Distinct neural substrates of duration-based and beat-based auditory timing

Sundeep Teki [1,2]

Manon Grube [2], Sukhbinder Kumar [1,2], Tim Griffiths [1,2]

[1] Wellcome Trust Centre for Neuroimaging, University College London, UK

[2] Newcastle Auditory Group, Newcastle University Medical School, UK

Outline

- Rhythm and Time perception
- Timing Mechanisms
  - Relative, beat-based timing
  - Absolute, duration-based timing
- Stimulus
- fMRI experiment
- Discussion

Introduction

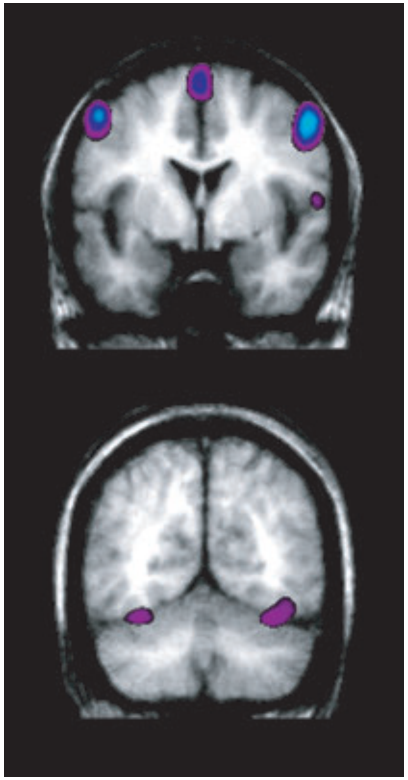
Rhythm and Timing

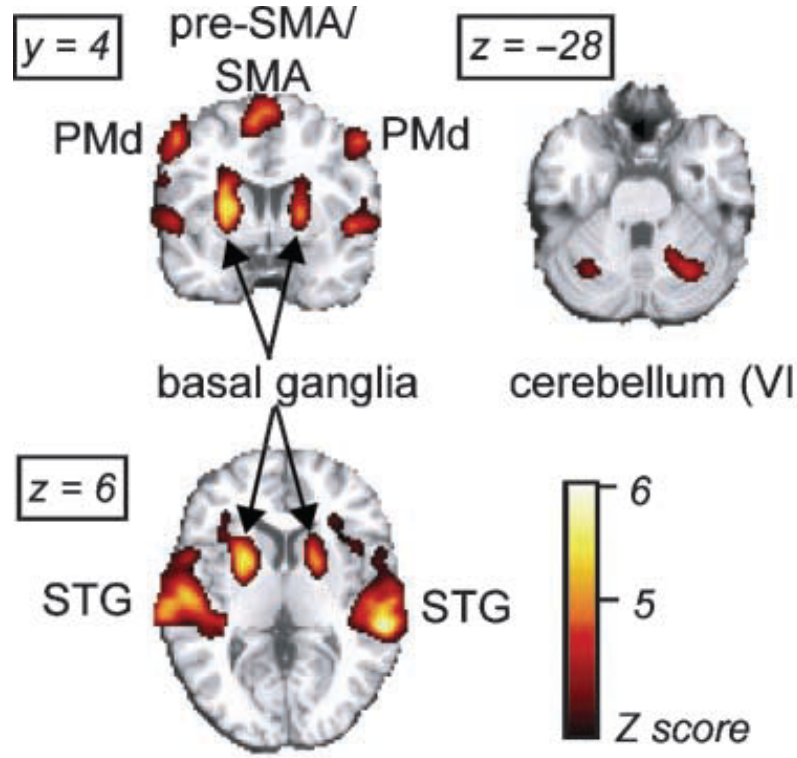
How does the brain perceive time?

Which brain regions are involved in time perception?

How do rhythms affect our perception of time?

Brain bases of rhythm perception





Listening to rhythms recruits several regions of the brain:

Cerebellum, basal ganglia; pre-SMA/SMA, pre-motor; STG, prefrontal cortex.

Bengtsson, Chen, Grahn and colleagues

Timing Mechanisms

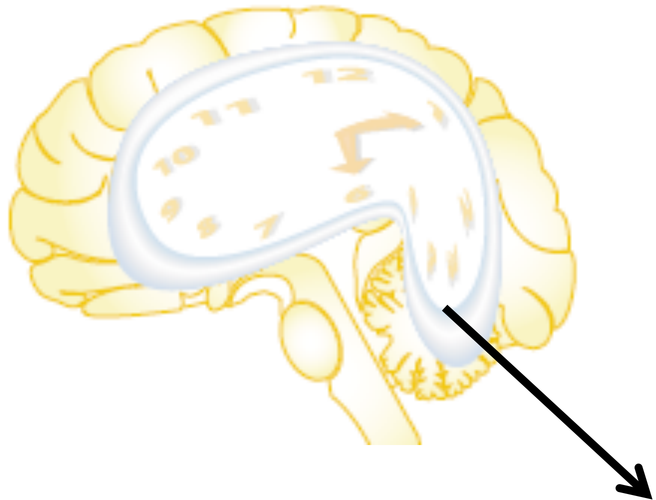
- **Relative, beat-based timing:**

  Timing of intervals relative to a regular beat (ΔT_i / T_{beat})

- **Absolute, duration-based timing:**

  Encoding absolute duration of individual time intervals (ΔT_i)

Relative, beat-based timing



Ignore the cerebellum!

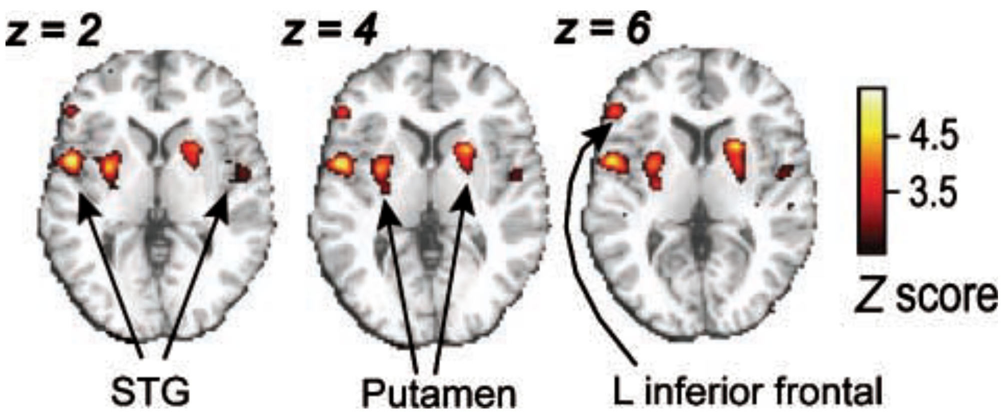
A regular beat offers beneficial temporal cues in perceptual timing

(Povel & Essen, 1985)

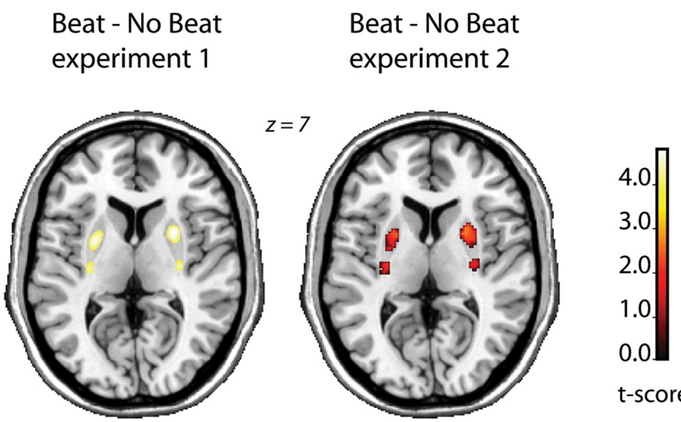
Parkinson’s patients show deficits in perceptual timing tasks.

