



From the Dynamic Structure of the Brain to the Emergence of Time Experiences

Virginie van Wassenhove

CEA.DSV.I²BM.NeuroSpin—INSERM Cognitive Neuroimaging Unit U992

Bât 145—Point Courrier 15, Gif sur Yvette F-91191 FRANCE

Virginie.van-Wassenhove@cea.fr

Virginie.van.Wassenhove@gmail.com

Abstract

Time perception remains an open question in cognitive neurosciences. Mechanisms for the encoding of time come in different flavors but the evidence remain sparse for the simplest questions, for instance, which areas in the brain constitute the most reliable sources for the encoding of time? Indeed, not one brain lesion in the cortex can account on its own for a total impairment in timing functions. The aim of this contribution is to highlight key concepts in the history of cognitive neurosciences that are relevant to the study of time perception. An alternative or a complementary approach to the classic clock model view is provided regarding ways in which the brain could automatically encode temporal properties.

Keywords

cognitive neurosciences, neural dynamics, amodal representation, discretization, phase encoding

1. Drawing Some Parallels between Spatial and Time Perceptions

The cognitive neurosciences of time perception are classically confronted with the lack of sensory specificity for time perception: perceptual systems (e.g. audition, vision) are defined by sensory receptors (cochlea, retina, respectively) and neuroanatomical pathways functionally specialized in the processing of specific physical attributes (mechanoreceptors dedicated to the transduction of moving particles, electrochemical chain reactions dedicated to the transduction of photons, respectively). This clear functional segregation of sensory pathways is in line with the distinct physical attributes to be analyzed and the psychological reality whereby one hears and sees the world. It also provides a guideline as to which neural system should be considered in light of the

sensory domain under scrutiny (with some notable exceptions as to the psychological reality of experiencing senses separately as will be seen below).

Although we speak of “time perception” and “space perception”, the terminology can be misleading in two ways. The first trivial issue is merely definitional in that space and time perceptions are not unitary phenomena; rather, each can be decomposed into functionally independent percepts (e.g. duration of events, ordering of events, simultaneity judgments for time; event localization, spatial scene analysis, dimensions of events for space). The second issue, less trivial, is that the subjective experiences of time and space are derived through information that can be extracted through all sensory modalities and as such, there is no “perceptual” system dedicated to space or time perception in the ways we talk about the auditory or visual perceptual systems. Temporal and spatial properties are constructed on the basis of information provided by various sensory modalities and as such, they are likely *amodal* perceptual constructs.

To provide a specific instance, the classic ventriloquism effect (Stratton 1897; Thomas 1941; Howard and Templeton 1966) in which the localization of a sound is displaced towards that of a simultaneous visual event can be explained on the basis of which sensory modality provides the most reliable information. Recent Bayesian modeling approaches can account for a stable spatial representation resulting from an optimal combination of auditory, tactile and/or visual information (Alais and Burr 2004; Ernst and Bühlhoff 2004; Ma and Pouget 2008). It is commonly assumed that vision is most reliable in providing spatial information whereas audition is more reliable in providing temporal information. In fact, the ventriloquism effect can be extended to the temporal dimension and indeed, auditory information biases the temporal perception of visual information (Bertelson and Aschersleben 2003).

Sensory-specific mechanisms have been described that provide workable models on how spatial information can be extracted at early stages of sensory processing (even before entering the cortex). One particularly simple and elegant neurophysiological theory for auditory space localization was proposed by Jeffress (1948) and verified in several mammalian and avian species in sub-cortical structures (e.g. Konishi 1986; see also Lestienne and Buser for description (2001, 43)). Briefly, the neural circuitry for computing auditory space actually relies on temporal information: it is composed of coincidence detectors and delay lines that allow computing the Interaural Time Differences (ITD) between the ears. As illustrated in Figure 1, a continuous sound source is located slightly on the right of the individual; the sound arrives slightly ahead (a few microseconds) at the right ear compared to the left ear, leading to a

slight phase delay of the auditory neural response in the left and right side of the early auditory system. In the Medial Superior Olive (MSO), the neurons receiving coincident information from both sides of the auditory nucleus will fire more than the others. In our example; the more right-tuned neurons (outlined grey) receive coincident information thereby encode the auditory temporal information into a place code and ultimately into an auditory spatial representation. If such highly specific models of spatial information encoding in neural systems are actively investigated in different species and for different sensory systems (e.g. Ashida and Carr 2011), the extraction of temporal information in each sensory system is poorly understood and mostly speculative. As illustrated, the problem can be complex as objective temporal information can serve the subjective representation of space in the brain.

