

# Chronotopic maps in temporal processing and perception

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## ABSTRACT

Neurons maximally tuned to specific durations in the hundreds of milliseconds to seconds are widely observed in studies using monkeys. These tuned neurons are observed in areas that are previously known to be involved in timing research—pre-supplementary motor area and basal ganglia. However, the role the duration tuned neurons and brain areas play in temporal processing remains unclear. Recent studies have added to the understanding of duration tuning in temporal processing by showing the existence of chronomaps. Duration tuned clusters at the voxel level, in human supplementary area have been shown to be topographically organized as duration maps, chronomaps. Chronomaps could thus provide the neuronal mechanism associated with duration tuning in timing areas involved in time processing and perception.

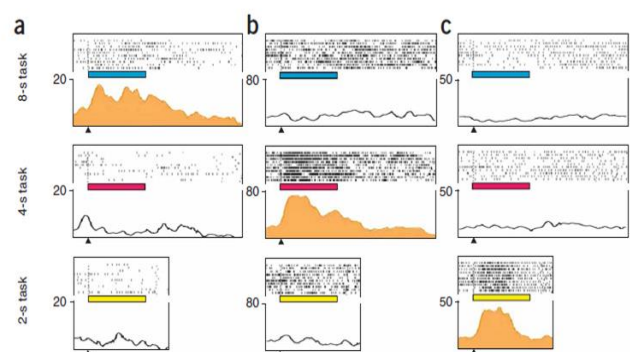
## KEYWORDS

Time perception, temporal processing, duration tuning, fmri, chronomaps, supplementary motor area.

## 1 Duration Tuning

Interval timing refers to durations in the hundreds of milliseconds to minutes range crucial for human behaviour, in decision making, speech processing, motor activity and music perception [1]. Studies using functional magnetic resonance imaging (fMRI) have found brain activity in certain key brain regions to be correlated with interval timing behaviour. These areas

include supplementary motor area (SMA), intra parietal sulcus, basal ganglia and cerebellum [1,2,4,5]. Electrophysiological studies on monkeys have found neurons from these timing brain areas to exhibit duration tuning [6,7]. When neurons are tuned, they preferentially fire for specific task durations. Mita *et al.* [6] found neurons in the monkey pre-SMA (human SMA) to fire preferentially for task durations. (Fig. 1). Two Japanese monkeys were trained to perform an interval-generation task that required them to determine a hold time of three different intervals before initiating a key-release movement. LED lights indicated the respective waiting times before key release: yellow light indicated 2 s, whereas a red or blue light indicated that the monkey had to wait at least 4 or 8 s.



Adapted from Mita *et al.*, 2009

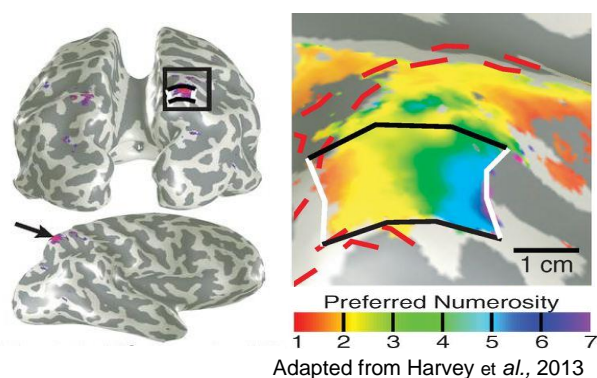
**Figure 1** Raster displays and spike-density functions illustrating selective neuronal activation during the 8-s task (a), 4-s task (b) and 2-s task (c). Mita *et al.* [6]

While the duration tuning in timing brain areas associated with interval timing are well observed the neuronal mechanisms tying the timing brain areas to the behaviour of interval timing remain unknown [1,2,3].

## 2 Representation of abstract stimulus features through maps

Representation of stimulus features through topographically organised sensory maps is well known. The tonotopic maps in the auditory cortex or the retinotopic maps of the occipital cortices. Could a similar topographical organisation of abstract features exist? Further, could such a topographical organisation be studied non-invasively in humans?

Harvey *et al.* [11] using ultra high-field fMRI (at 7 teslas) showed the existence of topographically organized numerosity maps in the human parietal cortex (Fig. 2). Numerosity refers to the size of a group of objects. Participants in the study were presented with visual stimuli of varying numerosity. The results showed that parts of the cortical surface corresponded to specific numerosity, in a topographical manner increasing from the medial to lateral ends. The results provided evidence that higher-order abstract features and their topographical organizational principles could be studied non-invasively.