(Artieda et al. 1992, Harrington et al. 1998, Grahn & Brett, 2009)

Relative, beat-based timing



Grahn and Brett, 2007



Grahn and Rowe, 2009

Basal ganglia, pre-SMA/SMA, and pre-motor cortex

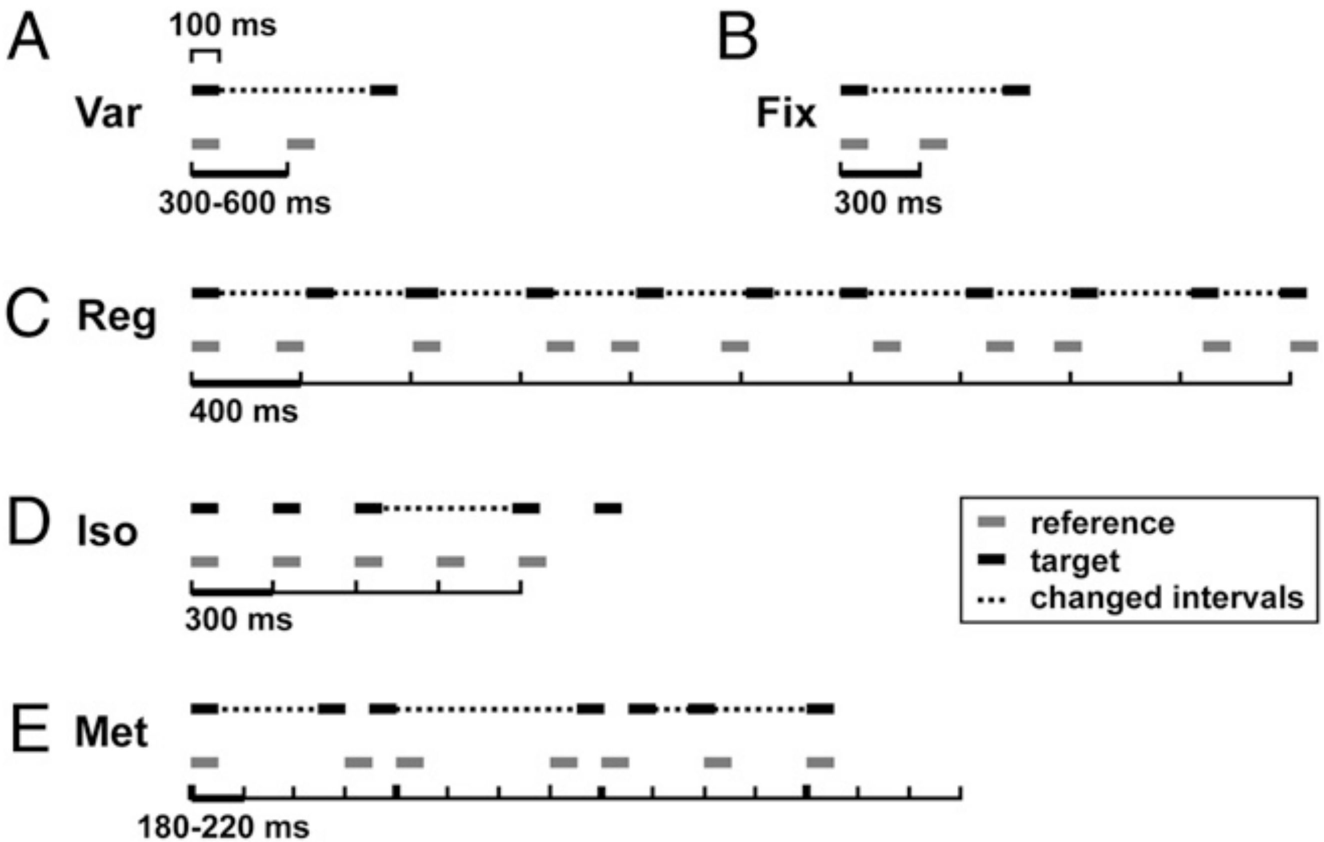
implicated in perception of beat-based and metrical rhythmic sequences.

Absolute, duration-based timing

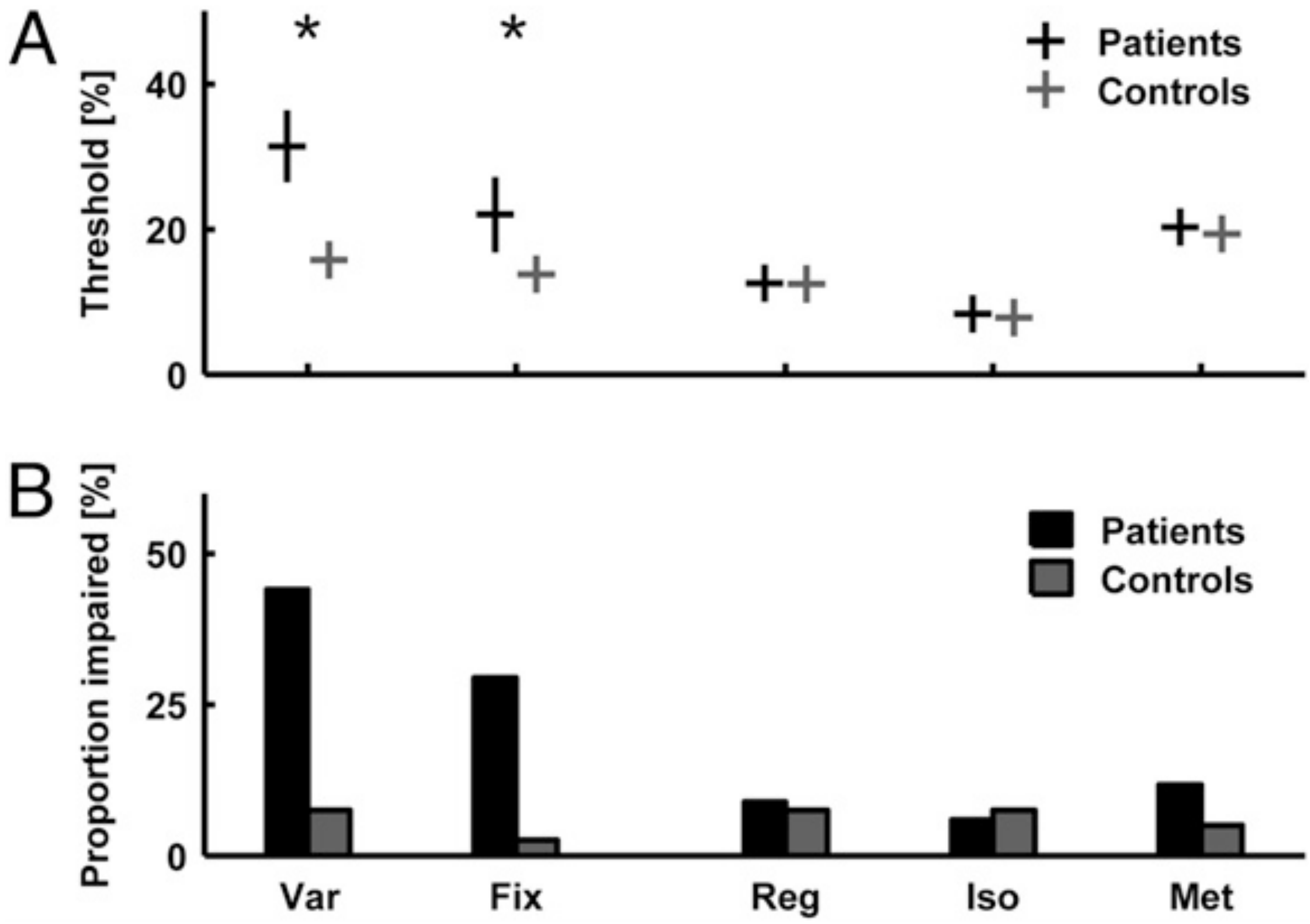
Cerebellum: Encoding of absolute duration of discrete time intervals.
(Ivry, 1993; Grube et al., 2010a,b)