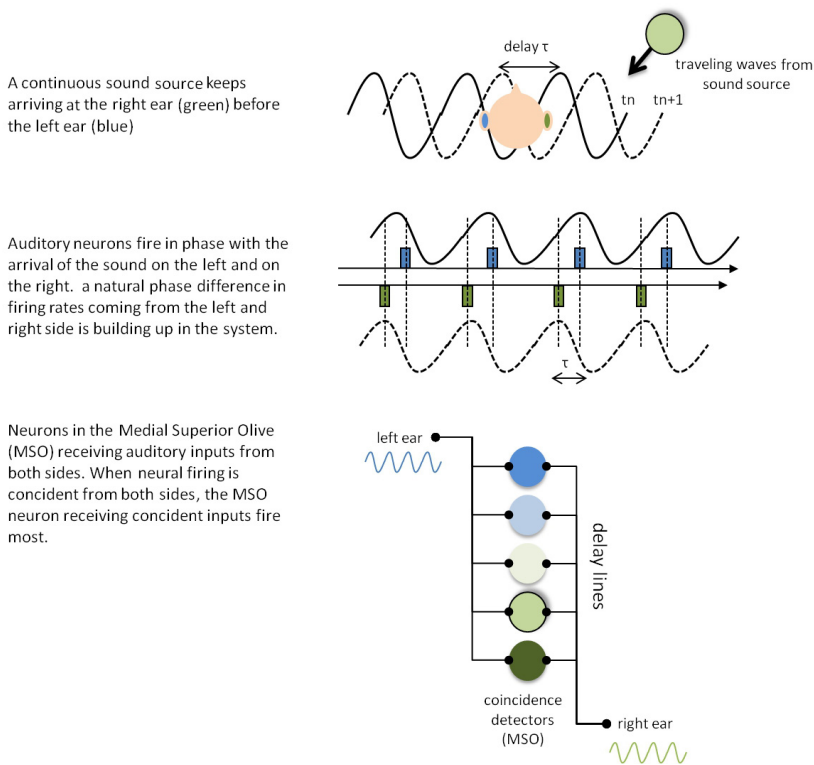


Figure 1. Schematic illustration of Jeffress' Place Theory of Auditory Spatial Localization (1948). Coincidence detectors of phase-delays between the left and right auditory inputs encode the spatial position of an auditory source, transforming temporal information on the microseconds scale into a place code.

Additionally, the extraction of features that ultimately contribute to the elaboration of the “where” and the “what” of sensory events follows distinct paths of information processing in the cortex. These cortical streams of information processing have been posited as the “dual-streams” hypothesis in vision (Ungerleider and Haxby 1994): information pertaining to the identity of objects (the “what”) follows a ventral cortical stream whereas information pertaining to the location of objects (the “where”) follows a dorsal stream. Figure 2 illustrates that this dichotomy has been put forward in the auditory system as well (Rauschecker and Tian 2000). More recently, it has been suggested that ordinal information pertaining to visual timing followed a third stream illustrated in Figure 2 as the “when pathway” (Batelli *et al.* 2008). This view of information processing in the brain is of course at the core of a classic and tricky “binding problem” (Treisman 1996) in cognitive neurosciences: if information about identity, space, and time of an object is segregated for processing, how does it bind together to form the unitary perceptual construct that we experience?

Distinct issues need to be kept in mind when drawing a parallel between space and time encoding in the brain. For instance, spatial representation is carried on with respect to particular reference frames (eye-centered,

