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Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing

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Sensory systems must rely on powerful mechanisms for organizing complex information. We propose a framework in which inhibitory alpha oscillations limit and prioritize neuronal processing. At oscillatory peaks, inhibition prevents neuronal firing. As the inhibition ramps down within a cycle, a set of neuronal representations will activate sequentially according to their respective excitability. Both top-down and bottom-up drives determine excitability; in particular, spatial attention is a major top-down influence. On a shorter time scale, fast recurrent inhibition segments representations in slots 10–30 ms apart, generating gamma-band activity at the population level. The proposed mechanism serves to convert spatially distributed representations in early visual regions to a temporal phase code: that is, 'to-do lists' that can be processed sequentially by downstream regions.

Preventing information overload in the visual hierarchy

Although neuroscience research is advancing quickly in terms of data acquisition and recording techniques, there is a strong need for computational principles that can guide future empirical investigations. General neuro-computational mechanisms might have evolved to serve similar computational purposes in different regions. Information overload (see Glossary), defined as the amount of information exceeding processing capabilities, constitutes a general neuro-computational problem. One example is the hierarchy of the visual system, in which sensory input converges on increasingly specialized representations (Figure 1A). This convergence constitutes an information overload problem because representations will overlap as several objects are viewed simultaneously. Consider the example in which several faces are presented at the same time [1,2] (Figure 1B). If not properly resolved, it might result in a percept where the faces are blended. This problem is related to the finding of illusory conjunctions [3]. When two objects are shown briefly, their features are accidentally combined to one object. The visual hierarchy also poses a problem for downstream memory networks. It is thought that that the identification of objects in inferior and temporal regions relies on pattern-recognition mechanisms implemented in networks with attractor dynamics [4]. Given that attractor networks can only operate on one object at a time, the simultaneous face presentation constitutes an information overload problem. Nevertheless, it has been argued that the visual system can process multiple objects in parallel [5], but how is this achieved physiologically? Here, we propose a solution to this problem in which an oscillatory mechanism serves to decompose the visual scene into sub-elements, allowing for sequential processing (Figure 1B).

A mechanism transforming spatial representations into a temporal code

We propose a neuronal mechanism that serves to prevent information overload by transforming spatial representations into a temporal code. This results in short 'to-do lists'. The mechanism is motivated by convergent evidence demonstrating that slower oscillations in the theta (5–8 Hz) and alpha band (8–13 Hz) are abundant in many brain regions, independent of species [6]. In particular, the alpha oscillations are inhibitory: that is, they rhythmically prevent firing [7]. In addition, gamma-band activity (30–150 Hz) reflecting neuronal processing is typically found to be phase-locked to the slower oscillations [8–12]. It has been proposed that oscillations with different frequencies

Glossary

Duty-cycle: the fraction of an oscillatory cycle in which processing occurs. This could be reflected by the window of spiking within an alpha cycle or the number of gamma cycles per theta cycle.

Figure–ground segregation: in complex visual scenes we are able to perceive different objects in isolation. This perceptual grouping requires that a given figure is segregated from its background. Both bottom-up and top-down mechanisms are implicated in this process [114].

Information overload: refers to a situation in which the incoming information exceeds the processing capabilities of a given system.

Phase coding: information encoded by the neuronal firing with respect to the phase of ongoing oscillations. Note that phase coding can complement other coding schemes such as rate and population coding. In the framework proposed here, the phase encodes the order of a set of neuronal representations [15].

Phase precession: hippocampal place cells fire at specific phases of the theta oscillations in the local field potential. As the rat advances through a place field, this preferred phase of firing systematically shifts as a function of the rat's position. This shift of preferred firing phase is termed phase precession [59].

Phase-to-power coupling: a class of cross-frequency coupling in which the power of activity at higher frequencies is phase-locked to slower oscillations. For instance, gamma power phase-locked to both theta and alpha oscillations has been reported [9,12].

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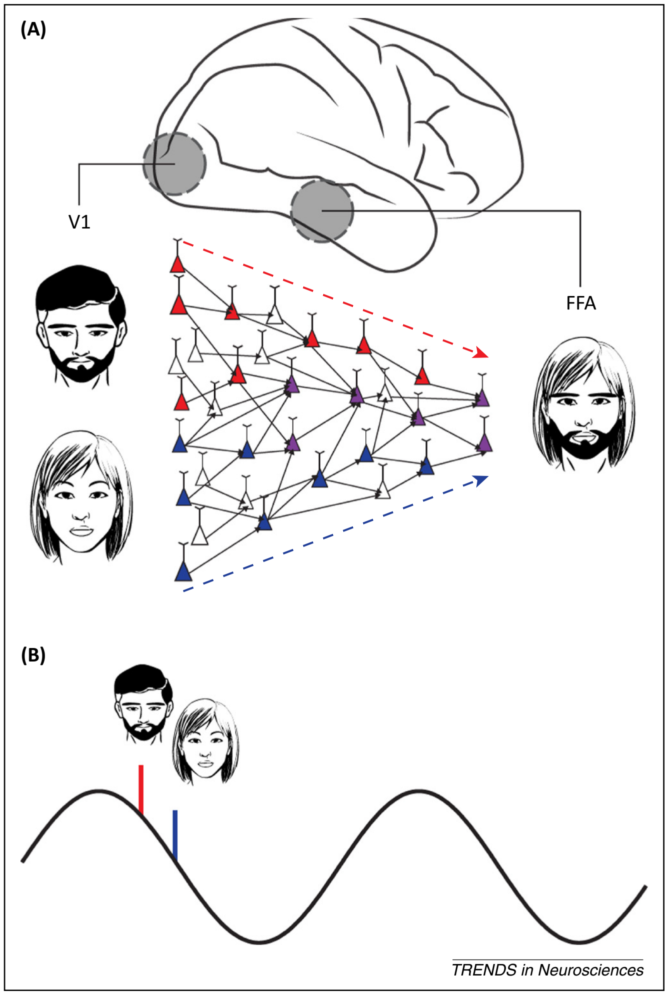