Absolute, duration-based timing

Patients with Spino Cerebellar Ataxia type 6:



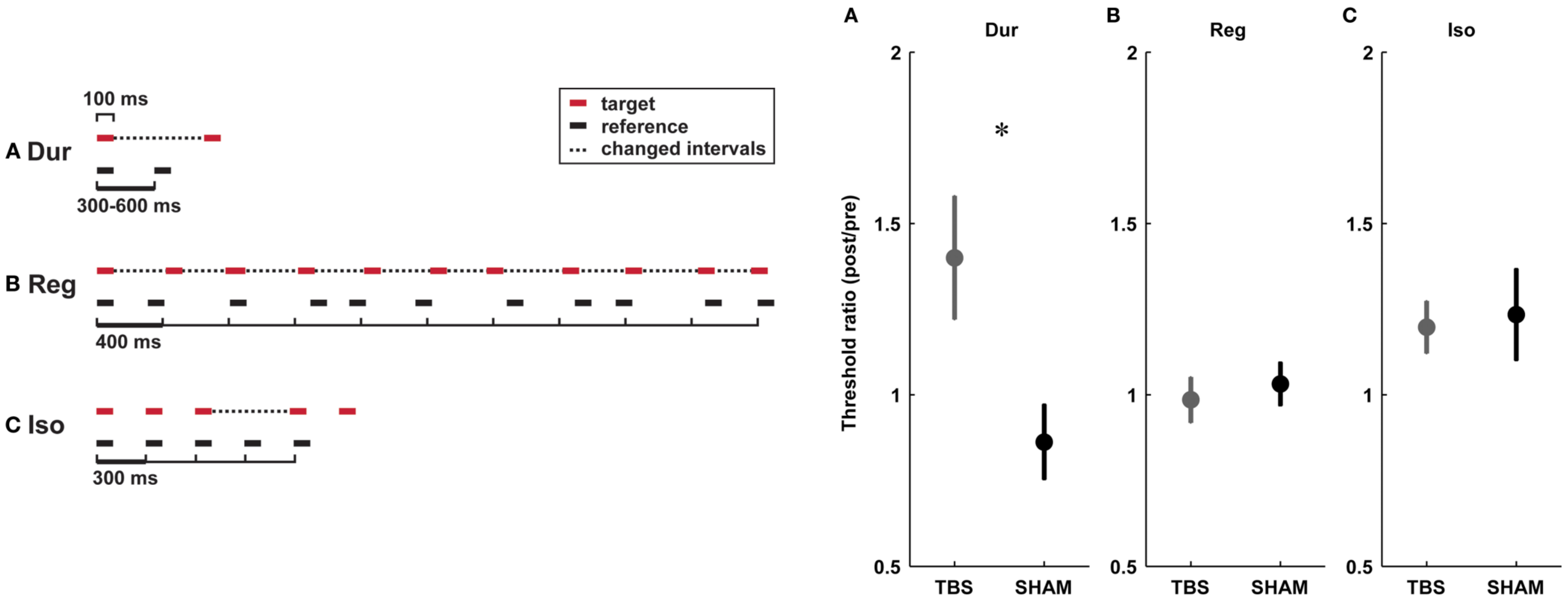
Absolute, duration-based timing



Patients are impaired specifically in absolute timing of single intervals but not in relative timing of rhythmic sequences with a regular beat. *(Grube et al., 2010: PNAS)*

Absolute, duration-based timing

Normal subjects with TMS over medial cerebellum:
impaired on only absolute timing task after TBS *(Grube et al., 2010: Frontiers)*



Cerebellum implicated in absolute, duration-based

perception of sequences without a regular beat.

Aim of the study:

Test for dissociation between the timing functions of cerebellum and basal ganglia according to the rhythmic context of time intervals.