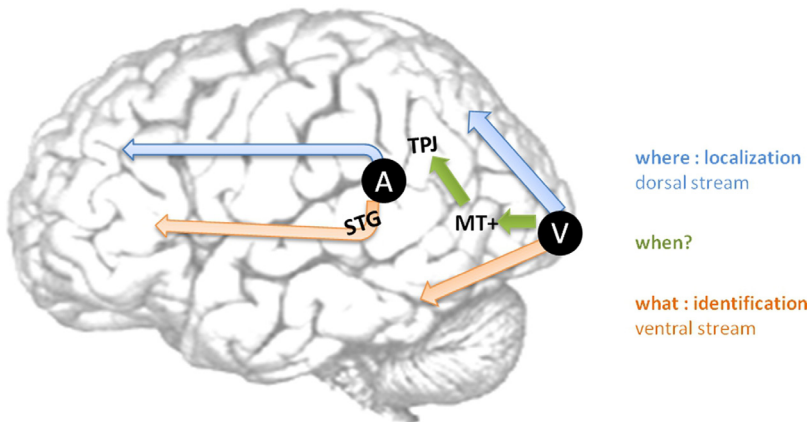


Figure 2. Processing streams in cortex. In white and gray, the dual-stream (or “what”/ “where” pathways) proposed by Ungerleider and Haxby (1994) and the analogous dichotomy described in the auditory system (Rauschecker and Tian 2000). In black, the recently suggested “when” pathway (Batelli *et al.* 2008). A: auditory cortex; V: visual cortex; MT: middle temporal (also known as V5); STG: superior temporal gyrus; TPJ: temporo-parietal junction.

object-centered) in various neural populations throughout the cortex. Recent evidence suggests that these reference frames can sometimes be mixed in parietal regions (Mullette-Gillman *et al.* 2005) arguing for the importance of multisensory or amodal representational formats for higher-level cognition. One question then is what would the reference frame for time be? Ultimately, it is likely to be the “self” when developing an understanding of time awareness at the level of time flow. But before reaching this stage, are reference frames diverse within each sensory modality? Are temporal properties eventually merging to form a unitary sense of time passing by? Are temporal properties object-centered? How does the arrow of time emerge in our conscious time representation?

In physics just as in psychology, temporal properties cannot easily be abstracted out or dissociated from physical events (personal communication with Etienne Klein). In other words, time cannot be dissociated from the information provided by our senses (incl. interoceptive, Craig (2002)). From a cognitive point of view, time is a property or feature that any object in the world associates with and as such, time perception research could encounter similar difficulties in its empirical approaches as those found with the qualia issue (Eagleman and Pariyadath 2009). Encoded temporal information eventually needs a centralized means to collect and synchronize information across senses but prior to reaching this stage the first problem needing to be addressed is whether multiplex encoding is a viable and testable approach. Here, I speculate that neural systems may have developed a means to encode temporal information not via specialized and centralized systems but by developing a parallel coding scheme as those used for other features or “multiplex encoding”.

2. From Phenomenology to Clock Model

In the last century, psychological time has been defined in reference to a quantity of elapsed time or duration which mechanistically presupposes the existence of a time counter in the brain (note here that time perception is constrained to its metric rather than its ordinal properties). Historical parallelism can be drawn between the notion of ‘time quantum’ in physiology (von Baer 1876) contemporary to the ‘specious present’ in psychology (Clay 1882; James 1890) and the ‘cinematographic hypothesis’ in philosophy (Bergson 1888): subjective time is seen as a compound of discrete durational units which replaced the classical notion of a continuous flow. This new concept elicited the quest for an internal unit of time perception.

The first approach was to consider the maximum length of a time moment (as specious present) but in light of considerable variations from seconds to minutes in the estimation of the maximal length (e.g. Wundt 1874), the question was reframed in finding the time unit or the *minimal perceivable duration*. This required the development of new psychophysical tools and concepts. First, subjective simultaneity that encompasses two distinct mechanisms (Piéron 1952): two events can be simultaneous or successive in time and, if they are successive, the ordering of events ought to be perceivable. As Fraisse (1957) wondered, “Peut-on percevoir l’ordre là où l’on ne pourrait même pas distinguer la succession ?” (“Can one discriminate order when not even succession is perceivable?”). The distinction between ‘simultaneity’ and ‘order’ has led to several types of psychophysical thresholds: the ‘fusion threshold’ as the amount of time whereby the observer can perceive several events and not just one (e.g. the critical fusion flicker (CFF) threshold in vision); the ‘temporal order threshold’ (TOT) as the amount of time required for two events to be correctly ordered in time (nearly equivalent across all sensory systems: interestingly, the CFF is also the TOT in vision); the ‘simultaneity threshold’ as the time separation required for two events to be correctly perceived as successive or simultaneous in time (see Vroomen and Keetels 2010 for a critical assessment of TOT and simultaneity threshold in multisensory contexts).