Figure 1. The convergence in the visual hierarchy creates a bottleneck in terms of information processing. **(A)** The visual system is hierarchically organized. Early visual regions code for low-level features in a retinotopic manner. Regions further down the ventral stream code for more complex features. For instance, face-selective cells have been identified in the fusiform face area [115]. Owing to convergence in the hierarchy, objects presented simultaneously will partly share the same neuronal representation in higher-order visual regions like the fusiform face area (FFA). This poses an information overload problem when perceiving the individual objects (illusory conjuction being an example [3]). **(B)** We propose a mechanism in which multiple objects are represented sequentially. This temporal code is organized in a phasic manner by alpha oscillations. The sequential activation allows downstream regions to process the objects individually.

interact in order to coordinate neuronal processing [6,13–15]. We first outline the proposed mechanism for how nested gamma and alpha oscillation can organize information processing.

A 'to-do list' organized by coupled oscillations

One strategy for preventing information overload is to make use of a pipeline relying on sequential processing [16]. We here propose a mechanism for how a visual scene can be converted into a temporal code. The mechanism we propose is highly inspired by models for phase coding in the rat hippocampus, in which sequences of spatial representations have been observed, that are coordinated by the 6–9 Hz theta rhythm [17]; reviewed in [15]. Assume that the early visual system is receiving input from numerous stimuli (e.g., several faces), but only has the capacity to process a limited number of those. These inputs (a, b, c, and so on) will compete for computational resources (Figure 2A). The subthreshold excitability of the representations is biased both by bottom-up mechanisms reflecting low-level properties of the visual stimuli and top-down mechanisms from higher-order visual areas [18]. One important top-down effect that we consider here is spatial attention. We also assume that an external pacemaker imposes a strong rhythmic inhibitory drive in the alpha band (8–13 Hz). The alpha oscillations are assumed to be highly synchronized across the early retinotopic visual regions, possibly due to the pacing by thalamic regions [19]. The spatial extent of alpha synchronization, however, needs further investigation. This is problematic using electroencephalography (EEG) and magnetoencephalography (MEG) owing to volume conduction and field spread. It could, however, be done using intracranial recordings in conjunction with visual perception and attention tasks. As a result, any of the representations are prevented from activating at the peak of an oscillatory pulse. As the inhibition decays within an oscillatory cycle, the neurons representing items a, b, and c will discharge in order of their respective excitability (Figure 2B). However, the neurons of the other presentations (d, e, and so on) will not fire, because they cannot overcome the inhibition in time. A second component of the model is based on the assumption that a fast inhibitory process involving GABAergic interneurons segments the representations in time [15,20]. The discharge of neurons for representation a activates an inhibitory network that momentarily prevents excitatory firing [21,22], implementing a winner-takes-all mechanism [23]. As the GABAergic inhibition wears off $\sim$10–30 ms later, the neurons for representation b will fire, and so forth. As a consequence, a population rhythm at gamma frequency is produced [24]. For the items to be properly separated by the inhibitory feedback, the gamma rhythm must be synchronized among the neuronal representations involved. Future work investigating the spatial extent of gamma-band synchronization in V1 is required to evaluate this prediction.

What prevents a given neuron, that for example is participating in representation a, from firing multiple times within an alpha cycle? It is well established that spikes and bursts are followed by strong after-hyperpolarization currents typically resulting from Ca-activated K currents with a duration of $\sim$100 ms [25]. This will diminish the likelihood of an excitatory neuron discharging multiple times within an alpha cycle. Further, it has been argued that bursts rather than single spikes are likely to carry the neuronal code [26]. Thus, if the actual representation is represented by a burst, the proposed scheme would be robust to some additional spiking. In short, the proposed mechanism will produce a sequence arranged according to subthreshold excitability. As a result a 'to-do list' is generated that is transferred to downstream regions. This allows for downstream regions to process each element one at a time. At the population level, the neuronal dynamics will be expressed as power in the gamma band that is phase-locked to the alpha oscillations, in other words: phase-to-power coupling [27,28]. The proposed mechanism is consistent with the idea of the 'gamma slide show', as proposed by [29] and the movement of cover attention clocked by gamma [111]. The mechanism we propose is also compatible with sequential visual search