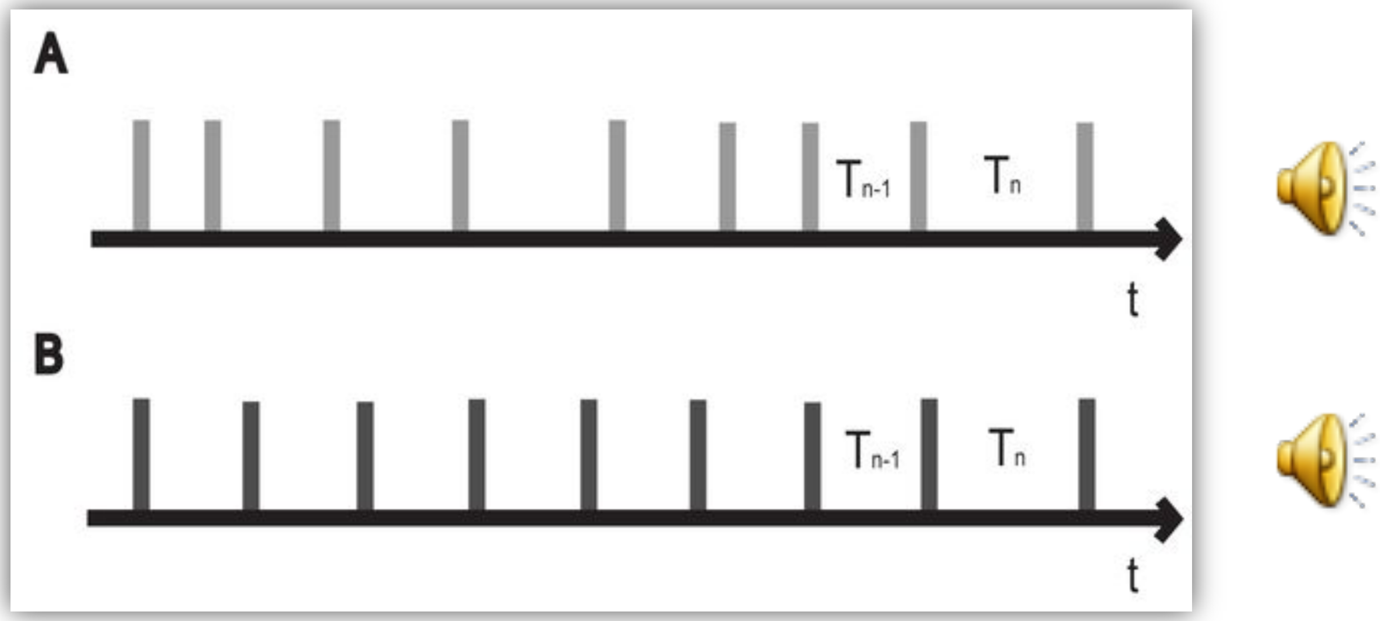
Hypotheses:

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

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

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

Stimulus and Task



- ***Judge the duration of the final compared to the penultimate interval***
  T_n > / < T_{n-1}

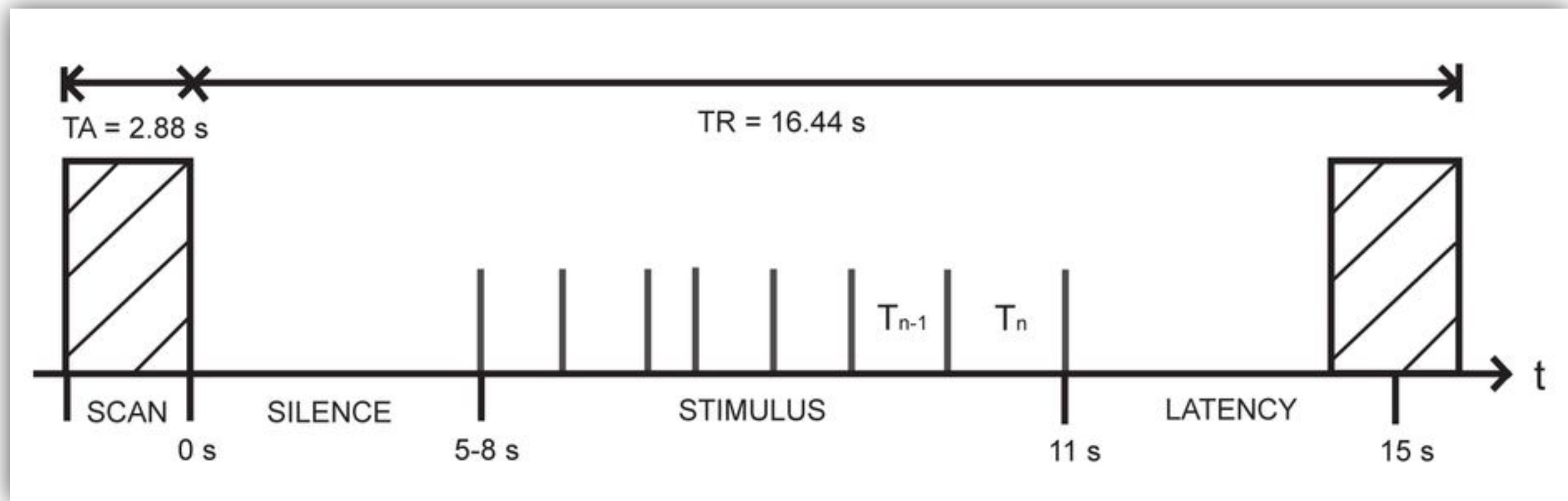
Sequence A: Irregular with 15% average jitter

Sequence B: Regular with an isochronous beat

Stimulus Design

- Click duration: 0.5 ms
- Inter-onset interval (ioi): 440 - 560 ms (roved in steps of 30 ms)
- Total no. of intervals: 7 – 10
- Max. Response time: 3 s
- 40 conditions/sequence: 5 ioi x 4 no. of intervals x 2 (shorter or longer)
- Time difference between final and penultimate interval ($T_n - T_{n-1}$):
  - 30% of ioi for irregular sequences
  - 15% of ioi for regular sequences

