Sundeep Teki

UCL

Context-dependent representation of auditory time

Auditory Cognition Group
Wellcome Trust Centre for Neuroimaging

Outline

I. Introduction

II. Perception of time (fMRI)

III. Working Memory for time (behaviour)

IV. Working Memory for time (fMRI)

V. Discussion

I. Introduction

Significance

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).*

Substrates

Motor structures:

Basal ganglia

Cerebellum

Supplementary motor area (SMA)

Pre-motor cortex (PMC)

Inferior Olive

Higher-order areas:

Prefrontal cortex

Parietal cortex

Sensory cortex

Insula

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

Models

Dedicated models

claim that timing is mediated by dedicated processes and areas in the brain e.g. cerebellum or striatum.

cf. Ivry - cerebellum

cf. Meck - striatum

Intrinsic models

propose that 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

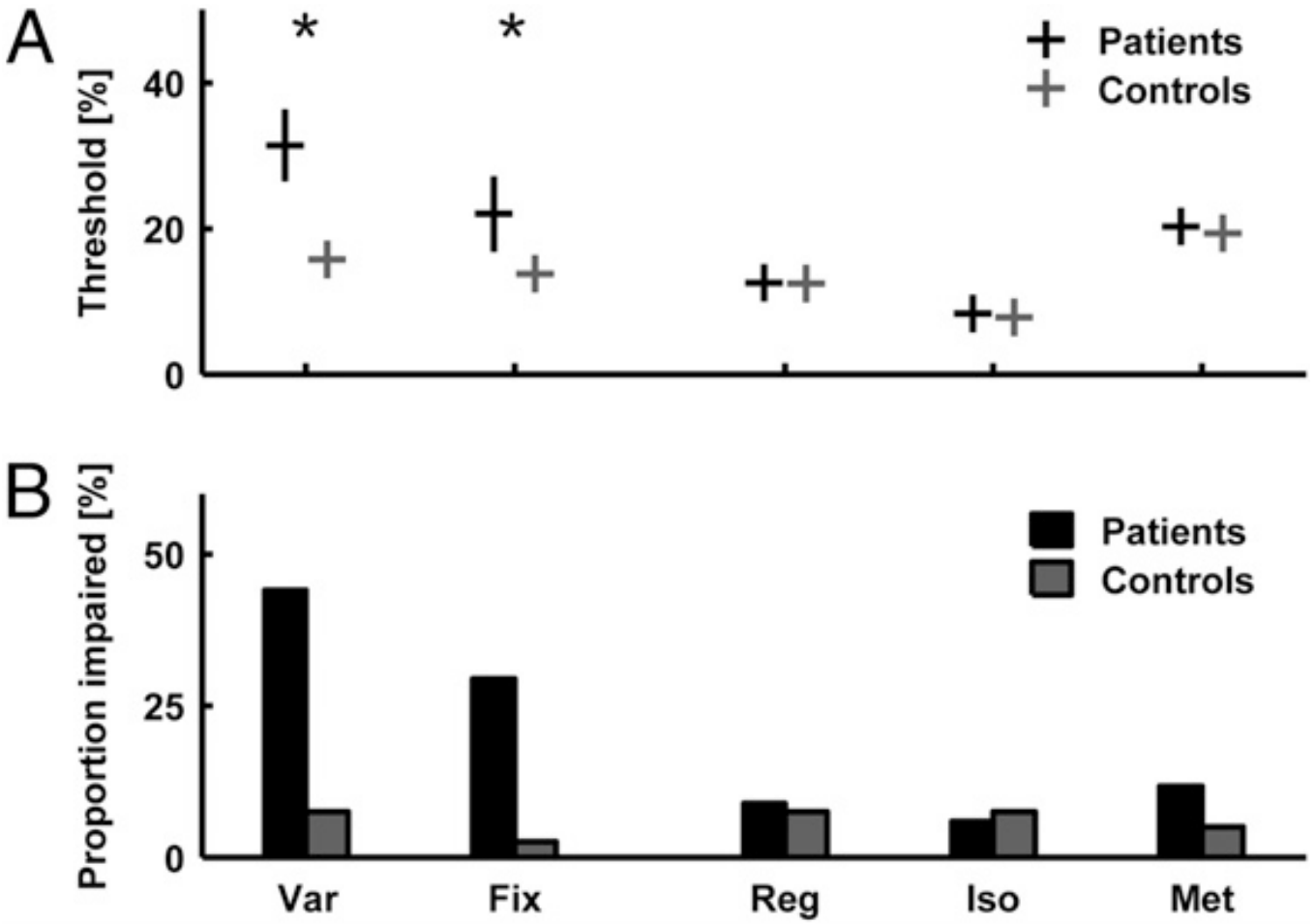
Sub-second	vs.	Supra-second	(Lewis and Miall)
Automatic	vs.	Cognitive	(Lewis and Miall)
Implicit	vs.	Explicit	(Coull and Nobre)
Event-based	vs.	Emergent	(Ivry et al.)
Duration-based	vs.	Beat-based	(Griffiths et al.)

II. Perception of time

Teki et al., 2011. *J Neurosci*

Duration-based timing

Encoding absolute duration of individual time intervals (ΔTi)



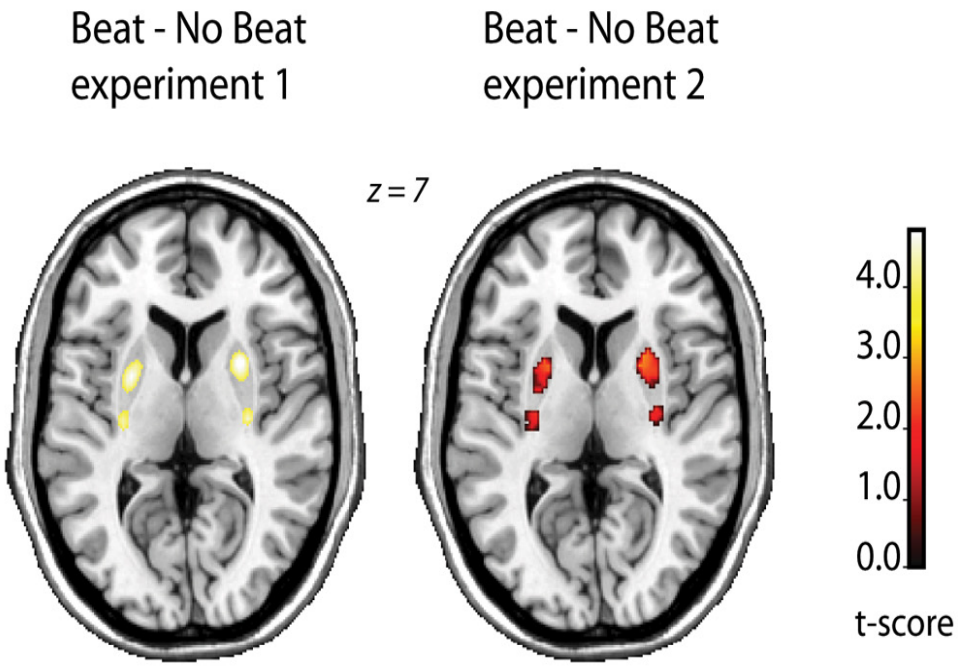
Grube et al., 2010. *PNAS*

Duration-based timing

- **Cerebellum implicated in absolute timing**

Beat-based timing

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

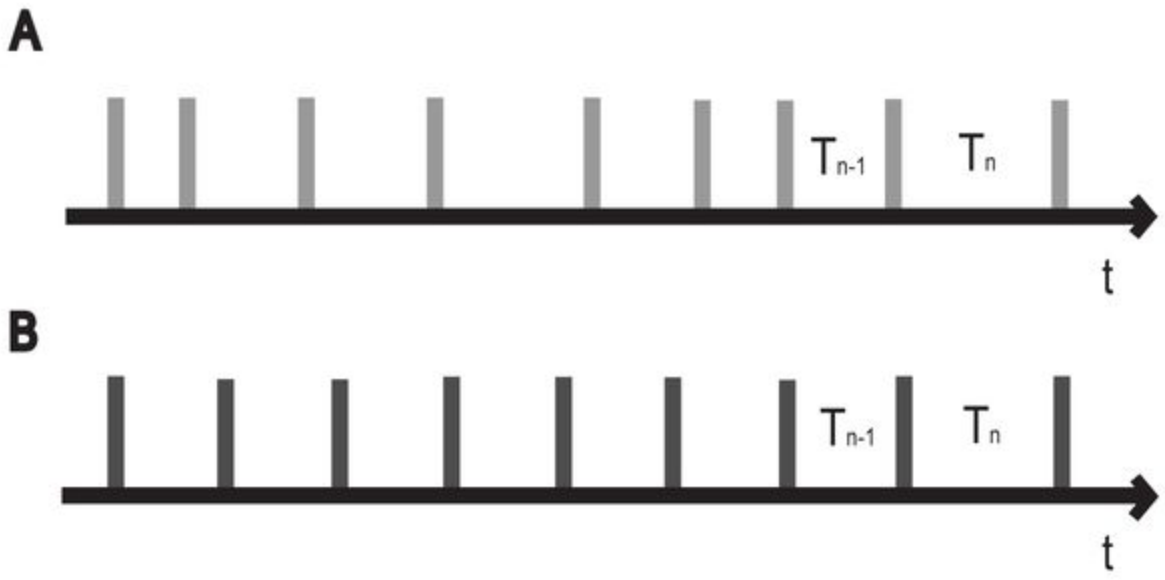


cf. Grahn et al.

Beat-based timing

- **Striatum, SMA, PMC involved in relative timing**

Paradigm

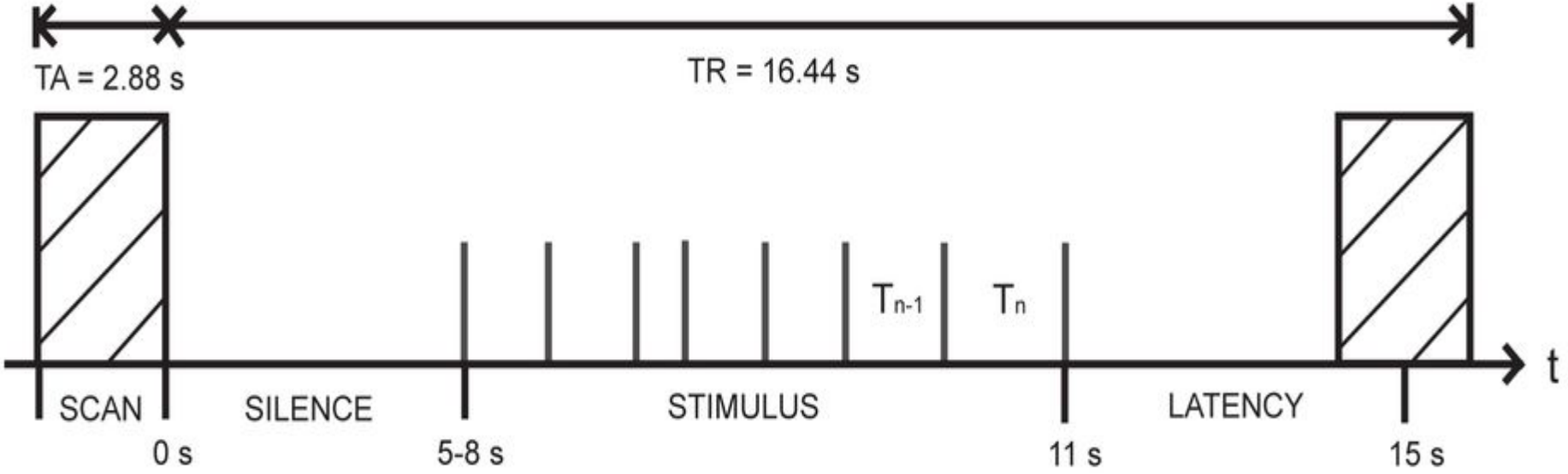


Task: T_n > or < T_{n-1}

Sequence A: Irregular with 15% average jitter

Sequence B: Regular with an isochronous beat

Design



EPI were acquired on a Siemens Allegra 3 Tesla scanner:

- 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

Hypotheses

H1: Beat-based timing more accurate than duration-based timing

H2: Cerebellum more involved in absolute, duration-based timing

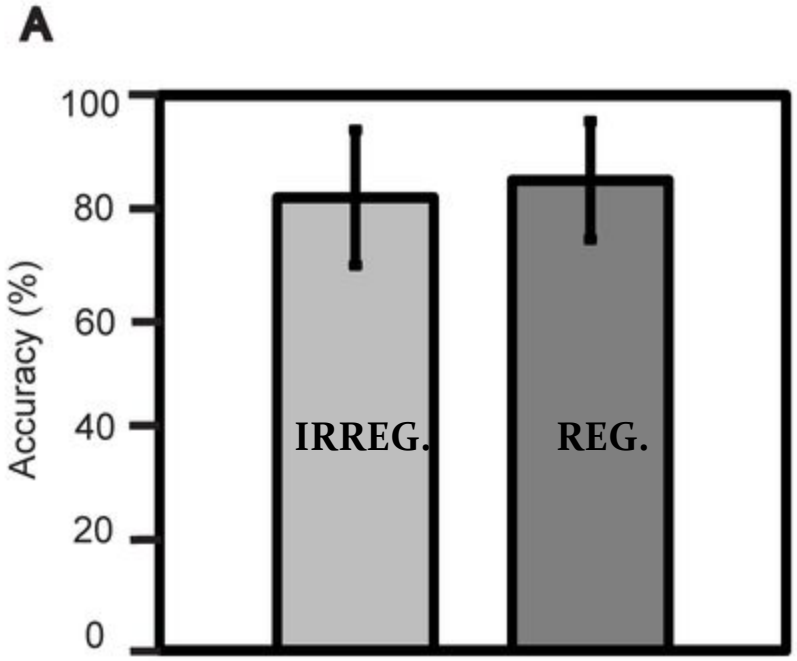
H3: Basal ganglia more involved in relative, beat-based timing

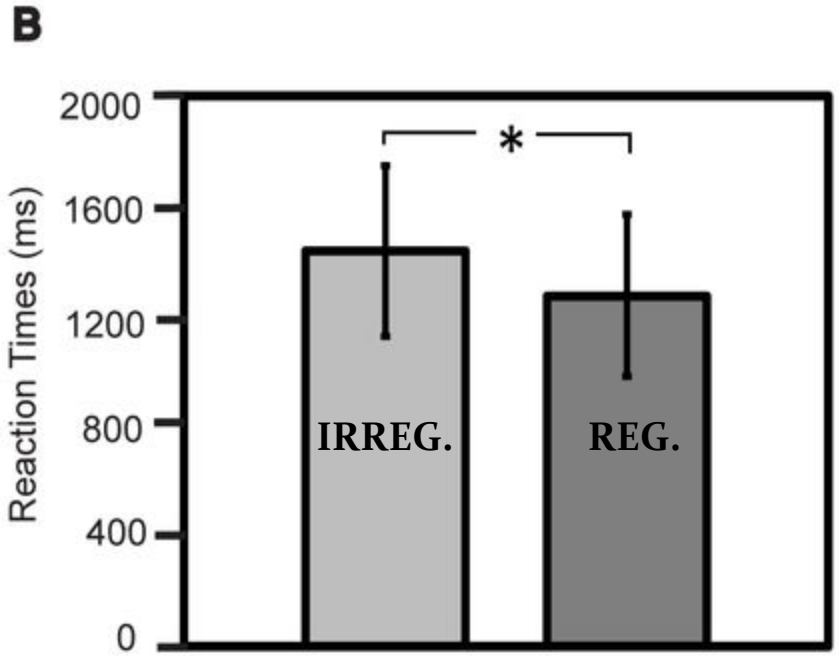
Analyses

Irregular > Regular (measure of absolute timing)

Regular > Irregular (measure of relative timing)

Behaviour in scanner



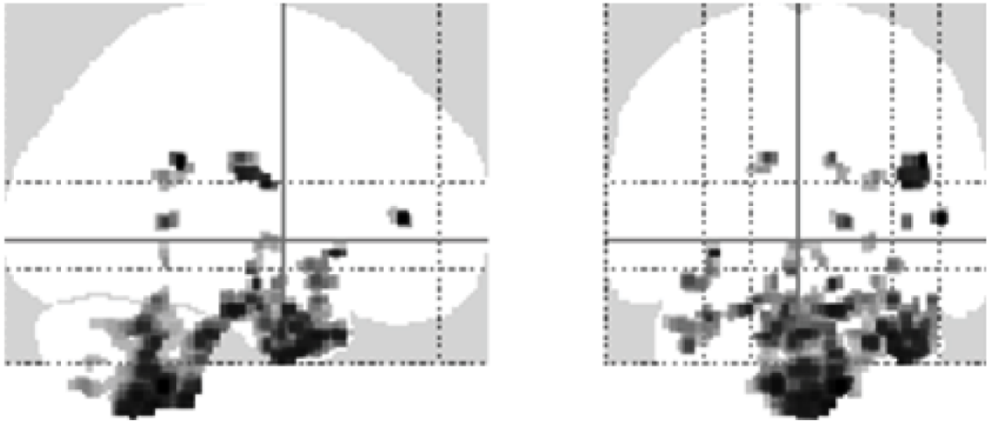


Mean	**81.53%**	**84.72%**	**1438**	**1275**
SEM	± 12.28%	±10.64%	± 297 ms	± 312 ms

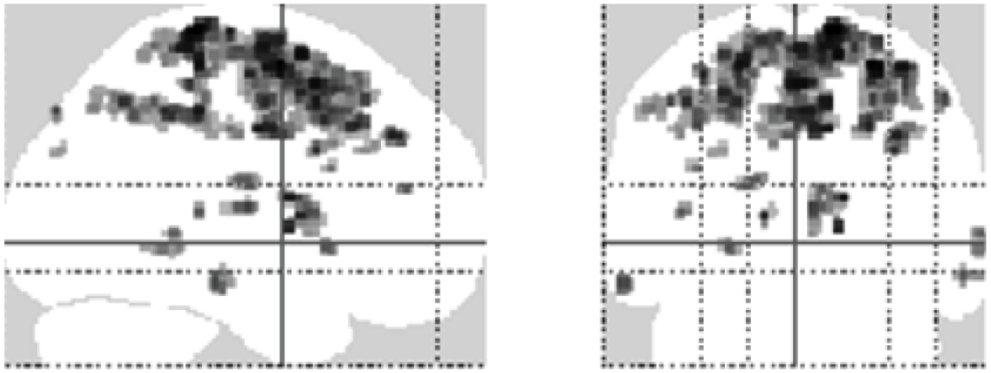
N = 18

fMRI results

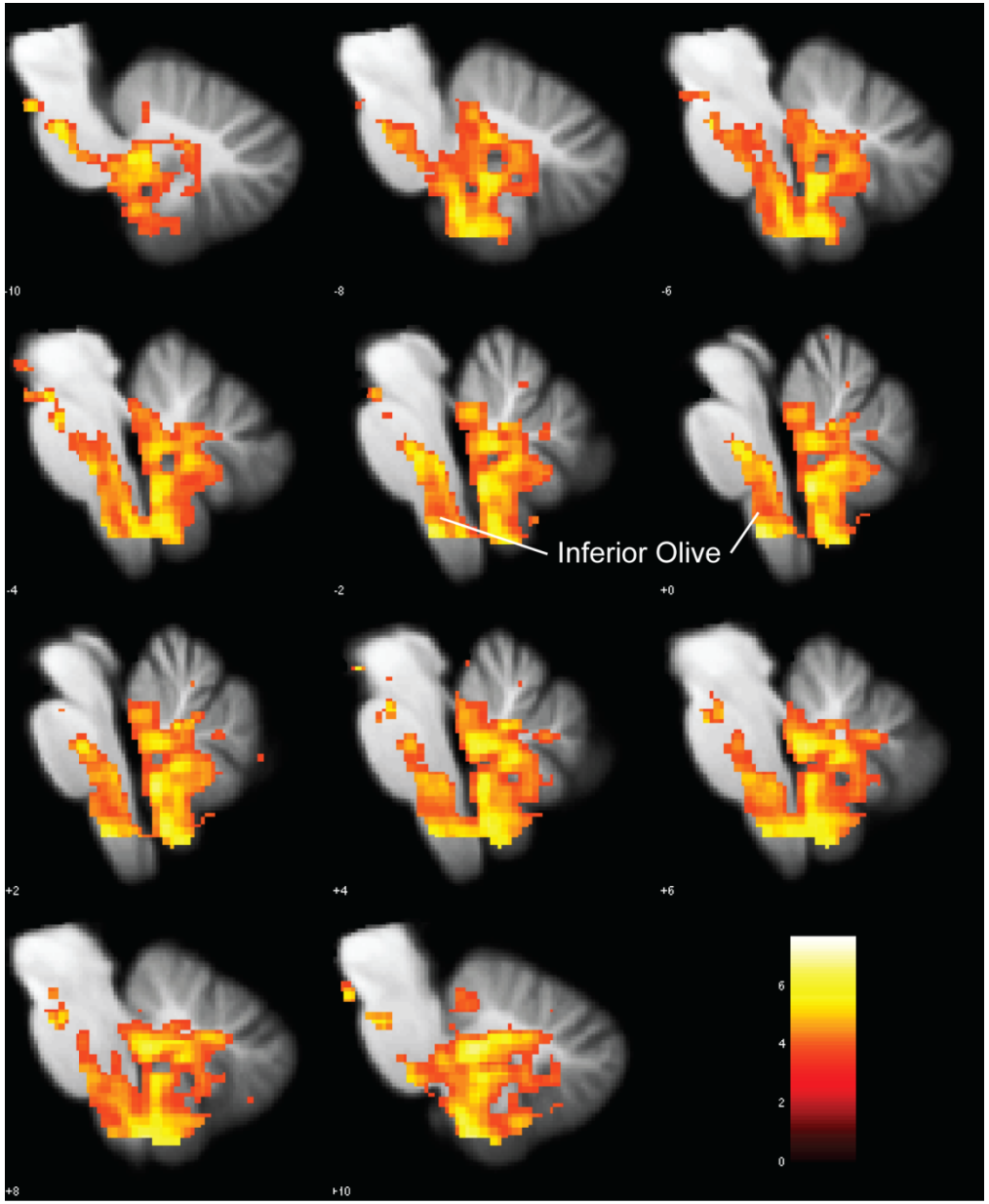
A Activations for absolute, duration-based timing



