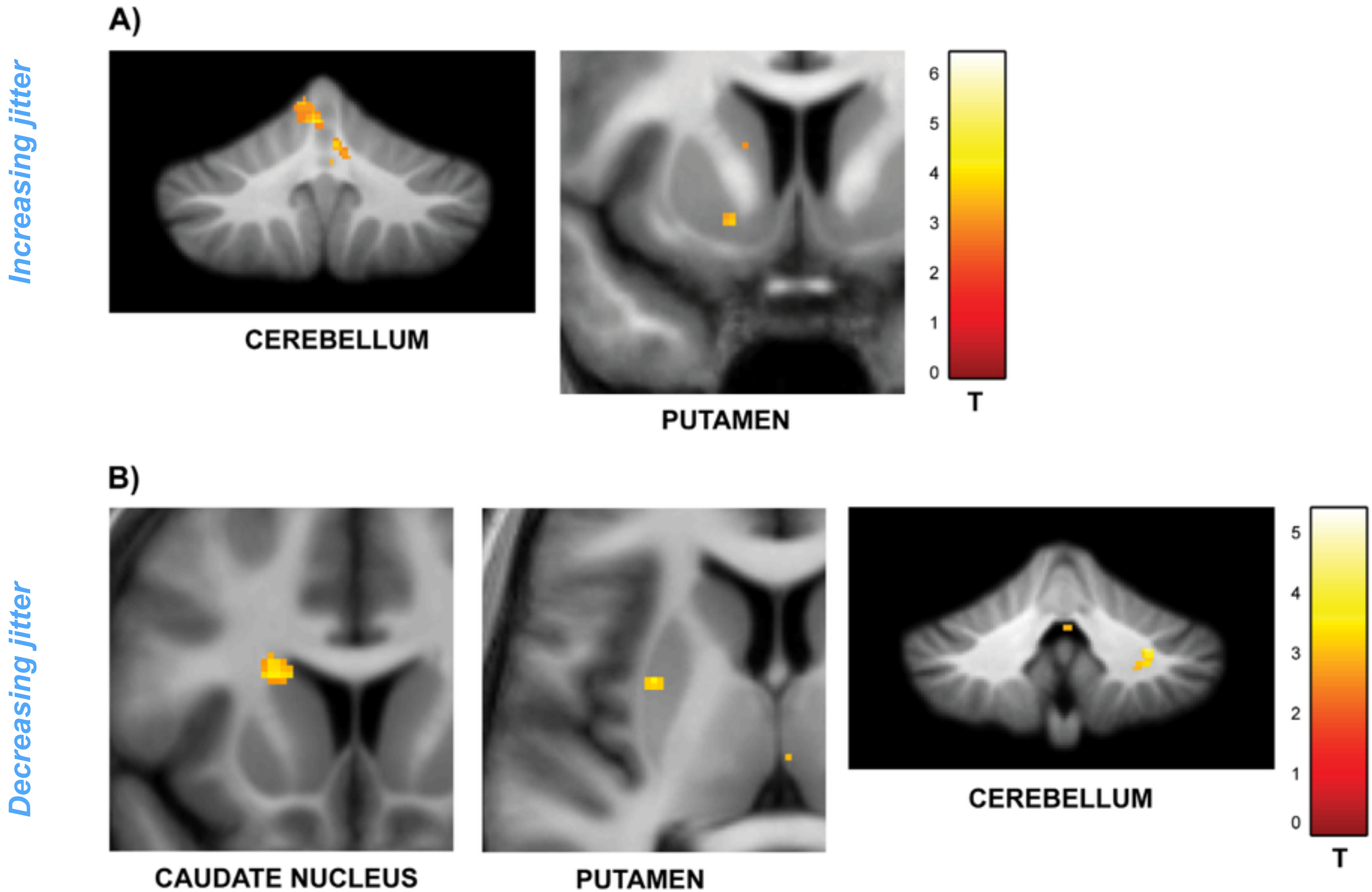




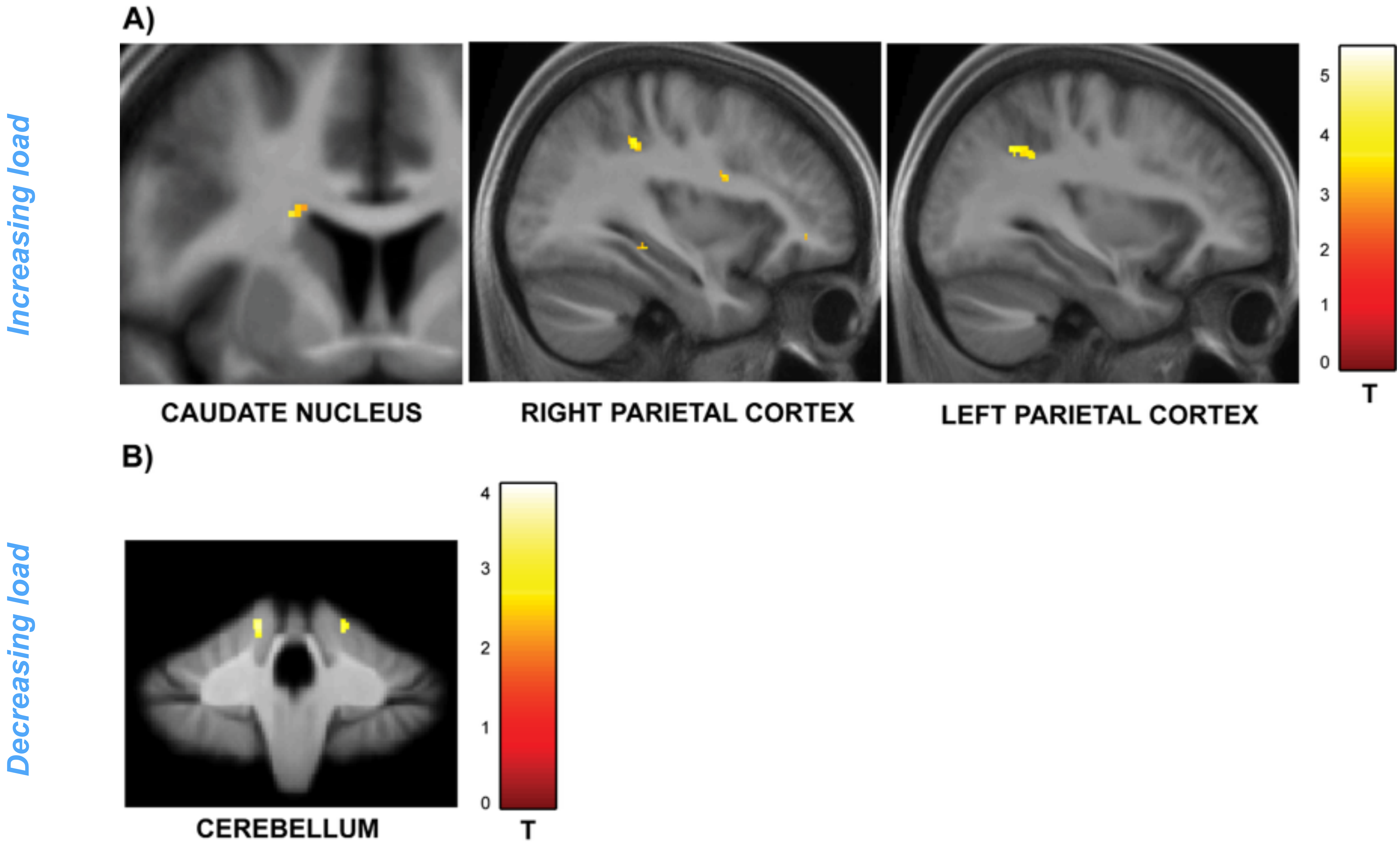
Significant effect of jitter (p=0.02; N=18)

No significant effect of load (p=0.36; N=16)
However, significant across 12/16 subjects: p = 0.04