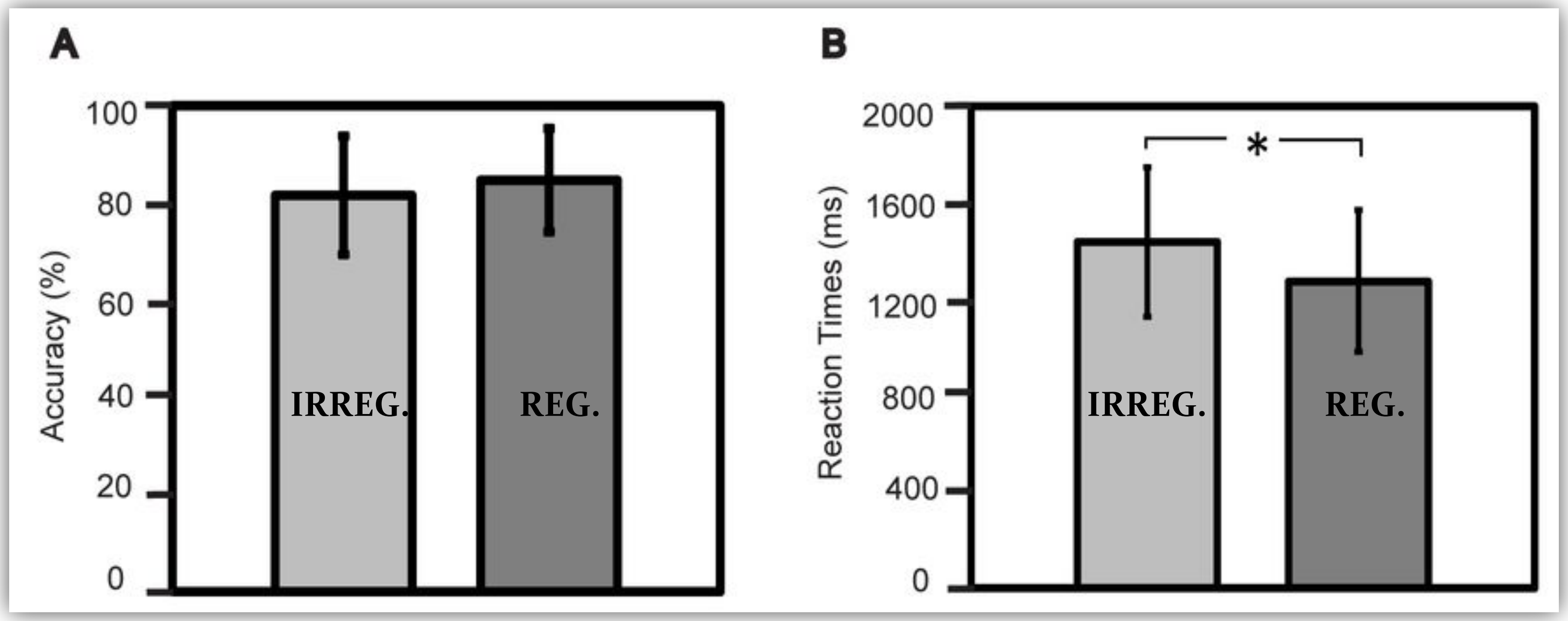
Sparse imaging paradigm



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
- 18 subjects (normal hearing, no current musical training)

Behaviour in scanner



81.53% ± 12.28%	84.72% ±10.64%	1438 ± 297 ms	1275 ± 312 ms

➢ **Relative timing more accurate and faster than absolute timing**

fMRI analysis

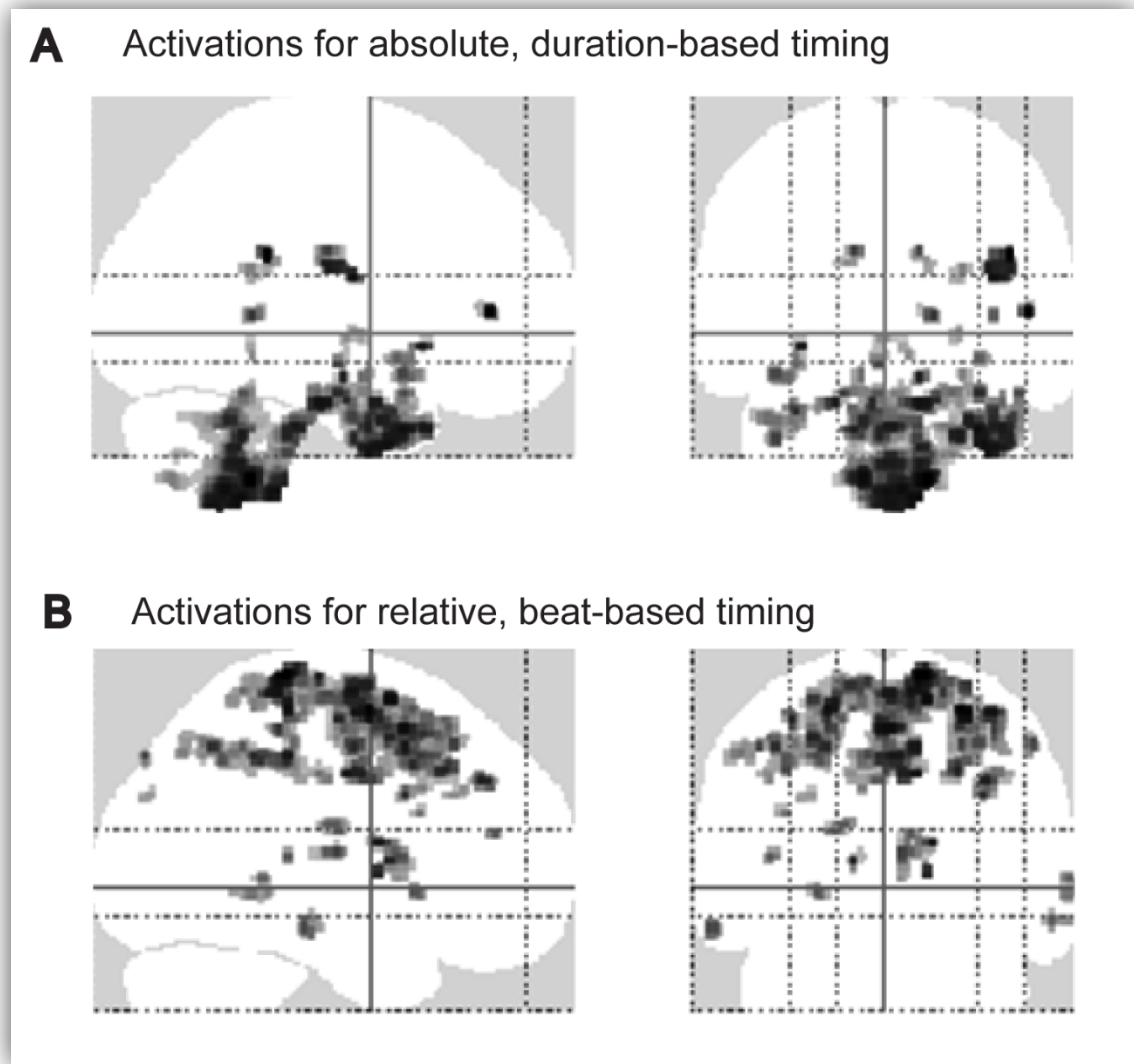
- *A priori* hypotheses for cerebellum for duration-based and basal ganglia for beat-based timing
- Whole brain analysis based on General Linear Model (SPM8)
- Random effects design

- Key contrasts:

  (a) Regular > Irregular (measure of relative timing)

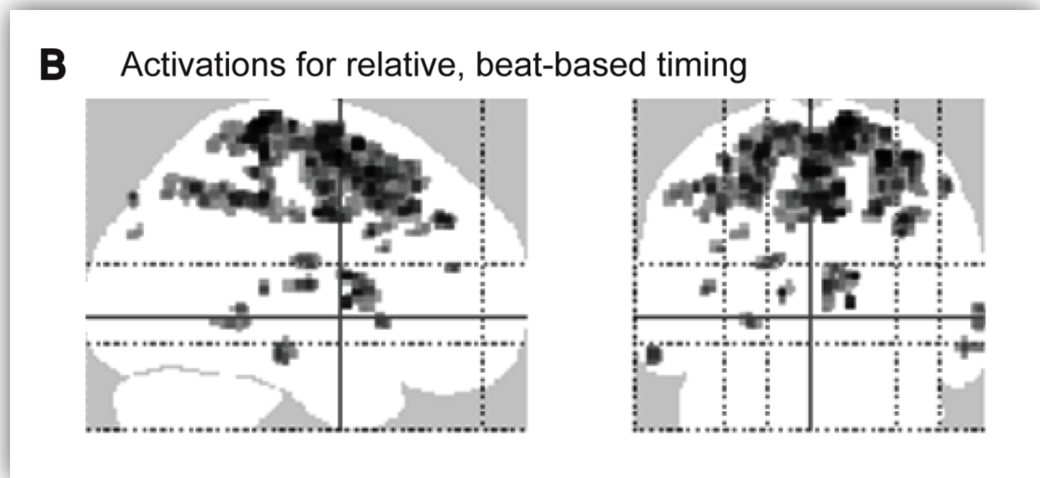
  (b) Irregular > Regular (measure of absolute timing)