B Activations for relative, beat-based timing

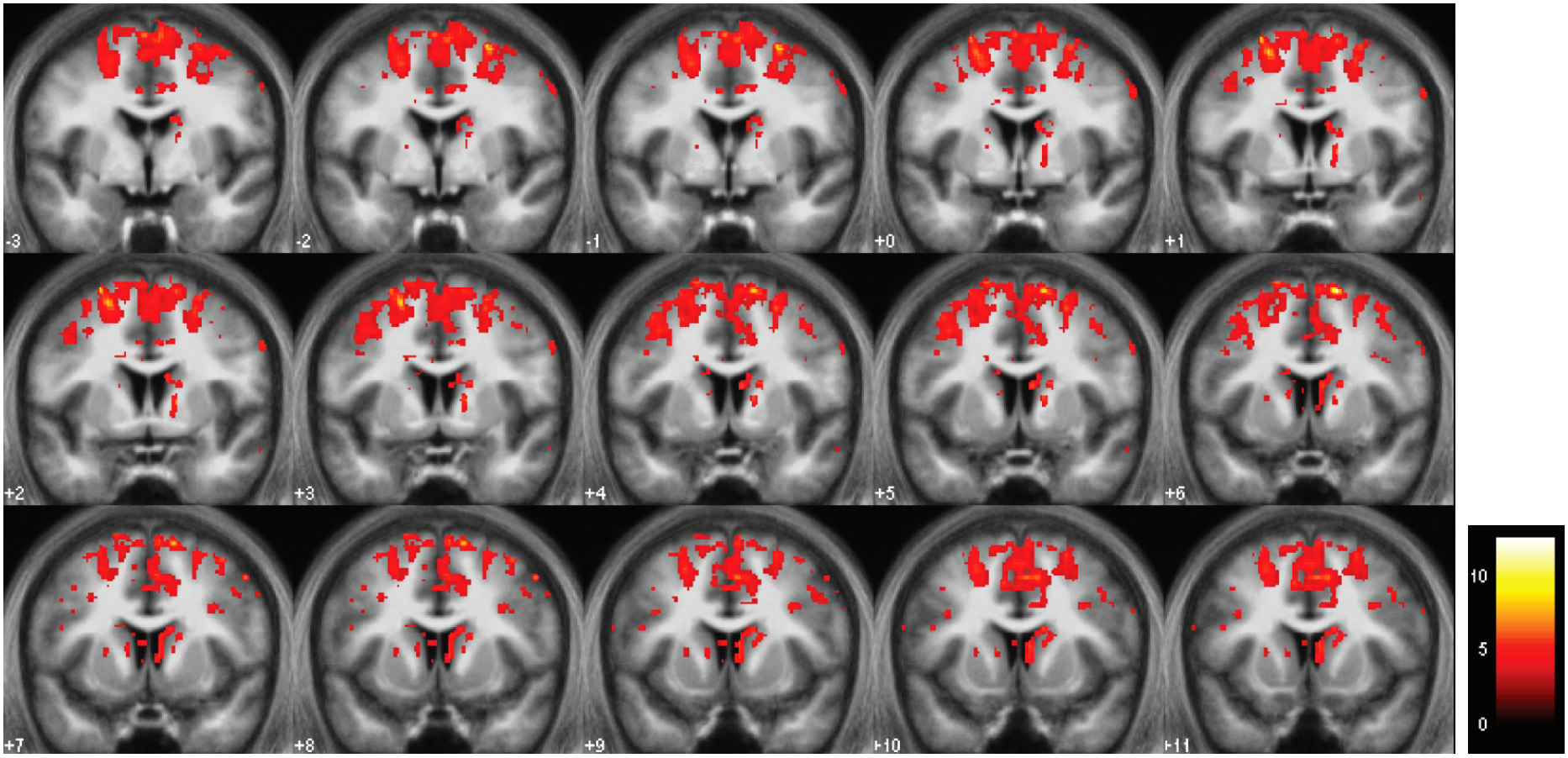


Duration-based timing



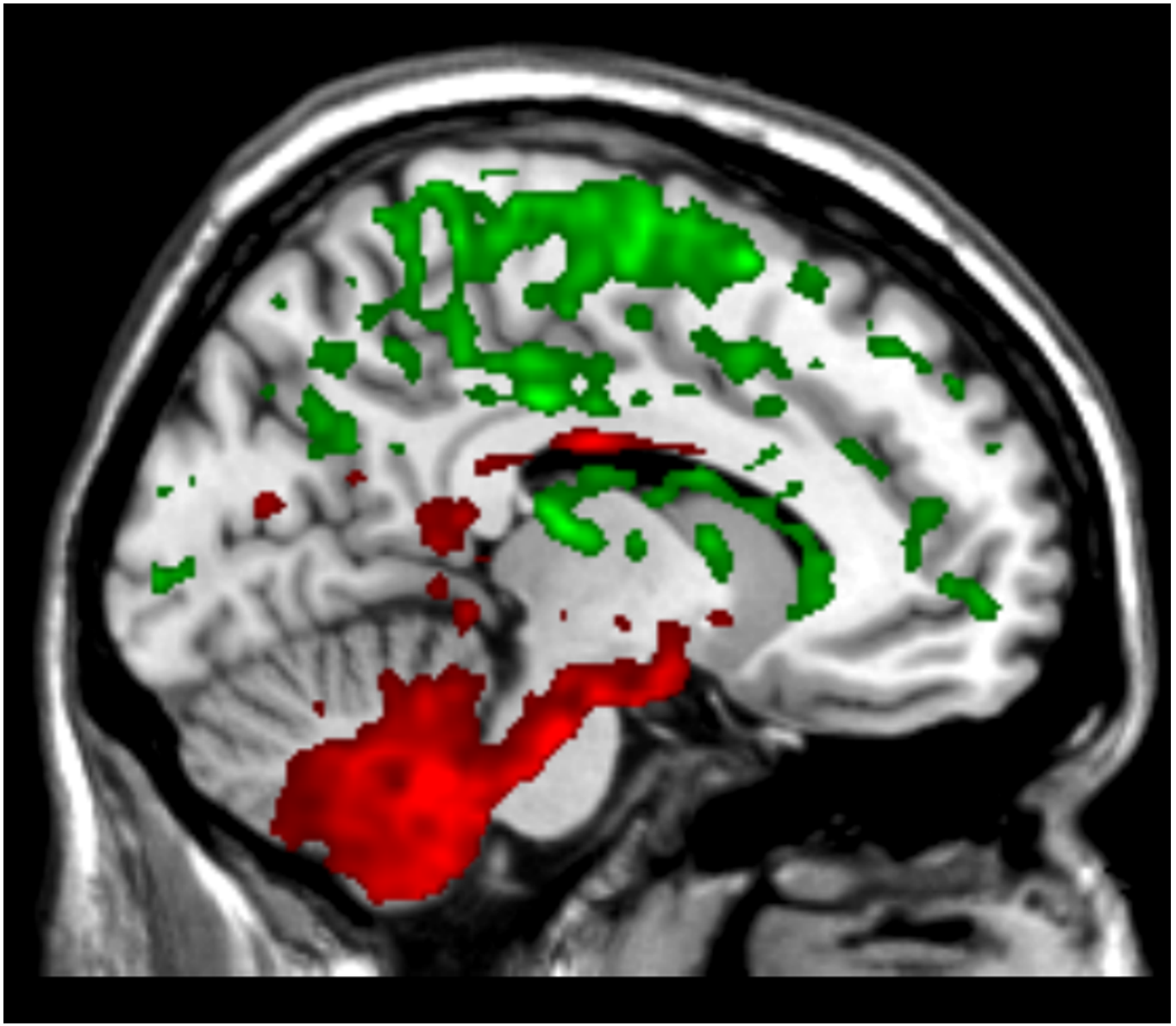
x = -10 to 10 mm

Beat-based timing

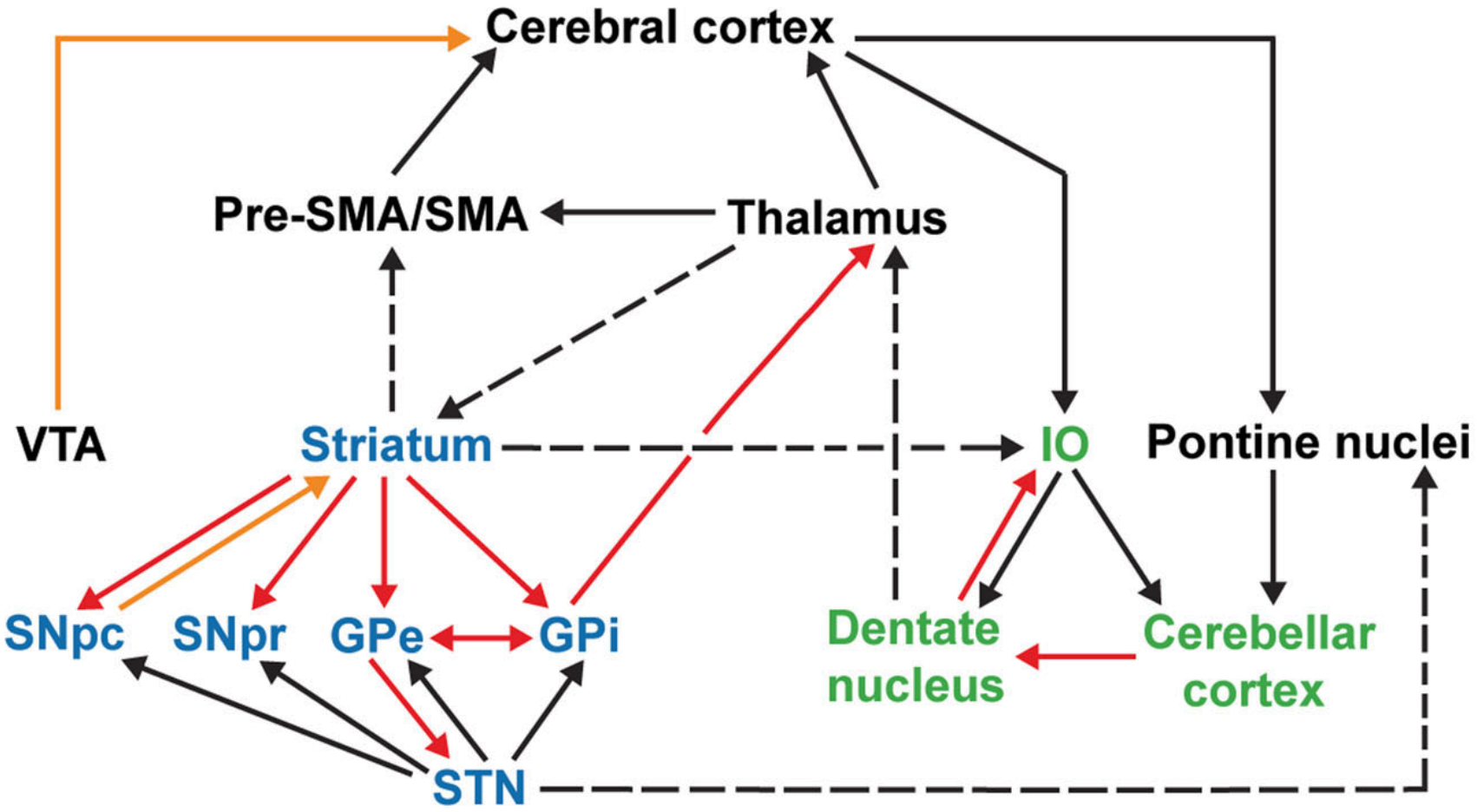


x = -3 to 11 mm

Functional dissociation



Unified Model



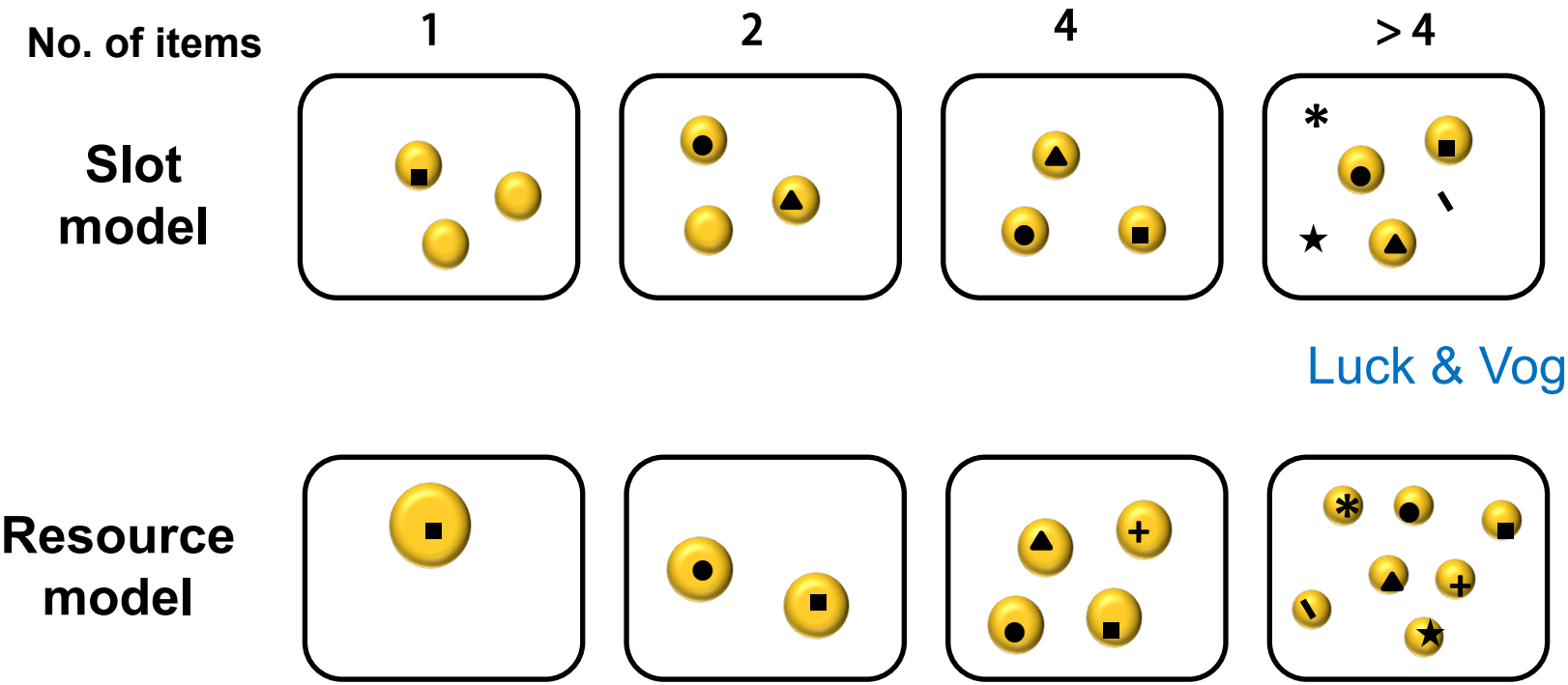
Teki et al., 2012. *Frontiers*

Allman, Teki et al., 2014. *Ann Rev Psychol*

III. Working memory for time (behaviour)

Teki and Griffiths (2014) *Elife (under review)*

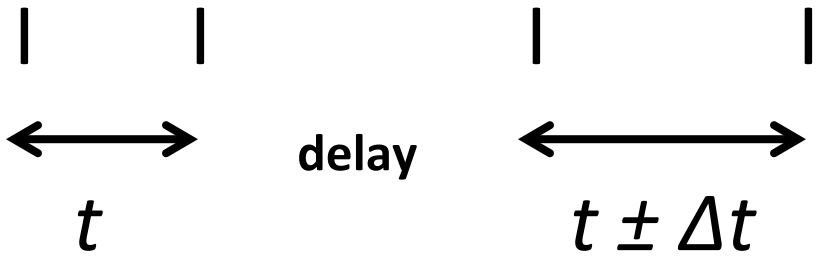
Models of working memory



Luck & Vogel (1997)