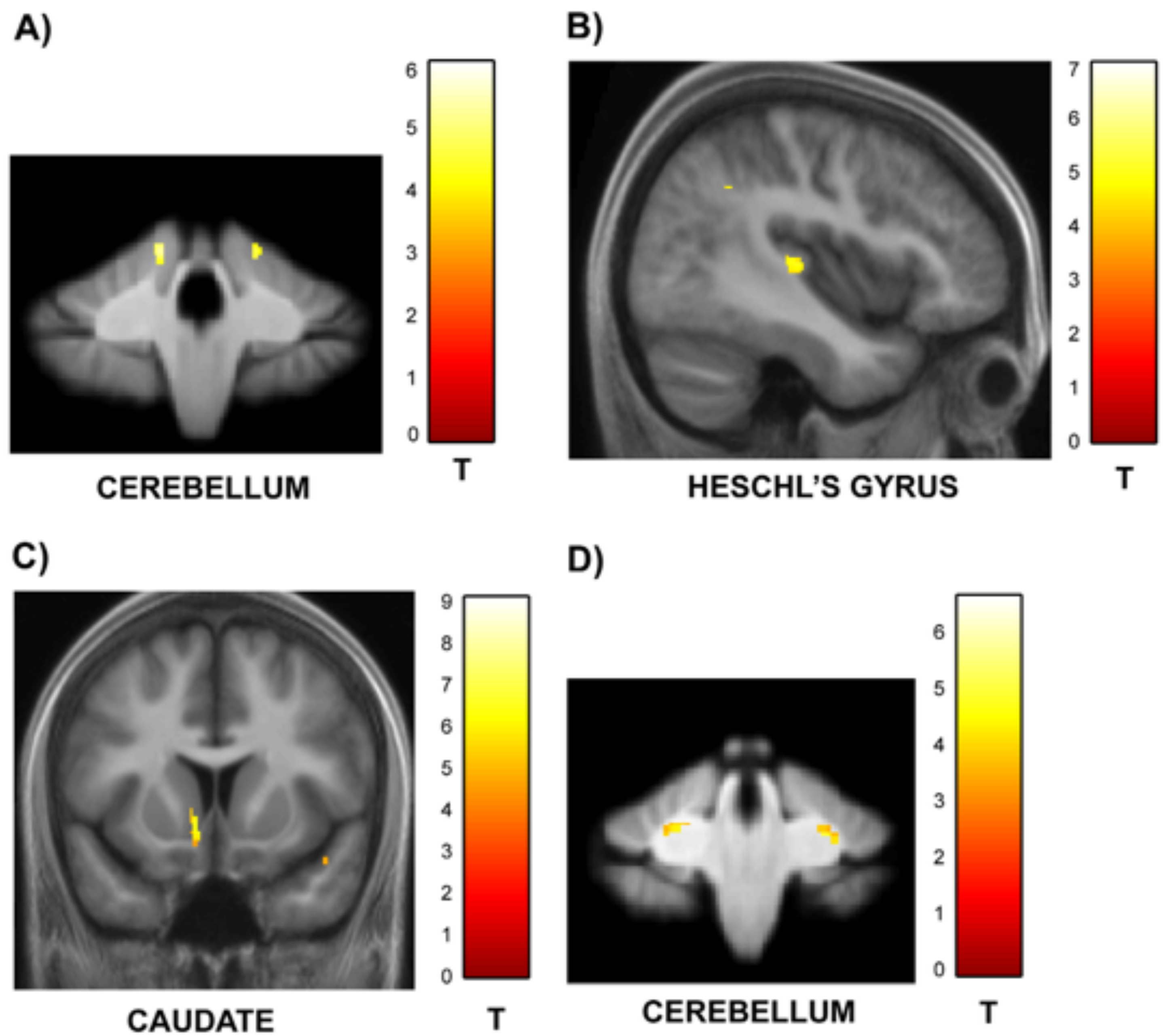
Effect of jitter



Effect of load



Gray matter volume correlation with behavior



A) Irregular sequences
B) Regular sequences
C) Sequences with high memory load
D) Sequences with low memory load

Summary

Encoding of a single time interval in working memory depends on:

a) the temporal context of the sequence
b) the number of intervals in the sequence

Both cerebellum and striatum involved in encoding time into memory but the level of activation depends on the temporal context of the sequences.

Striatum and inferior parietal cortex activity modulated by the number of intervals to be maintained in working memory.

Open questions:

Oscillatory code underlying memory encoding of time intervals?

- Beta modulation with jitter

  (cf. Iversen et al., 2009; Fujioka et al., 2012, Teki, 2014, Merchant et al., 2014, 2015)

- Alpha modulation with no. of intervals

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