fMRI Results



MNI space; t-value > 4.00 and extent threshold > 10 voxels

I. Relative Timing



STRIATO- **THALAMO-** **CORTICAL NETWORK**

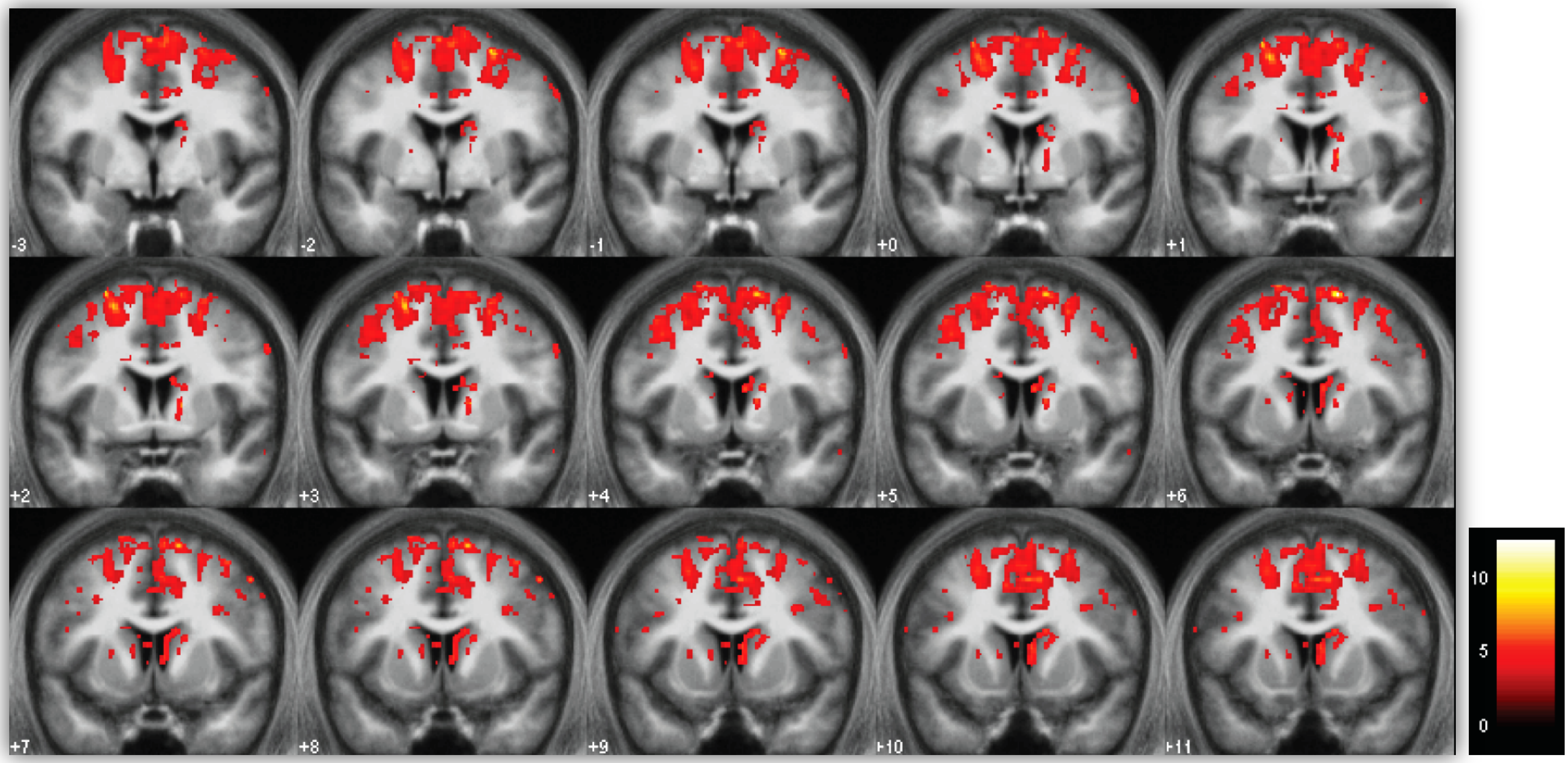
Caudate Nucleus
Putamen
Internal Capsule

Thalamus

Pre-SMA/SMA
Pre-motor cortex
Dorsolateral prefrontal

Also: Superior Temporal Gyrus

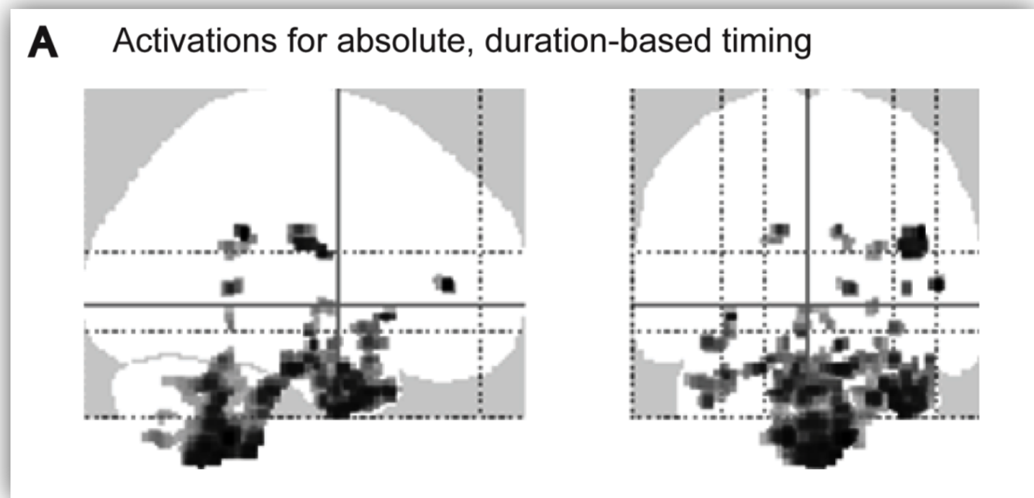
Striatal, premotor and prefrontal activations



x = -3 mm to + 11 mm

$p < 0.001$ (unc.)