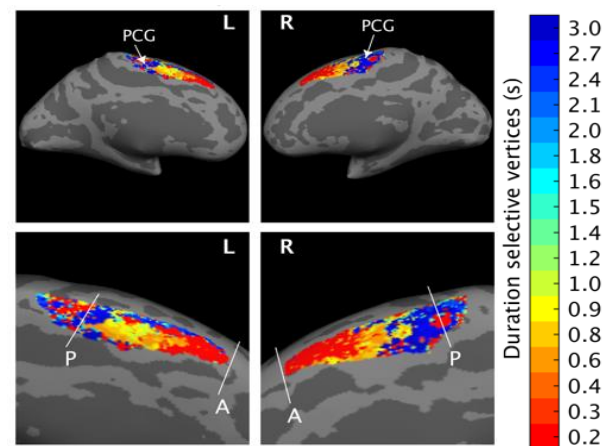


**Figure 2** High-field fMRI data was acquired while subjects were shown visual stimuli of varying numerosity. Numerosity maps showing preferred numerosity increasing from the medial to lateral ends

(white lines) of the region of interest (ROI) (black and white lines). Harvey *et al.* [11]

## 3 Representation of durations through chronotopic maps

Like the topographical organisation of numerosity, could task durations have a similar map like organisation. Protopapa *et al.* [8] provide the first evidence for a topographical representation of durations in the human supplementary area.



Adapted from Protopapa *et al.*, 2019

**Figure 3** Chronotopic maps showing the topographic organization of duration-sensitive vertices in bilateral SMA with the progression in the rostro-caudal direction, with vertices sensitive to the shorter duration (vertices in warmer colors) located in the anterior and those sensitive to the longer duration (vertices in colder colours) in the posterior SMA.

A, anterior; L, left; P, posterior; PCG, precentral gyrus; R, right; SMA, Supplementary Motor Area. Protopapa *et al.* [8]

Protopapa *et al.* [8] used data from ultra-high field fMRI (at 7 Teslas) and showed the results to be independent of task design and analysis approaches. In Experiment 1 of the study, volunteers participated in a temporal discrimination task. The resulting data were analysed using a general linear model (GLM) approach. While in Experiment 2 of the study, participants performed temporal and spatial discrimination tasks. The data were analysed with neural population receptive field approach [9]. Chronotopic maps,

topographic organisation of durations in the range of 0.2 to 3s, was observed in the SMA both the left and right hemispheres (Fig. 3). The progression of the maps was seen in a fixed, rostro–caudal direction, with vertices sensitive to the shorter duration located in the anterior and those sensitive to the longer duration in the posterior SMA. Chronomaps were also found to exist in a task independent manner, topographic organisation of durations were observed even in a control condition when subjects were instructed to focus only on the spatial aspect of the stimuli and ignore their temporal properties.

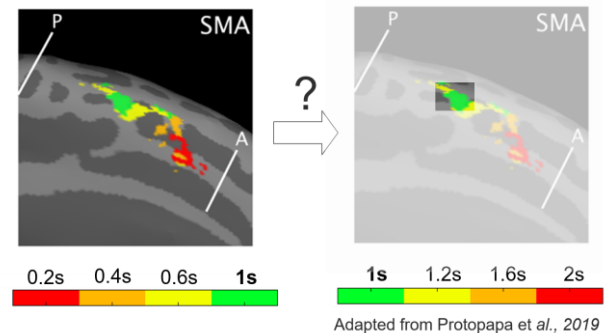
Protopapa et al. [8] connected the previously reported neuronal duration tuning in monkeys' medial premotor cortex [6,7] to a representational format in humans. Although, previous duration tuning seen in monkeys were exclusively associated with motor-timing behaviour, Protopapa et al. [8] showed the presence in human premotor cortex of a duration tuning mechanisms in a purely temporal perceptual task.

Harvey et al. [10] have now gone further by describing the existence of topographic maps of stimulus duration in ten different cortical locations, from occipital to parietal to frontal lobe.

#### 4 Properties of chronotopic maps

While Protopapa et al. [8] was successfully able to show the existence of chronotopic maps, the results further raised some interesting questions. Are the chronotopic maps organised in an absolute or relative manner (Fig. 4)? The maps in Fig.3 are from tasks in visual domain, would the maps change if the durations were presented in the auditory domain? Are chronomaps experience based or present from birth? Harvey et al. [10] showed the topographic organisation in multiple areas, how do these

representations vary and contribute to the encoding and perception of durations?



**Figure 4** Are chronotopic maps encoding duration in an absolute or relative manner? The left panel shows the chronotopic map from Experiment 1 of Protopapa et al. [8]. How are the clusters encoded for 1s duration (in green)? If the range of durations that 1s is presented in changes (right panel), does the spatial position of the green clusters remain the same or change in the new chronotopic map? If the green clusters retain their spatial position, then the durations are organised in an absolute manner. If they change their spatial position based on the duration range the durations are encoded in a relative manner.

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