Bays & Husain (2008)
Ma et al. (2014)

WM for time

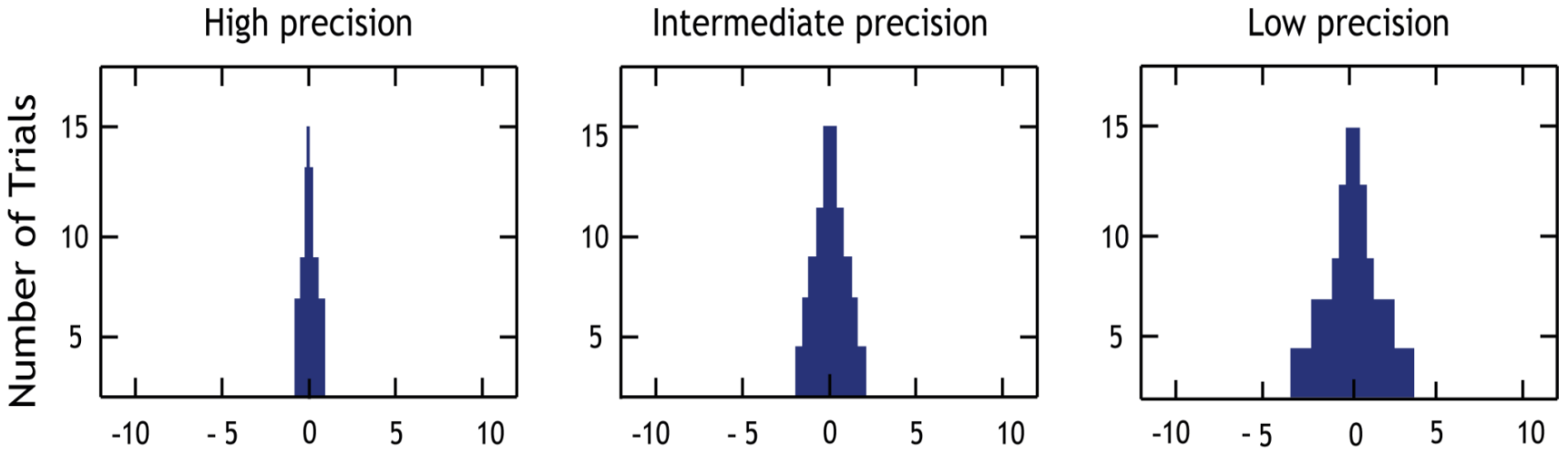


- discrimination task
- binary/categorical measure
- no variation of memory load
- isolated intervals; no variation of rhythmic structure

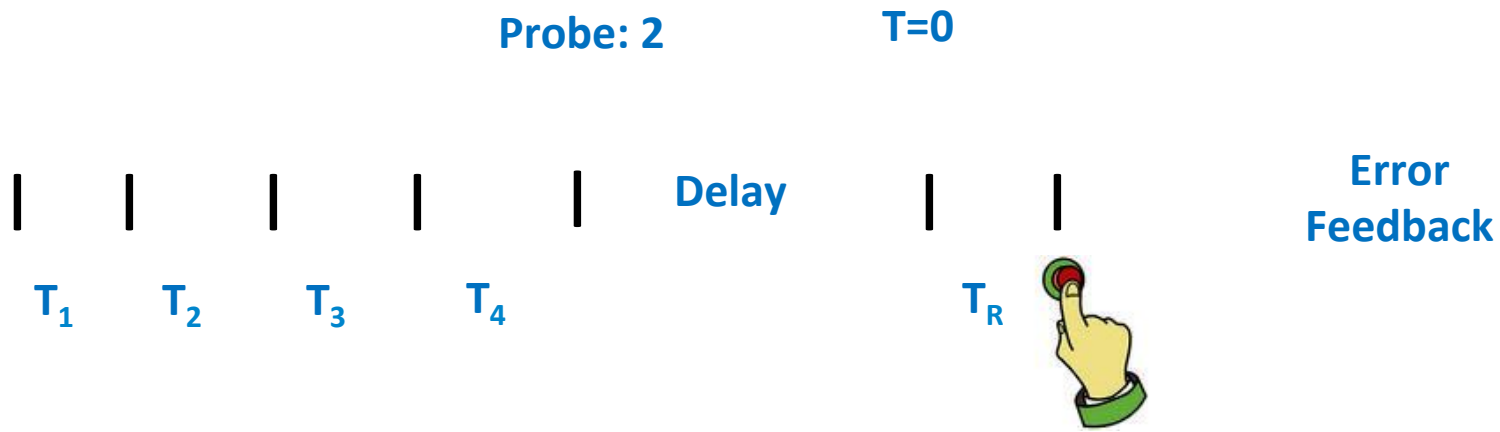
Output measure

Precision: a continuous index that quantifies fidelity of memory

Precision = 1 / standard deviation



Paradigm



Perceptual time matching response = T_R (adjusted for RTs)

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

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

Experiments

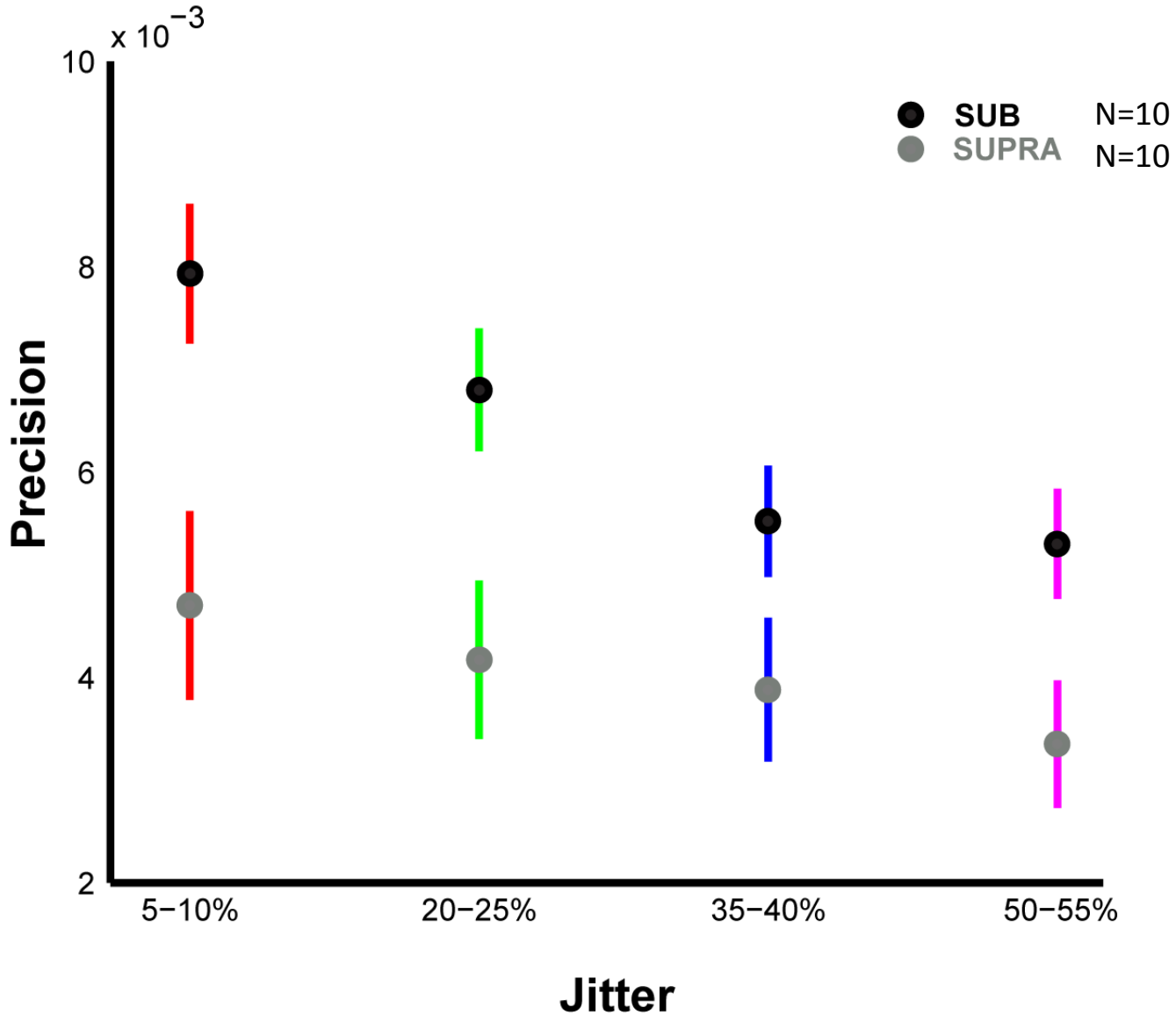
1: 'SUB'

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

2: 'SUPRA'

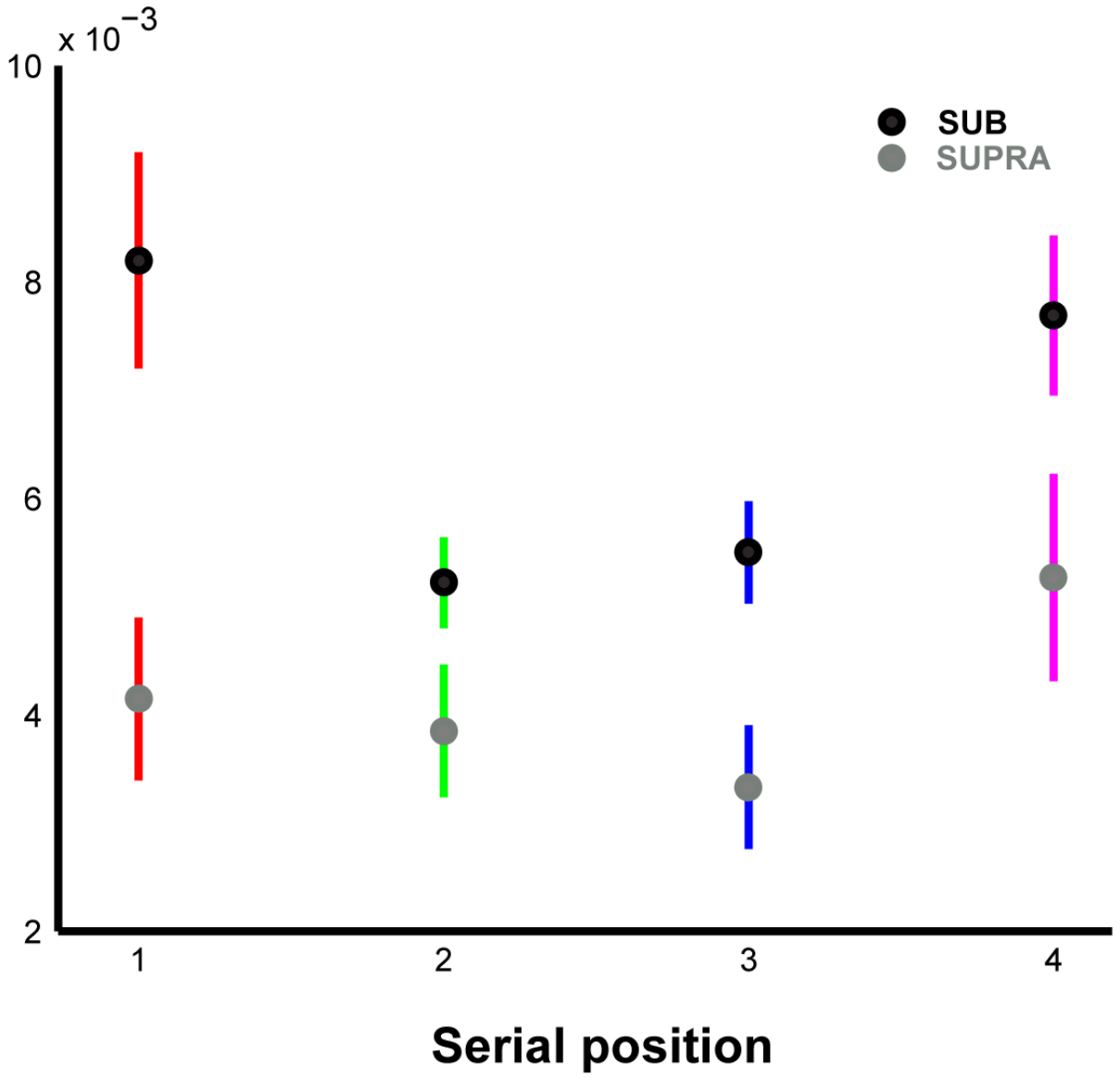
- No. of intervals: 4
- IOI: 1.0 - 1.2 s
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