II. Absolute Timing



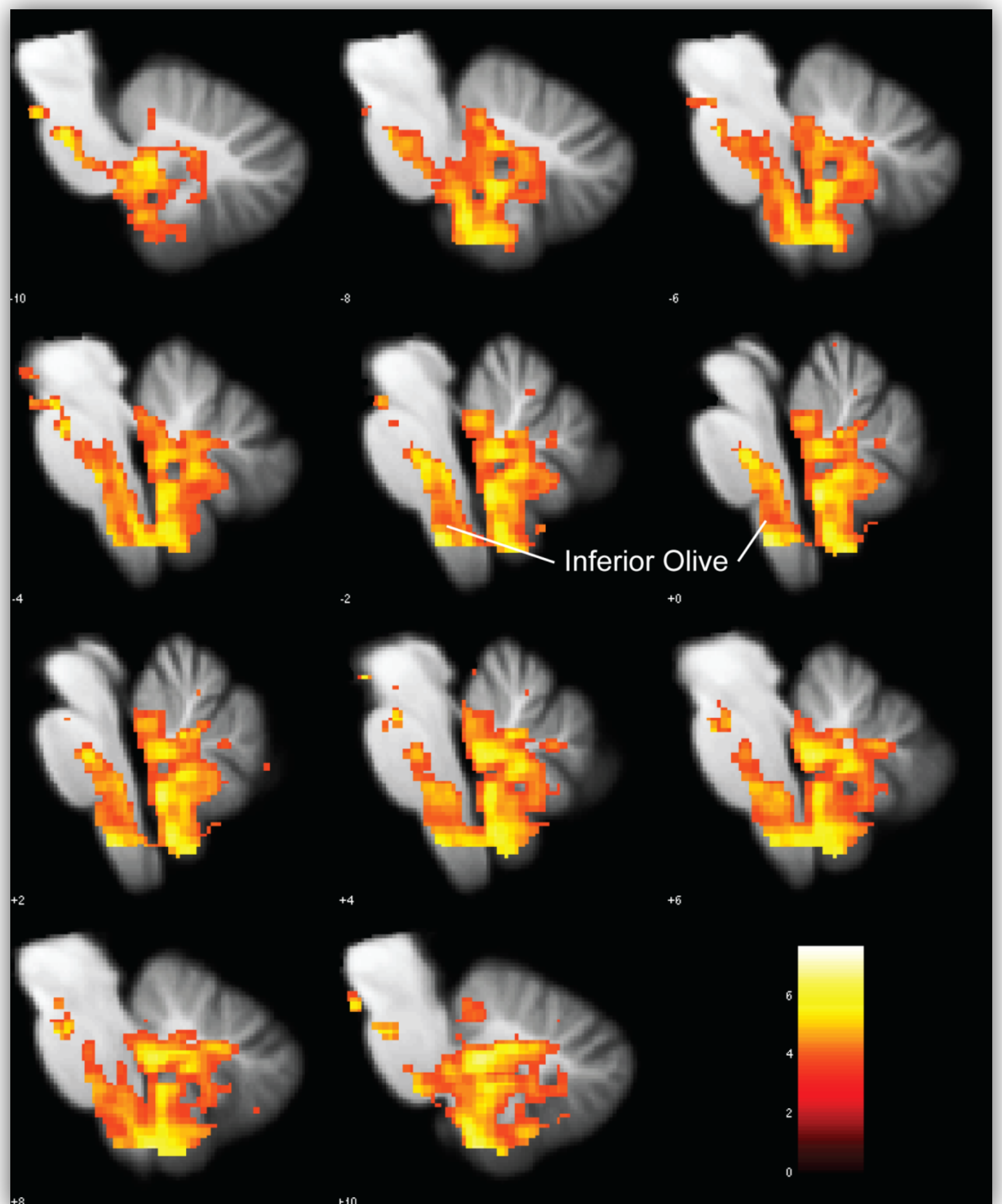
OLIVO- CEREBELLAR NETWORK

Inferior Olive

Vermis
Cerebellum
Dentate Nucleus
Cerebellar Lobules IX and X

Also: Superior Temporal Gyrus, Cochlear nucleus

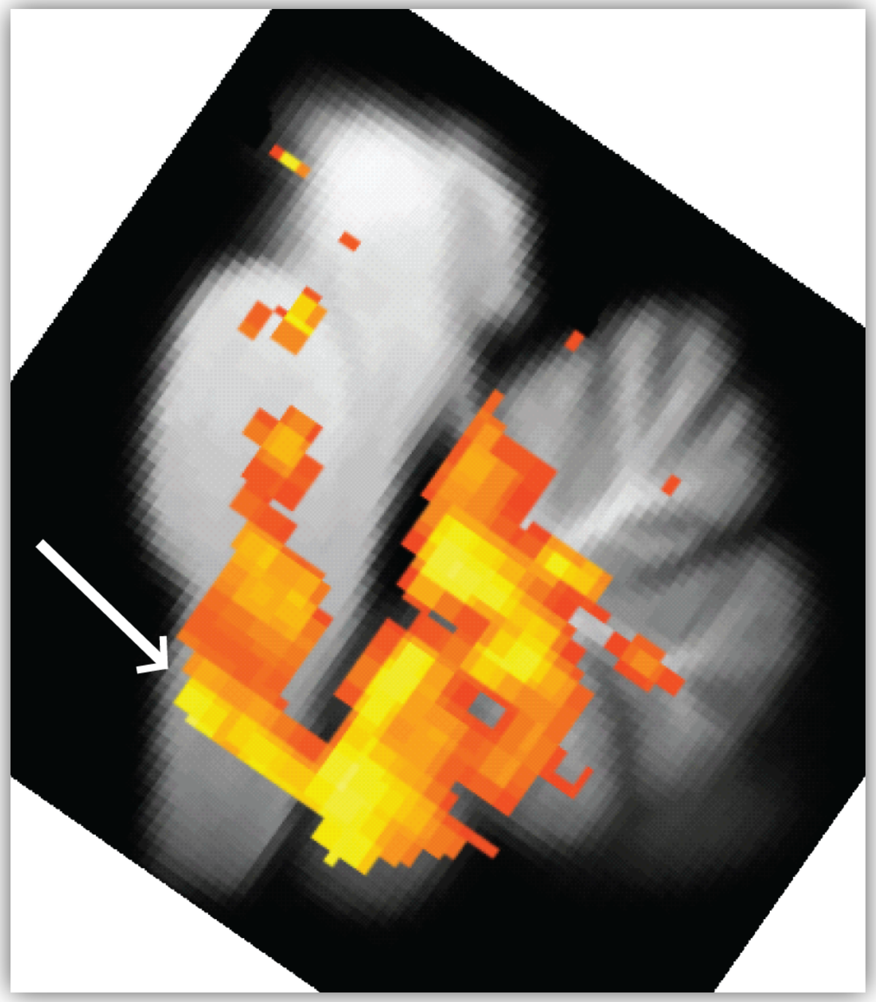
Olivocerebellar activations



x = -10 to +10 mm

$p < 0.001$ (unc.)