For estimating the duration of an event, a clock model soon formally emerged with Treisman’s proposal (Treisman 1963; Figure 3a) in which time is quantified as the amount of internal (brain time) units cumulated through a certain physical duration. This model has been refined over the years with empirical data leading to the updated fairly consensual view in Figure 3b. An internal pacemaker defines the rate at which temporal information evolves and its rate can be modulated by arousal. A gate between the pacemaker and the counter (Fig. 3a) or accumulator (Fig. 3b) regulates the counting: when the gate is closed, no accumulation of time units can flow to the accumulator; when it is open, units are gathered in the accumulator. Attention can modulate the timing at which the gate turns on or off. At the end of the interval to be estimated, the units in the accumulator are compared with an internal duration reference held in memory. Numerous variants of the clock model exist implicating one or several sensory modalities.

With the field of cognitive neurosciences developing, the brain started to be considered as a computational system that operates on discrete units of information (irrespective of the content of the information, i.e. discretization for time, speech, etc.). Three useful levels of description were proposed by Marr (1982): the computational level, comprising the set of operations needed to

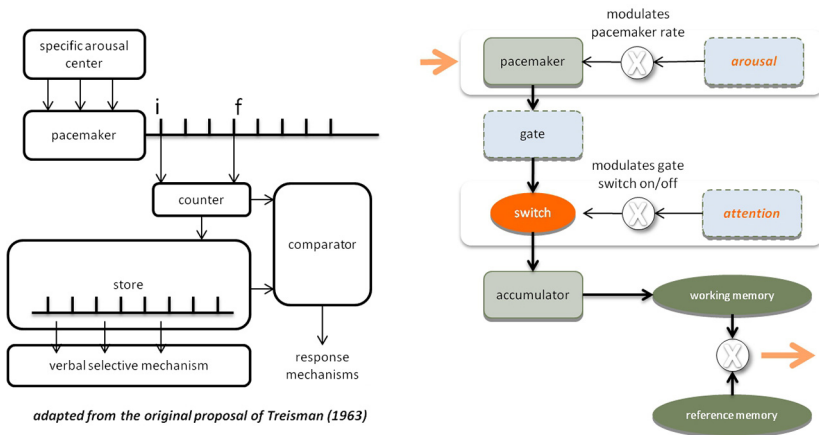


Figure 3. Clock model hypothesis. Three major components constitute the clock: a pacemaker, an accumulator or counter and a comparator.

perform a particular transformation; the algorithmic level, comprising the set of rules and the representations on which computations ought to operate; the implementation level, comprising the constraints brought about by the system that realizes the operations (here, the brain). In this context, the clock model (Figure 3) provides a computational sketch as to the requirements needed to establish the duration of an event with the assumption that an internal reference exists held in memory. An implementation for this model is the cortico-striatal beat frequency model (for review, see Buhusi and Meck 2005) depicted in Figure 4. Briefly, a set of oscillatory inputs from cortical neurons in the prefrontal cortex are integrated by striatal spiny neurons which compare their readout with duration stored in memory. Evidence for this model has cumulated notably for interval timing in the order of a few seconds in rats; in humans, supporting evidence come from non-invasive recordings in particular as indexed by the Contingent Negativity Variation (CNV) with electro- and magneto-encephalography recordings (EEG and MEG, respectively) showing a slow accumulation-like response during time estimation (whether perceptual or motor; Macar and Vidal 2004). The implicated cortical regions are the pre- and supra-marginal gyrus (pre/SMA), also appearing in Figure 4. Additional support is found with the consistent implication of the supplementary motor area (SMA) and the inferior frontal gyrus (IFG) in a recent meta-analysis of the functional Magnetic Resonance Imaging (fMRI) literature on temporal processing (Wiener *et al.* 2011).