Exp 1 & 2: Precision vs. jitter



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

Exp 1 & 2: Precision vs. position



Experiments

1: ‘SUB’

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

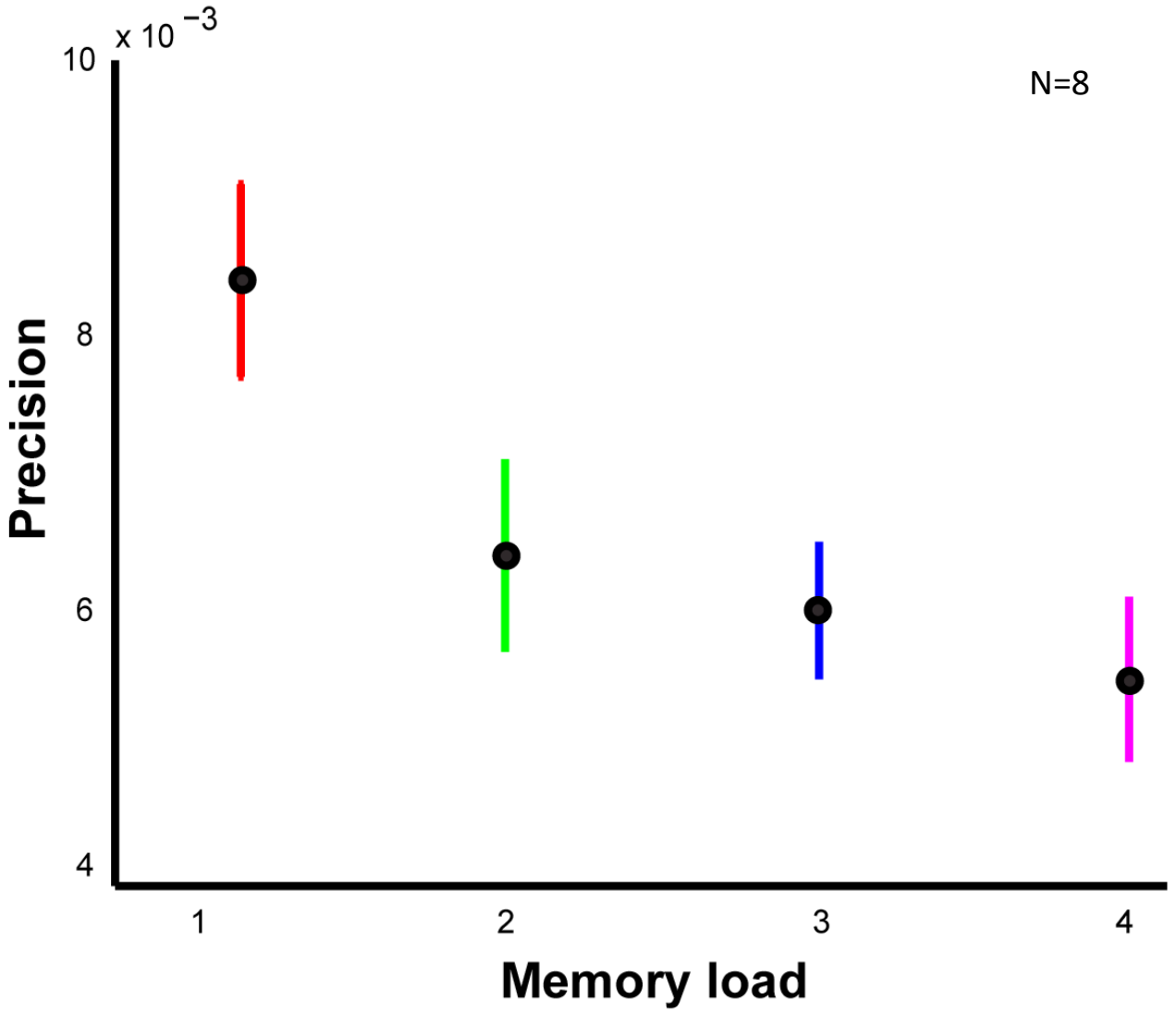
2: ‘SUPRA’

- 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%

Exp 3: Precision vs. WM load



- ***Significant effect of WM load (p=0.01)***

Experiments

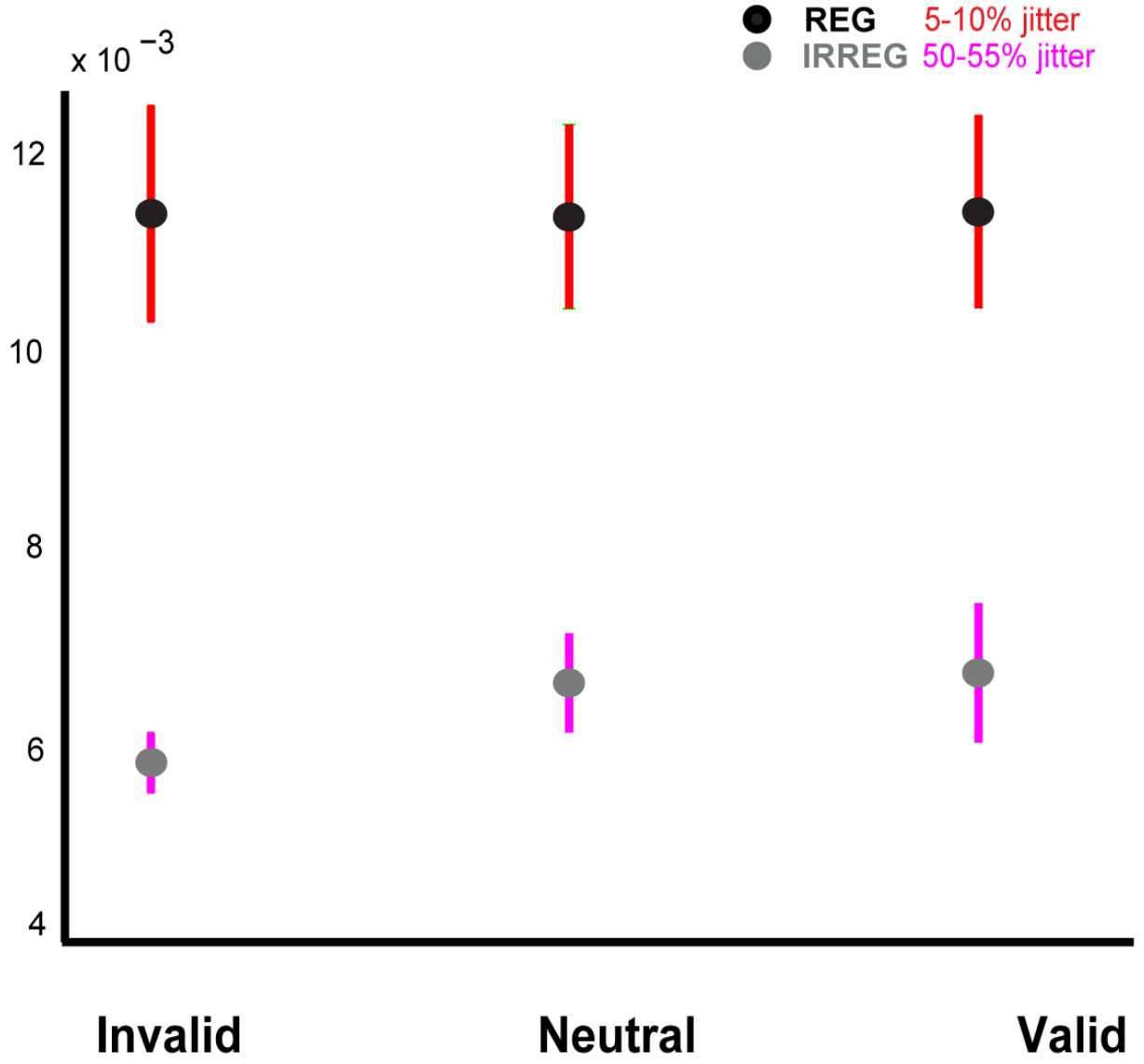
1: ‘SUB’
- No. of intervals: 4
- IOI: 500-600 ms
- Jitter levels: 5-10%, 20-25%, 35-40%, 50-55%

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%

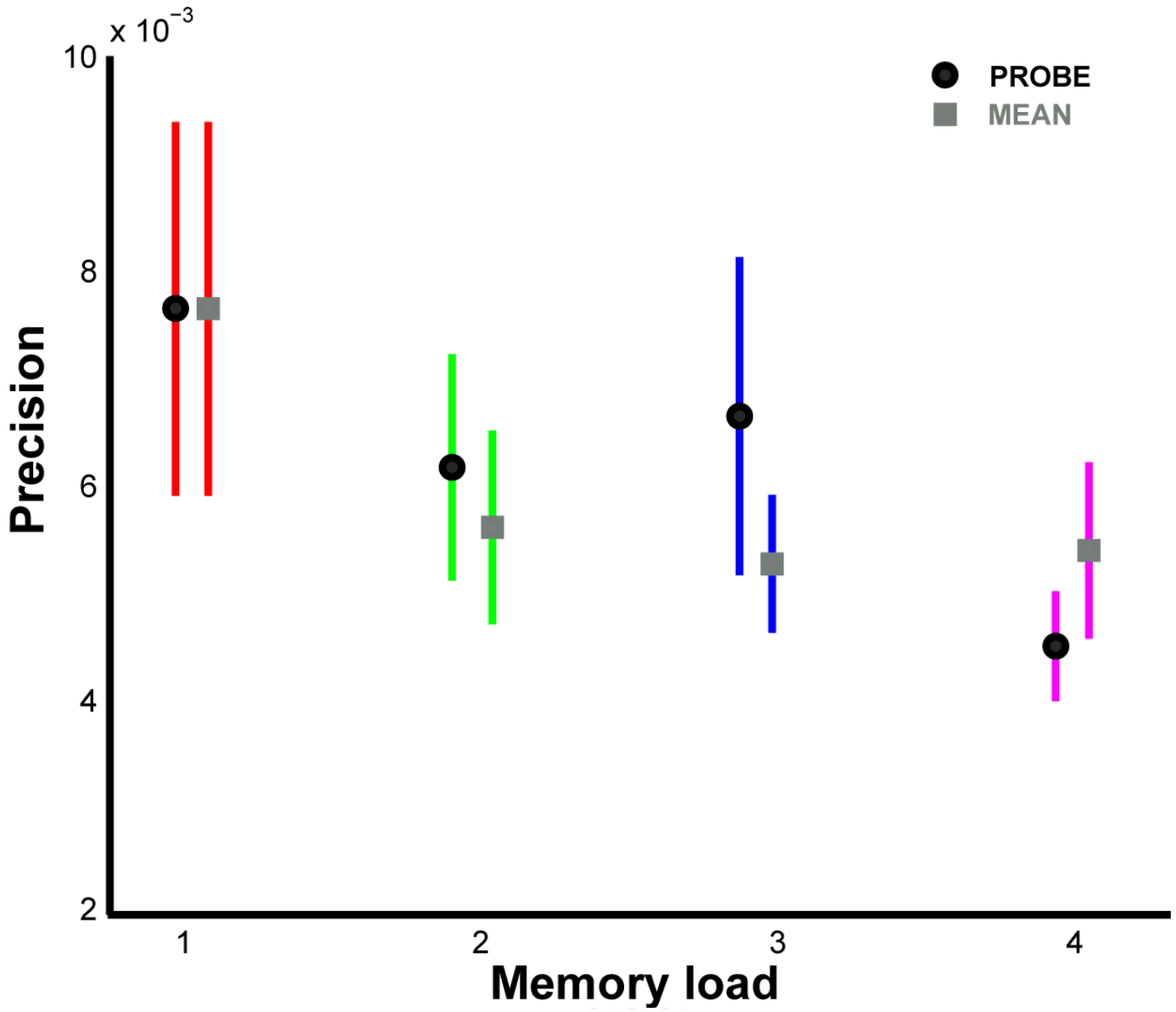
4: ‘CUED’
- **No. of intervals: 4**
- **IOI: 500-600 ms**
- **Jitter levels: 5-10%**
- **Cue: Valid (56.2%), Invalid (18.8%), Neutral (25%)**

Exp 4: Precision vs. cue



- ***No significant effect of cueing in either REG or IRREG context***

Control analysis



IV. Working memory for time (fMRI)

Teki and Griffiths (2014)