Inferior Olive

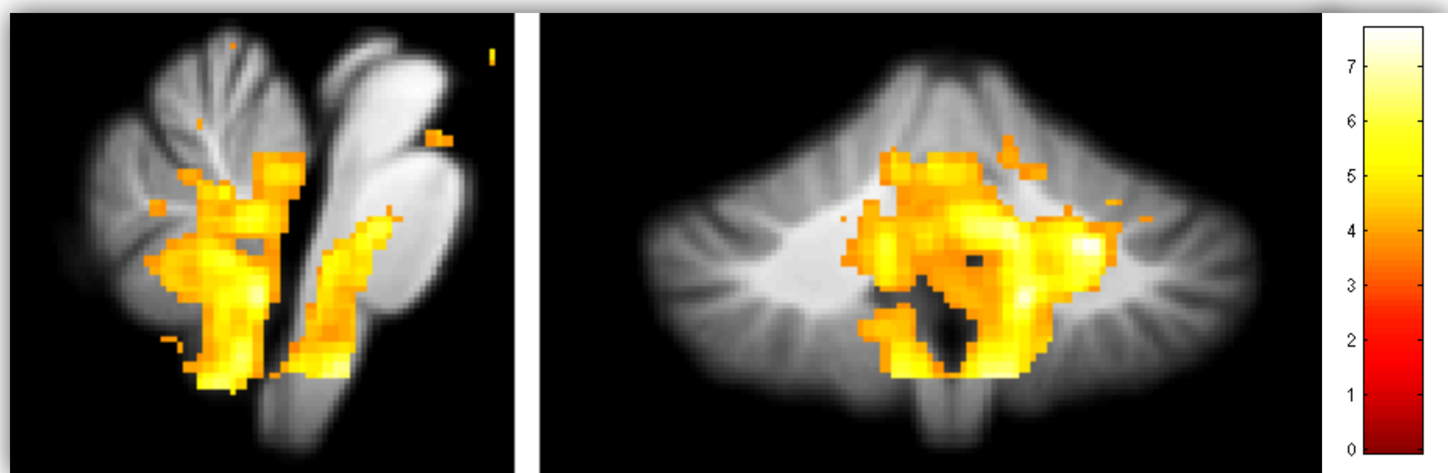


activations in inferior olive

anatomical section of inferior olive

Xu et al. (2006)

Cerebellum



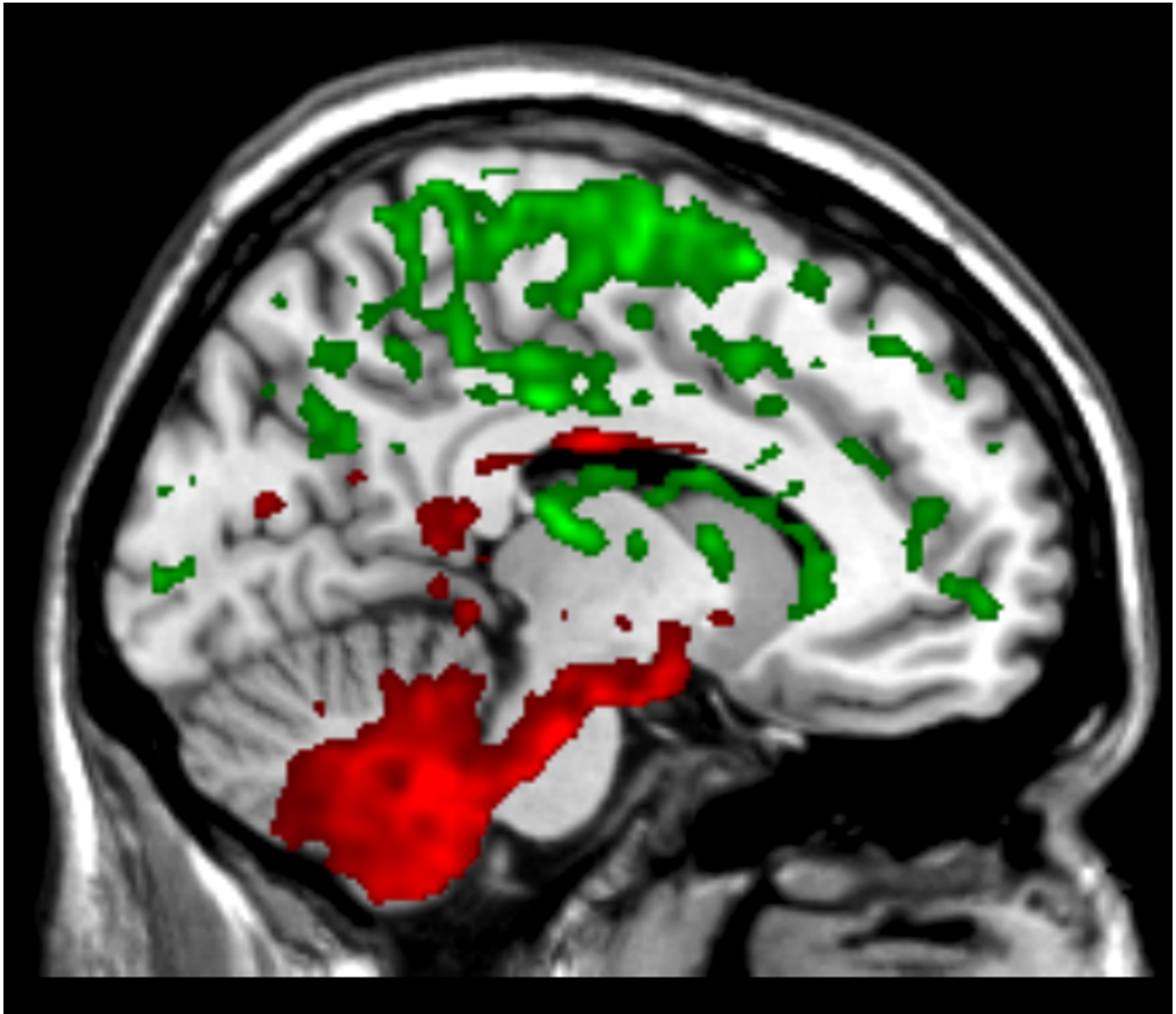
x = 0

Dentate nucleus

x = 9

$p < 0.001$ (unc.)

Functional dissociation



Inferior Olive and Timing

- sole source of climbing fibre input to the Purkinje cells
- display subthreshold oscillations at ~5-15 Hz
- oscillations are synchronized via gap-junction coupling
- electrical coupling controlled by deep cerebellar nuclei
- organized into dynamic, functional subgroups
- capable of acting as a synchronized timing device *(Llinas, Yarom, de Zeeuw et al.)*

- Implicated in visual and tactile timing using fMRI *(Bushara)*

Inferior Olive: A supra-modal timing system?

- receives visual input

- auditory input from cochlear nucleus

- input from the caudate nucleus and cortex

Conclusions

- We directly compared the timing functions of cerebellum and basal ganglia in the same experiment using fMRI.

- Results consistent with previous work:

  Absolute, duration-based timing in the Cerebellum *(Grube et al.)*

  Relative, beat-based timing in the Basal ganglia *(Grahn et al.)*

- First study to implicate inferior olive in auditory timing using fMRI

- Distinct timing mechanisms and underlying subsystems:

➢ **Olivocerebellar network:** **absolute, duration-based timing**

➢ **Striato-thalamo-cortical network:** **relative, beat-based timing**

Teki et al., J Neuroscience (2011)

Acknowledgments

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