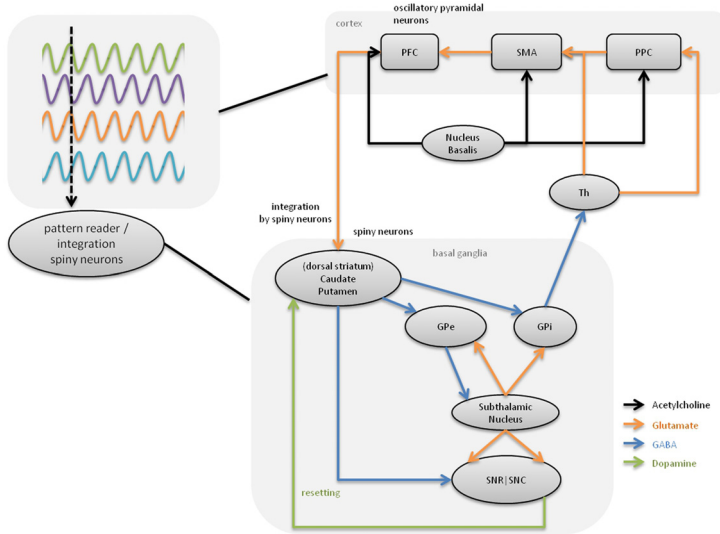


Figure 4. Implementation of the clock model hypothesis as “cortico-striatal beat frequency model” (adapted from Buhusi & Meck 2005). This model implies a centralized clock of reference and has received a substantial amount of evidence for interval timing (above the second range). BG: basal ganglia; GPe: globus pallidus external segment; GPi: globus pallidus internal segment; PPC: posterior parietal cortex; PFC: prefrontal cortex; SMA: supplementary motor area; SNR: substantia nigra pars reticulata; SNC: substantia nigra pars compacta; Th: thalamus.

One difficulty in establishing the validity of the model for interval timing is that a majority of paradigms used to test the clock model hypothesis entail learning a duration (hence, storing a duration in memory and forming a reference) with which to compare another novel duration. This leads to a circular testing of the model since the components of the model are also present in the task itself. More recently, some studies have failed to replicate the early CNV findings opening new avenues to approach the time perception problem. Additionally, neurophysiological work in monkeys suggests similar accumulation-like responses in the lateral intraparietal cortex (LIP) that may be specific to elapsed time (Janssen and Shadlen 2005) bringing evidence for alternative and complementary views perhaps relevant for shorter time estimations than the above the second temporal scales. I now introduce a different kind of literature not a priori focused on time estimation but which may provide an

alternative approach in conceiving the brain system as a psychological time maker device in a more distributed manner.

3. Neurophysiological Temporal Structuring: A Logistical Platform for the Discretization of Events in Time

In line with the notion of temporal discreteness, Ernst Pöppel (1971, 1997, 2009) provided a compelling view of time perception based on the natural dynamics of brain systems. With ongoing periodicities of milliseconds to seconds, brain oscillations naturally lend themselves as temporal processing units or ‘temporal frames’ parsing the sensory field into cycles of brain-time. This view has recently been refined as pre-semantic temporal representations (Pöppel 2009) and finds substantial evidence in various sensory systems characterized by specific temporal constants in relation to perception (vanRullen and Koch 2003; Holcombe 2009).

Brain rhythms naturally echo the time scales of perceptual structuring in various sensory modalities but also of posited high-levels internal representations in cognition. For instance, a ~ 30 ms unit has been posited as a possible unit for time perception. This temporal scale corresponds to the temporal order thresholds observed across sensory systems (i.e. within 30 ms, order of events is lost) and consequently, information is integrated over this time scale (Pöppel 1971, 1997). Note that in the process of discretization for the purpose of (auditory, visual...) perceptions, temporal information is lost by virtue of integration. Brain oscillations provide a natural logistical platform for brain computations. Interestingly, they also present a hierarchical structure at both local and global spatio-temporal scales (Buzsáki 2006; Llinás *et al.* 1998). Just as one naturally conceives neuroanatomical connectivity to impose a set of hard constraints on the information flow in the brain, so does the set of temporal processing scales in the architecture of the brain system itself (and this, at different levels of observation). Recent advances in neurosciences provide fascinating insights on the temporal structuring of information processing (Buzsáki 2010; Wang 2010), some of which are alluded to here in the context of the emergence of time perception.