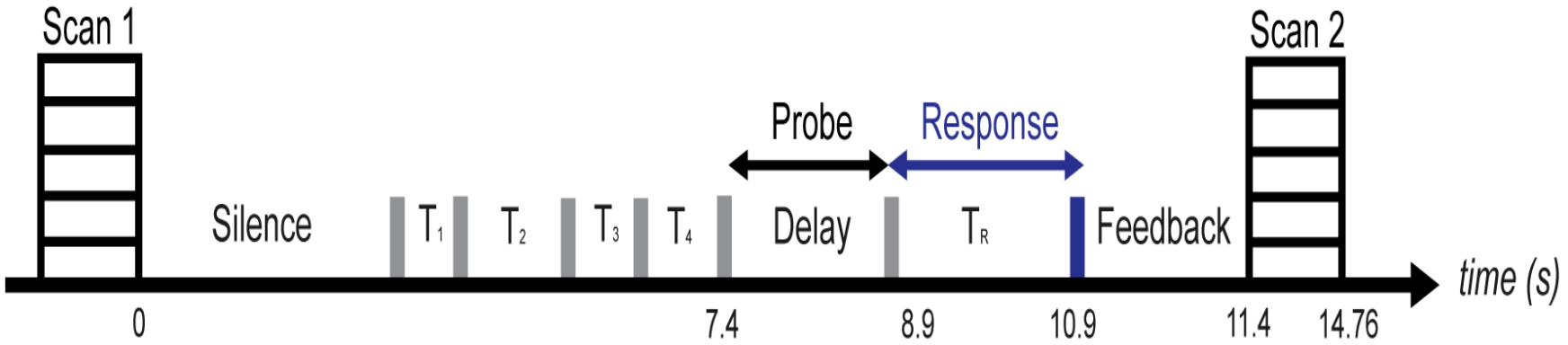
Aims

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%	

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)

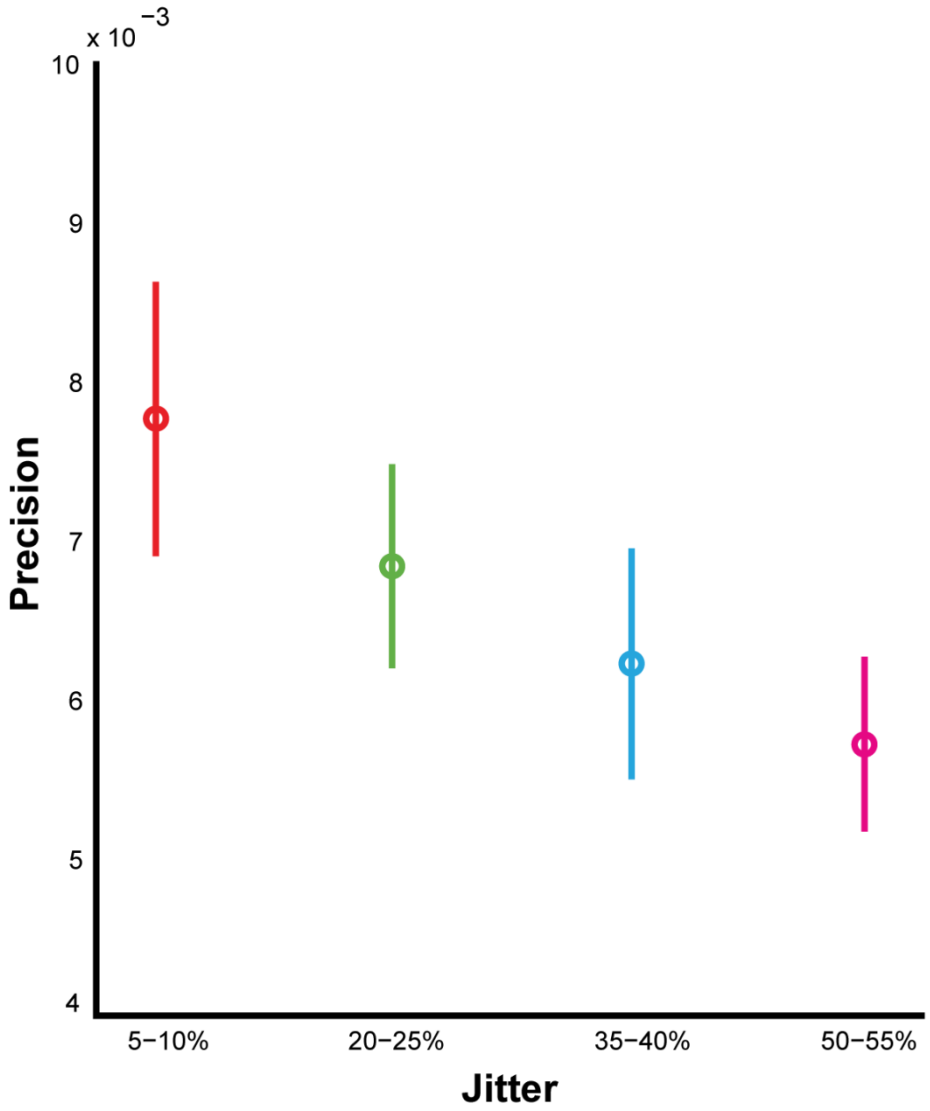
B. Effect of varying WM load (for fixed temporal regularity)

C. Effect of context:
Common (32) trials in rhythm and WM blocks with
4 intervals and 20-25% jitter

D. Effect of learning: block 2 vs. 1

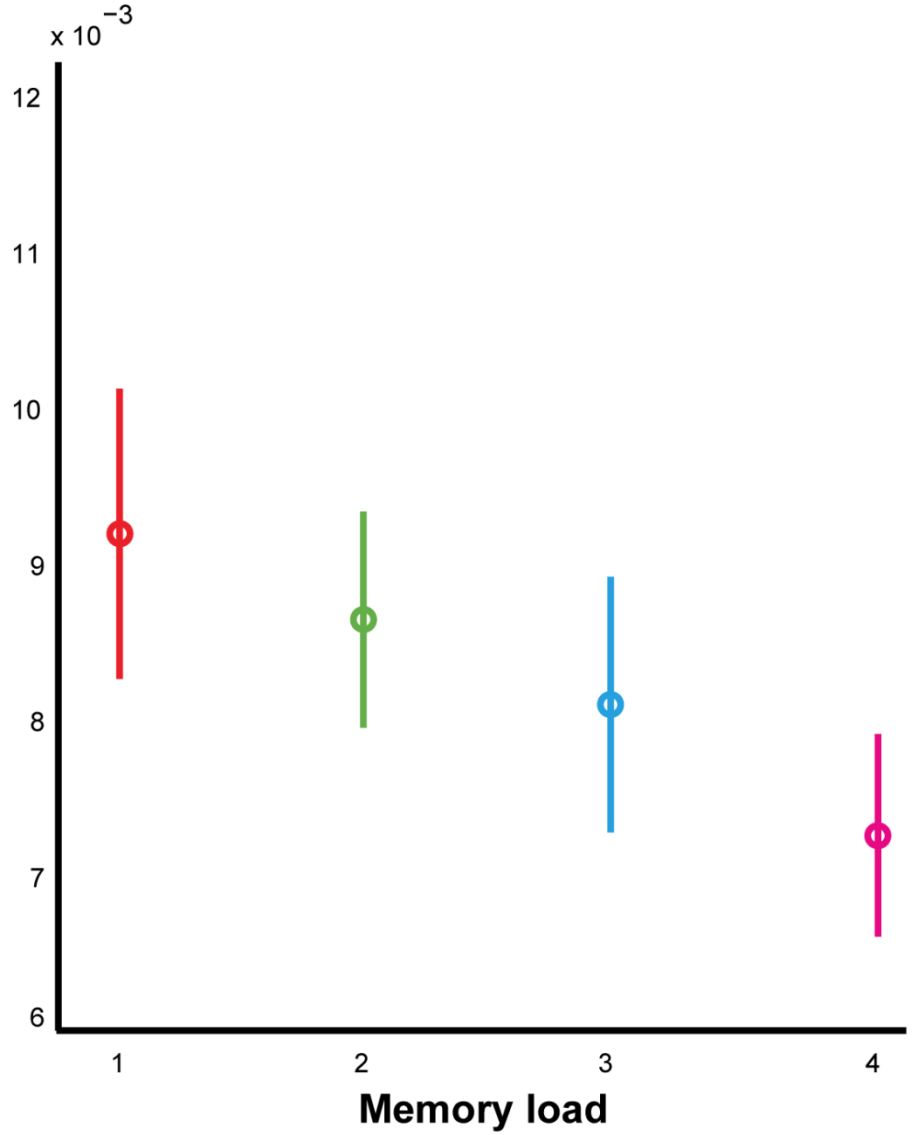
E. VBM analysis: GM volume correlation with behaviour

Behaviour in scanner: Jitter



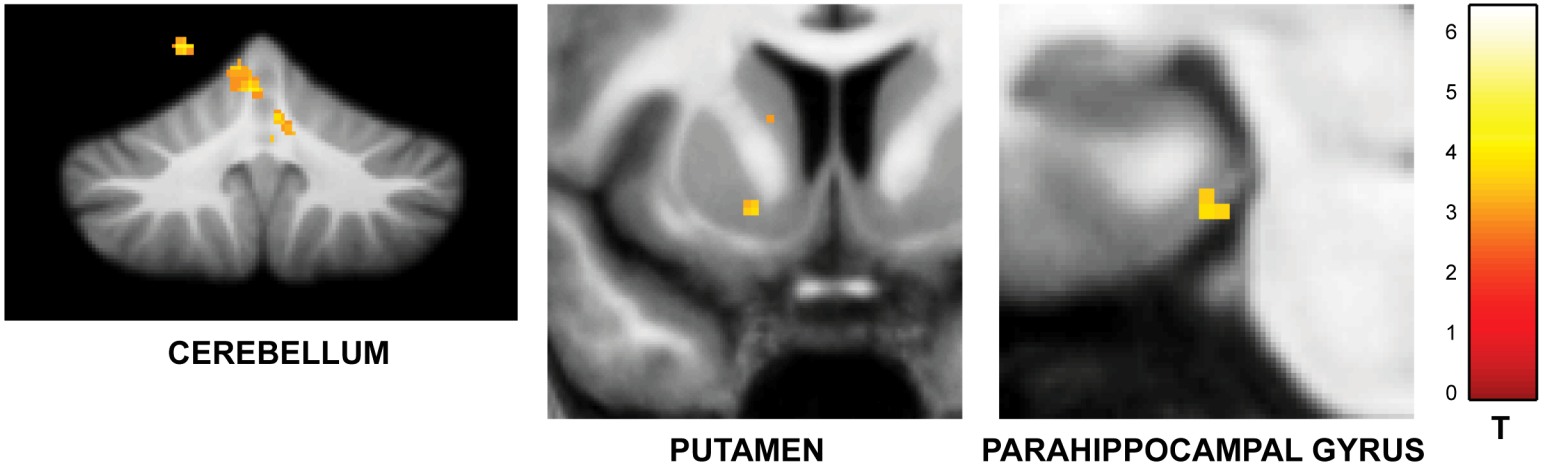
- ***Significant effect of jitter (p=0.02; N=18)***