3.1 Oscillations and Spikes

Neural activity recorded non-invasively with EEG and MEG requires the synchronization of thousands of neurons at once (Figure 5). EEG and MEG recordings are closely related to the activity invasively recorded as Local Field

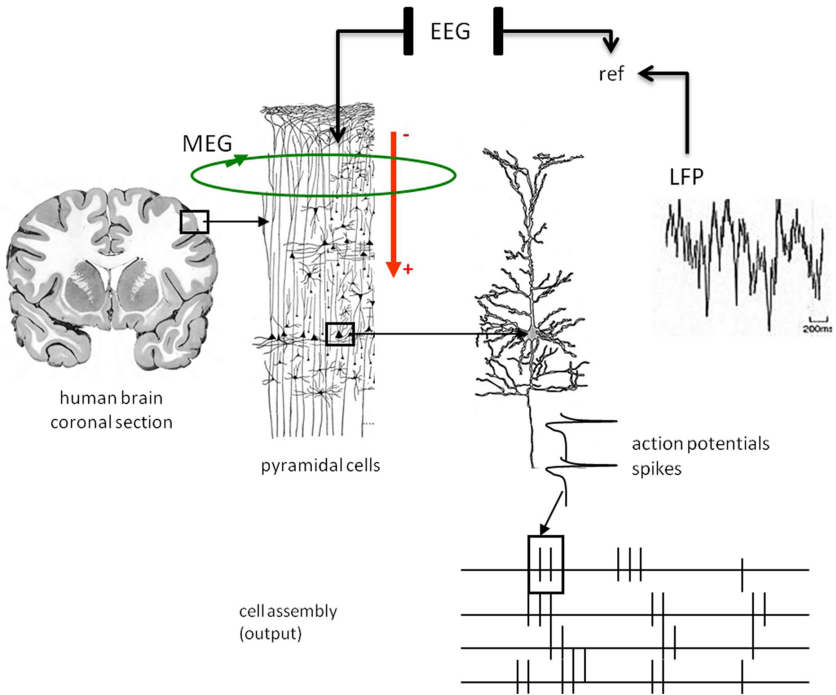


Figure 5. Mesoscopic observations of brain function. Electro- and magnetoencephalography (EEG, MEG) record non-invasively the extracellular electric and associated magnetic flux of thousands of neurons originating in the dendritic arborization of pyramidal cortical cells. Local Field Potentials (LFPs) are comparable signals. Action potentials generated at the single neuron level originate from the differences of electrical charges in and out of the cellular milieu.

Potentials (LFP). LFPs are a mesoscopic characterization of neural function and reflect the sum of external electrical current flows in the dendritic arborization of local neural assemblies. Hence LFPs can be conceived as the sum of information flowing in (inputs) a particular neural assembly; they also reflect the “slower” synchronization (tens of milliseconds) amongst the different neurons of an assembly, constrained by their anatomical configuration in the assembly. However, these techniques do not capture action potentials or neural spikes which are extremely rapid (few milliseconds). Neural spikes are the output in this information processing scheme and reflect the charge differences

between the intra- and extra-cellular ionic (electrical charges) concentration. Yet interestingly, recent investigations suggest a tight link between cellular spiking and extracellular oscillations: namely, the moment at which a spike occurs during an ongoing oscillation may serve as a temporal coding scheme.

3.2 *A Case Study: Hippocampal Place Cells*

The discovery of the importance of the neural spike timing with respect to ongoing oscillations has been thoroughly addressed in the hippocampus. As rats freely move in a maze, recordings of the hippocampus cells revealed that theta oscillations (~4 Hz) provide an ongoing temporal reference frame with regards to the position of the rat in the maze (Figure 6). Different cell assemblies were found to code for a particular location in the maze. As the rat moves in the maze, various electrophysiological patterns correlated with behavior. First, it was found that the temporal delay in maximal firing rate between two neural assemblies (e.g. neural assembly tuned for place 1 and neural assembly tuned for place 2) reflected the distance needed for the rat to go from point 1 to point 2 in the maze. Second, the neural tuning of place cells assembly shifts together in time in successive theta cycles: specifically, as the rat passes a particular location in the maze, neurons tuned to that location start firing earlier in time with respect to the ongoing theta rhythm. This phenomenon named “phase recession” or “compression mechanism” has been proposed to translate distances into time (Skaggs *et al.* 1996; Buzsàki 2010). This sophisticated coding scheme is under intense investigations in the hippocampus.

In the cortex, large-scale oscillations are clearly functionally relevant for cognition (e.g. Siegel *et al.* 2012). Different oscillations directly relate to the time-scale of information encoding. One possibility for the automatic encoding of temporal information ultimately serving the purpose of time experience is that, similar to the theta temporal reference frame, low-oscillations could provide a temporal reference frame (i.e. a distributed “brain clock”) allowing various cortical regions to be in-sync with each other. Event times may be encoded as neural assemblies spike at particular moment (or phase) of ongoing oscillations. This hypothesis is currently under investigation.

3.3 *Temporal Multiplexing in the Brain and Oscillatory Hierarchy*

Just as several anatomical streams define the flow of information from a spatial point of view, information can be encoded with different temporal granularities across brain areas dedicated to the processing of particular information. In other words, just as spatial multiplexing of information can be seen in

the streams model outline above (Figure 1), so can multiplexing occur at different temporal scales. It has recently been proposed that making use of temporal multiplexing in encoding information stabilizes neural representations (Panzeri *et al.* 2010). However, the typical oscillations observed in brain function (from infra-slow ($< 1\text{Hz}$) to as much as 600 Hz) should not be conceived as independent channels of information processing. Rather they appear to define an interdependent hierarchy of information processing in time. Specifically, low frequency oscillations modulate cortical excitability in up and down states modes. Said simply, particular moments in time are more prone to elicit further cortical processing than others. This can be illustrated by

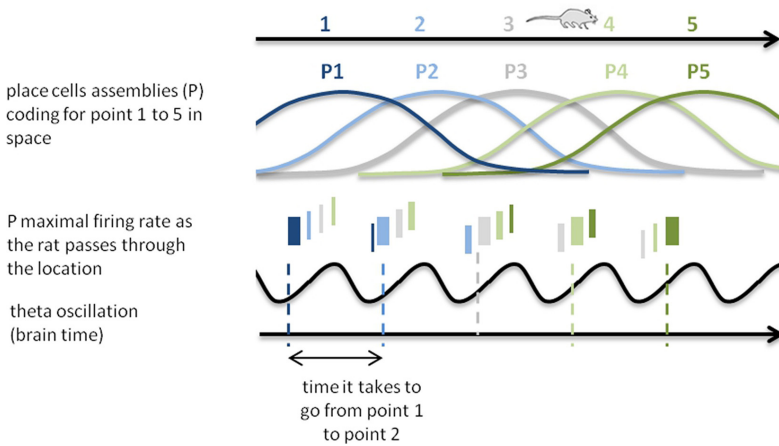


Figure 6. Hippocampal cell assemblies (*adapted from Buszàki, 2010*). The response profile of five cell assemblies (P1-P5) are here depicted with different shades of grey. Each cell assembly is tuned to five different positions (1-5) in a maze. When the rat passes one of those locations (e.g. 2), neurons of the corresponding cell assembly (e.g. P2) maximally fire. In other words, cells in P2 code for position 2. More interestingly, the time at which maximal firing takes place in one assembly (e.g. P1) with respect to another (e.g. P2) appears to be tightly related to the time it takes the rat to go from one location (1) to another location (2) in the maze. Specifically, as the rat moves across the maze, the cell assembly tuned to the location that the rat is about to pass starts firing earlier in time with respect to the ongoing theta oscillation. Hence, the position of the maximal firing in the cell assembly encodes the location of the rat with respect to the ongoing temporal reference frame provided by the theta oscillation.

recent neurophysiological findings in which the timing of visual inputs with respect to a low neural oscillation (delta, 1-2Hz) determines whether gamma bursts will be observed or not (>40 Hz) (Lakatos *et al.* 2005, 2008). A similar cross-frequency coupling between the phase of a slow oscillation and the power in a higher frequency band is observed in humans between theta (4-7Hz) and gamma bands (Canolty *et al.* 2006). In the context of this cross-frequency dependency, about 7 ± 2 neural assemblies per gamma cycle can be present within a theta period (Bragin *et al.* 1995; Lisman and Idiart 1995).

This suggests that a brain moment in time (for instance seen as a period of theta oscillation) is neither immune to the past nor to the future but rather integrates over time several moments of information that has been encoded with a finer temporal resolution across cell assemblies (for instance in the gamma range). Reaching back from recent neural functioning observations to their implication on perception and cognition (ultimately what neurosciences ought to explicate!): if a particular rhythm imposes a temporal reference frame to our perception, it entails that a perceptual moment is not quantifiable along a single stream of analysis but rather implicates some time before and some time after the physically instantaneous event. The segmentation or multiplexing of temporal information across different scales raise once more the problem of informational binding likely to necessitate a central stage able to integrate information into a coherent whole or the experience of the “flow of time” (van Wassenhove 2009).