Behaviour in scanner: WM load

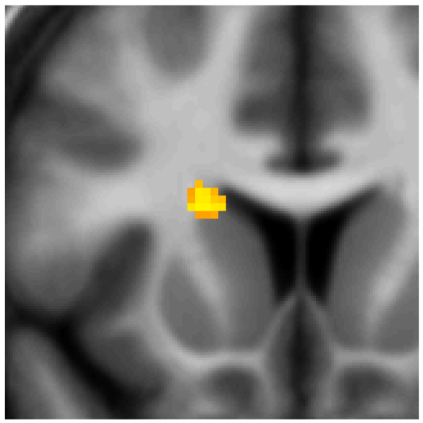


- ***No significant effect of load (p=0.36; N=16)***

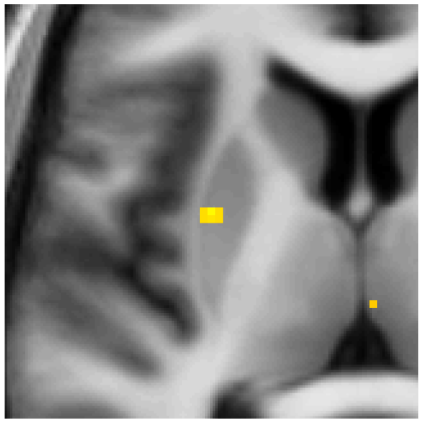
A1. Effect of increasing jitter



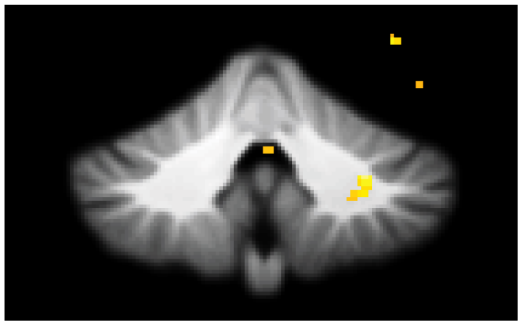
A2. Effect of decreasing jitter



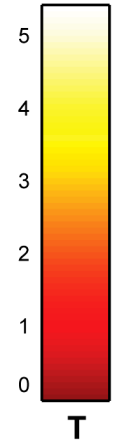
CAUDATE NUCLEUS



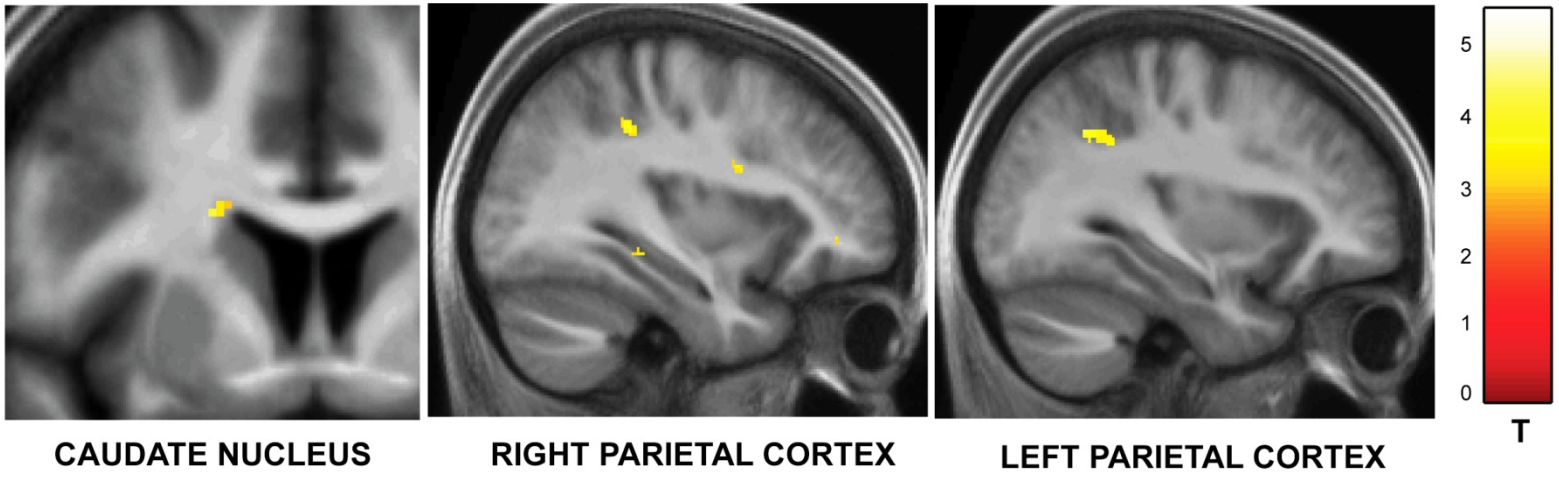
PUTAMEN



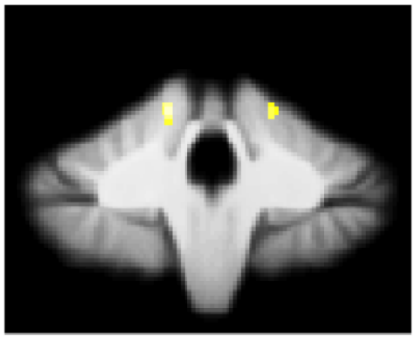
CEREBELLUM



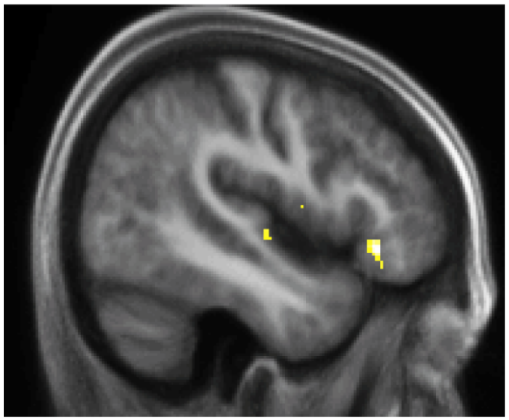
B1. Effect of increasing load



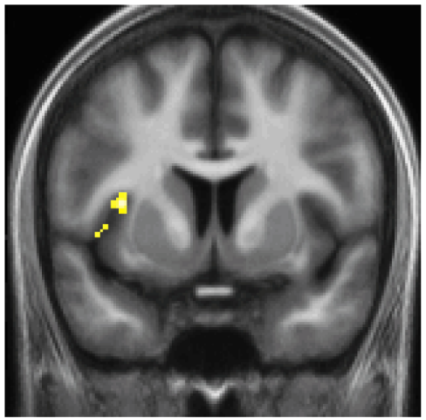
B2. Effect of decreasing load



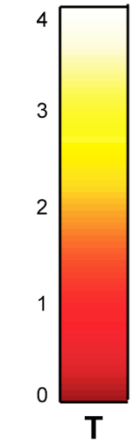
CEREBELLUM



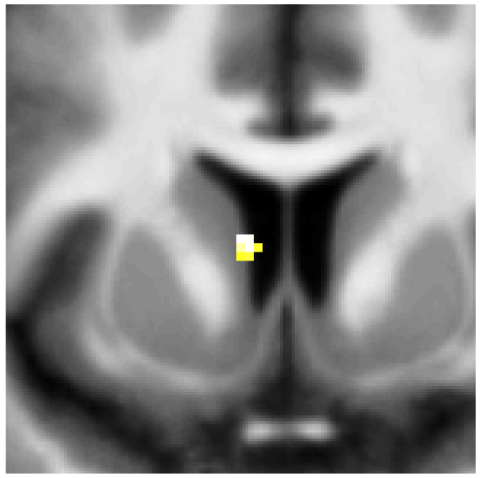
ORBITOFRONTAL CORTEX



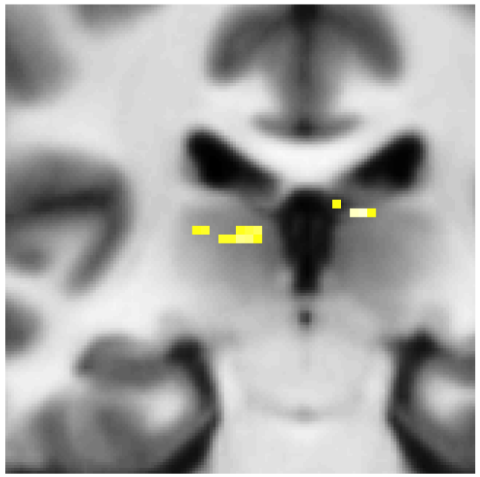
INSULA



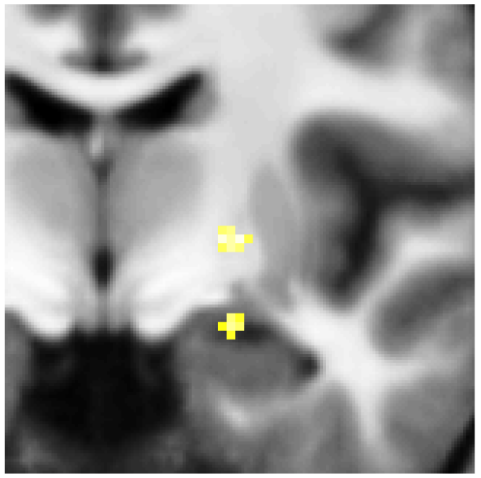
C1. Rhythm vs. WM



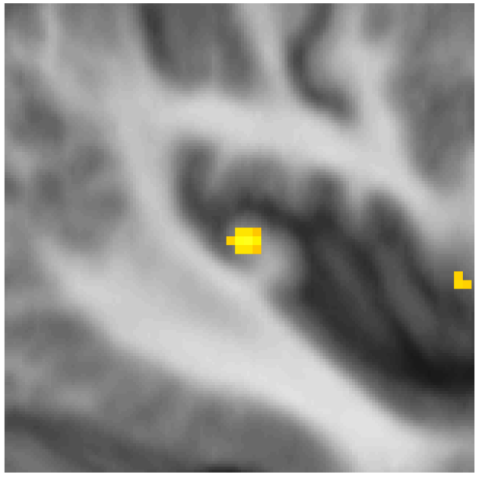
CAUDATE



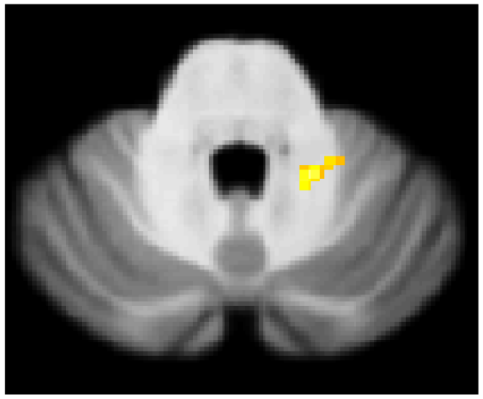
THALAMUS



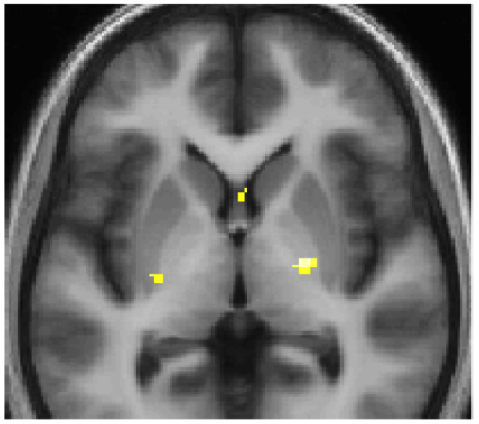
HIPPOCAMPUS



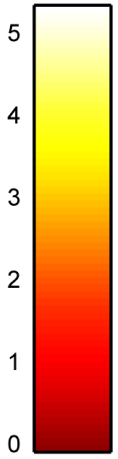
HESCHL'S GYRUS



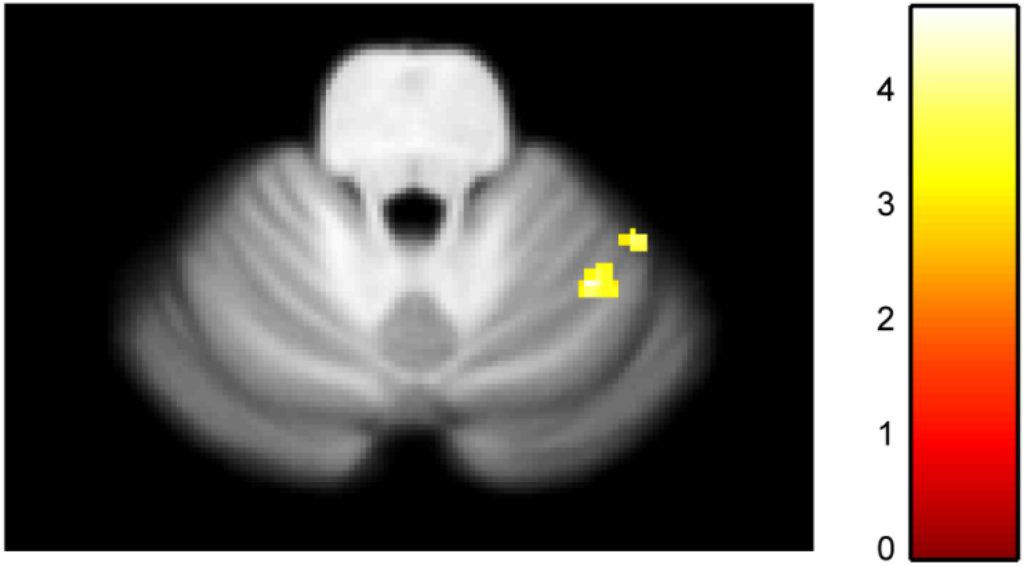
CEREBELLUM



PUTAMEN/PALLIDUM

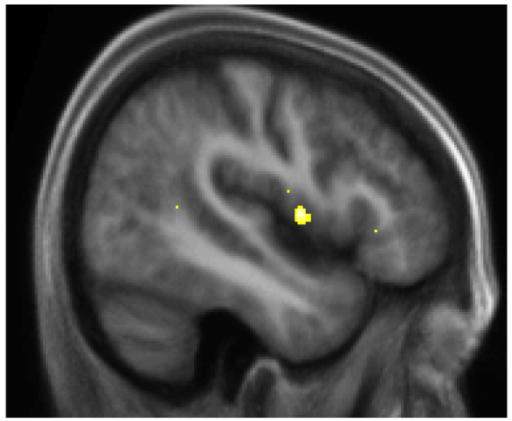


C2. WM vs. Rhythm

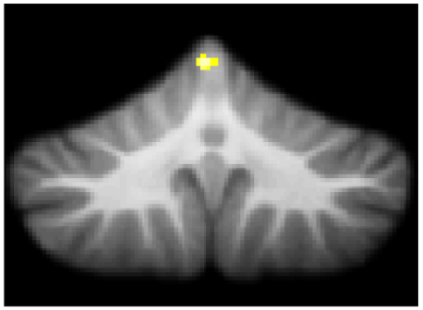


CEREBELLUM

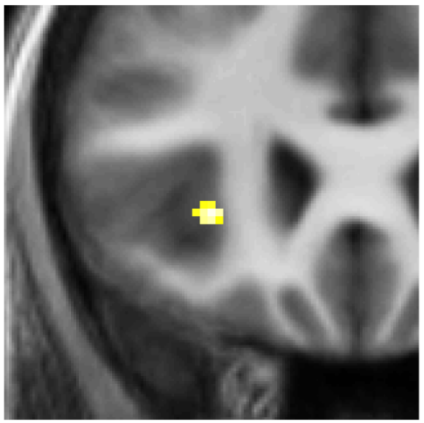
D1. Learning (rhythm)