3.4 (Re)Constructing Time in the Brain for Synchronizing with the External World

Some limitations with regards to brain oscillations need to be addressed. For instance, could they predict the differences of duration perception observed in audition and in vision? It is well known that auditory temporal perception is more precise than visual temporal perception and auditory events are often judged as longer than visual events of the same objective duration. The very same encoding mechanisms or brain rhythms should not lead to such differences across sensory modalities pending no other mechanism intervenes. One possible difference for duration perception in audition and vision would be the mere result of experimental confounding, i.e., the lack of intensity-matching between the two sensory modalities since intensity-duration trade-offs have been observed in audition (Moore 1997) and vision (Eagleman *et al.* 2004). Alternatively, different temporal coding schemes or local dynamics may take place in each sensory modality that would affect the access to temporal features. This is a working hypothesis. One additional thing to keep in

mind is that ultimately, the brain needs to function in a dynamic environment and as such needs to be in-sync with it. One approach is thus that neural dynamics serve a function to keep track of natural asynchronies: for instance the speed of light is faster than the speed of sound but its transduction is also slower. Yet the time it takes transduced auditory and visual information to reach the first entry point to the cortex (primary sensory cortices) still greatly differ and are out sync: if ~12 ms suffice to reach primary auditory cortex, ~50 ms are needed to record the first significant spiking in the visual cortex. Keeping a unitary linear timescale for time encoding in neural systems is doomed to fail unless mechanisms allowing the syncing of information such as the one observed across auditory and visual modalities are considered (Lakatos *et al.* 2008).

4. Iterative Temporal Processing: A Glimpse into Creativity and Free Will?

Finally, time research should have a dominant role to play in the recent revival of studies on the question of free will. Numerous neuroimaging studies have shown that cortical dynamics prior to the onset of a stimulus can reflect and predict the decision that a subject will make in the following hundreds of milliseconds (and sometimes seconds!). Direct interpretations of this observation suggest that even before a participant knows what the stimulus might be, his or her decision regarding that event might have already been taken. Neural activity recorded with diverse neuroimaging techniques tends to be mapped out on a linear time scale (the arrow of time). As has just been made evident, the brain is a highly dynamic and complex system that encompasses several multiple anatomical scales of observation in turn constrained by their temporal scales. As such, a linear and serial view of perceptual and conscious phenomena is a very simplified approach biased by our own psychological mapping of time itself.

Let's take a simple example in this context. If different subsystems operate at different time-scales, a 500 ms moment may be the "present" for that particular subsystem within which order doesn't matter with respect to informational content while in another subsystem, a present moment may be in the order of 50 ms. If the motor system operates on a time scale of 500 ms, mapping out events within that window of physical time would not necessarily provide an insight on true causality in the conscious brain (i.e. in brain time); rather it provides an insight on what the "present moment" is for that system. This illustrates the difficulty in interpreting the classic free will experiments (Libet 2004).

It is also becoming increasingly clear that the brain is a predictive system which can use prior knowledge to draw inferences about the world (Friston 2010). The nature of predictions the brain can make is a matter of another debate which is not the focus of this paper but needless to say that numerous areas of research are being pursued to better understand the implications of predictions. With respect to time perception and time processing the implication is quite puzzling: observing the predictive brain dynamics at time t implies that we are actually recording predictions of what's about to happen at time $t+1$ (future to happen) and the comparison of t with $t-1$ (the just recent past). This again illustrates that temporal information in the brain is shuffled at various levels of information processing and ought to be lawfully reconstructed to provide our often faulty but sufficiently accurate time experiences.

The predictive and iterative structure of cortical computations has ultimately endowed the human brain with the linguistic, mathematical, and musical languages. At the core of these abilities lie symbolic manipulations and syntactic structures that use "iterative" processes, in which the outcome at one computational level serves to predict the output at a different computational level. Let's now apply such principles to temporal structure in the human brain. The fascinating result that this endows us with is the ability to imagine the future, not simply by remembering the past but by creatively arranging imagined events and projecting them in a temporal space that only exists in our mind. Iterative temporal structures enable us to consciously predict and express scenarios as to the results that a decision taken in the objective now will have in the objective few years for our subjective self. The underlying mechanisms for such complex cognitive functions remain unexplored and set the stage for a promising future for time research.

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