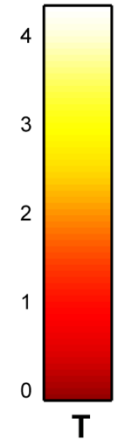
FRONTAL OPERCULUM



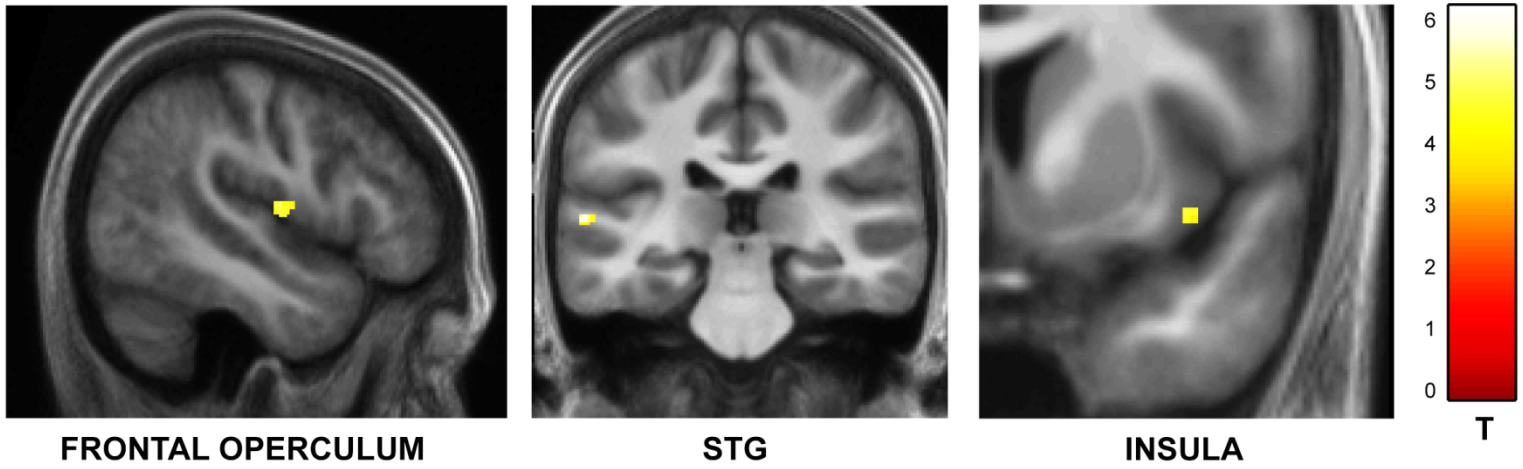
CEREBELLUM



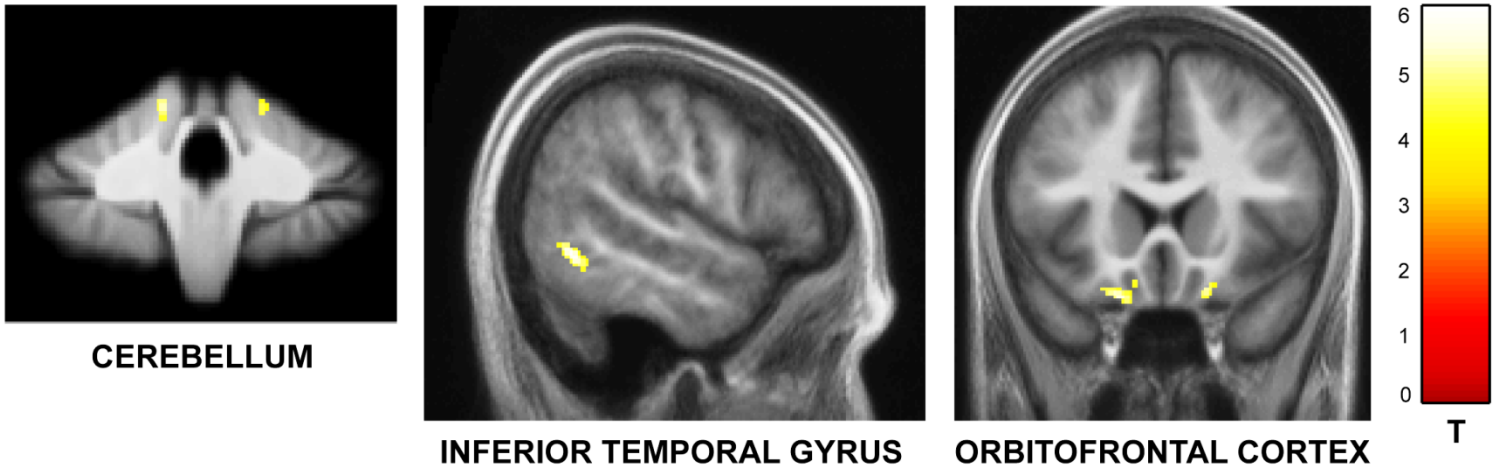
INSULA

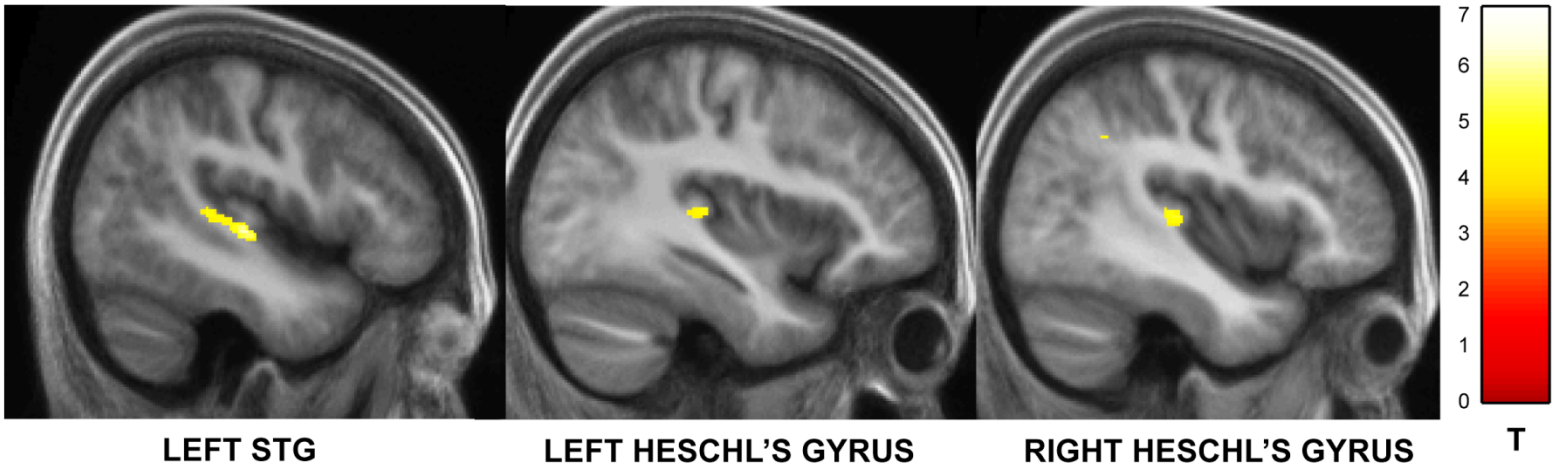


D2. Learning (WM)

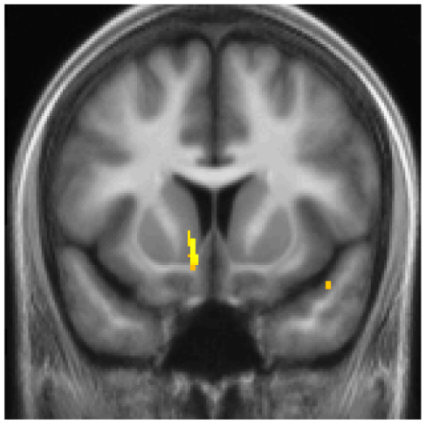


E1. GM volume correlation with performance on rhythm blocks

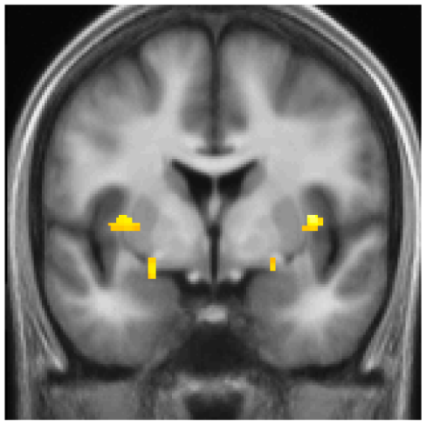




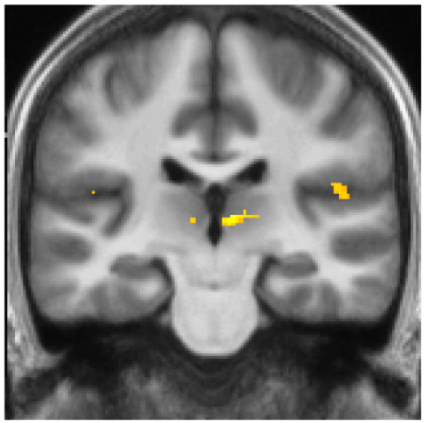
E2. GM volume correlation with performance on memory blocks



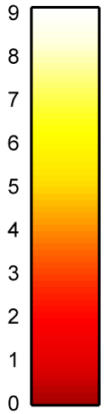
CAUDATE

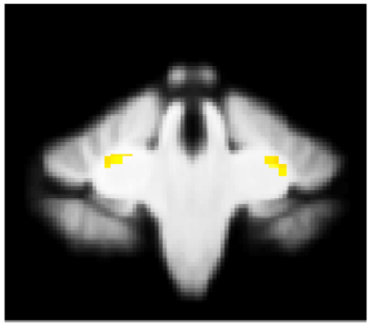


INSULA / AMYGDALA



THALAMUS





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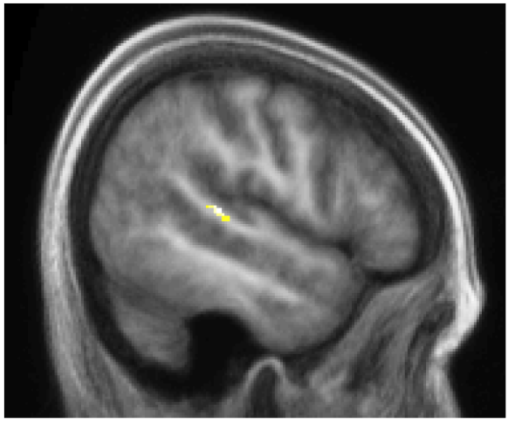
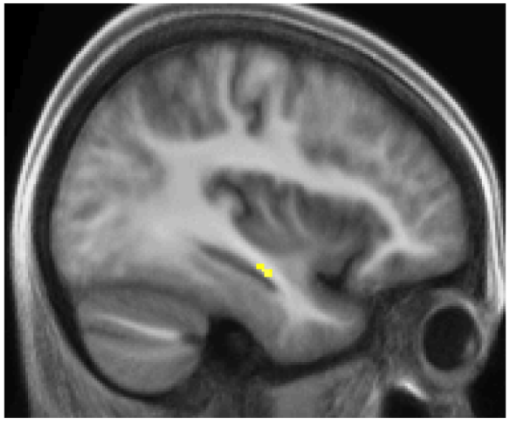


STG



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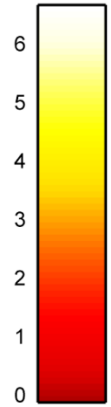

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wellcome trust

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