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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

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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].
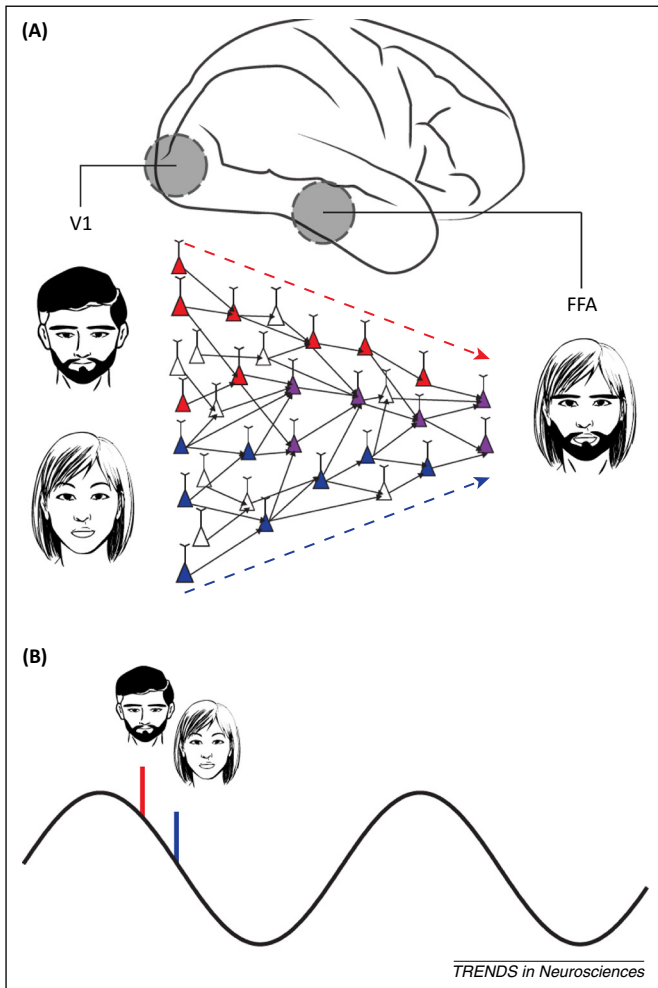

Figure 1. The convergence in the visual hierarchy creates a bottleneck in terms of information processing. **(A)** The visual system is hierarchically organized. Early visual regions code for low-level features in a retinotopic manner. Regions further down the ventral stream code for more complex features. 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 ∼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 ∼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
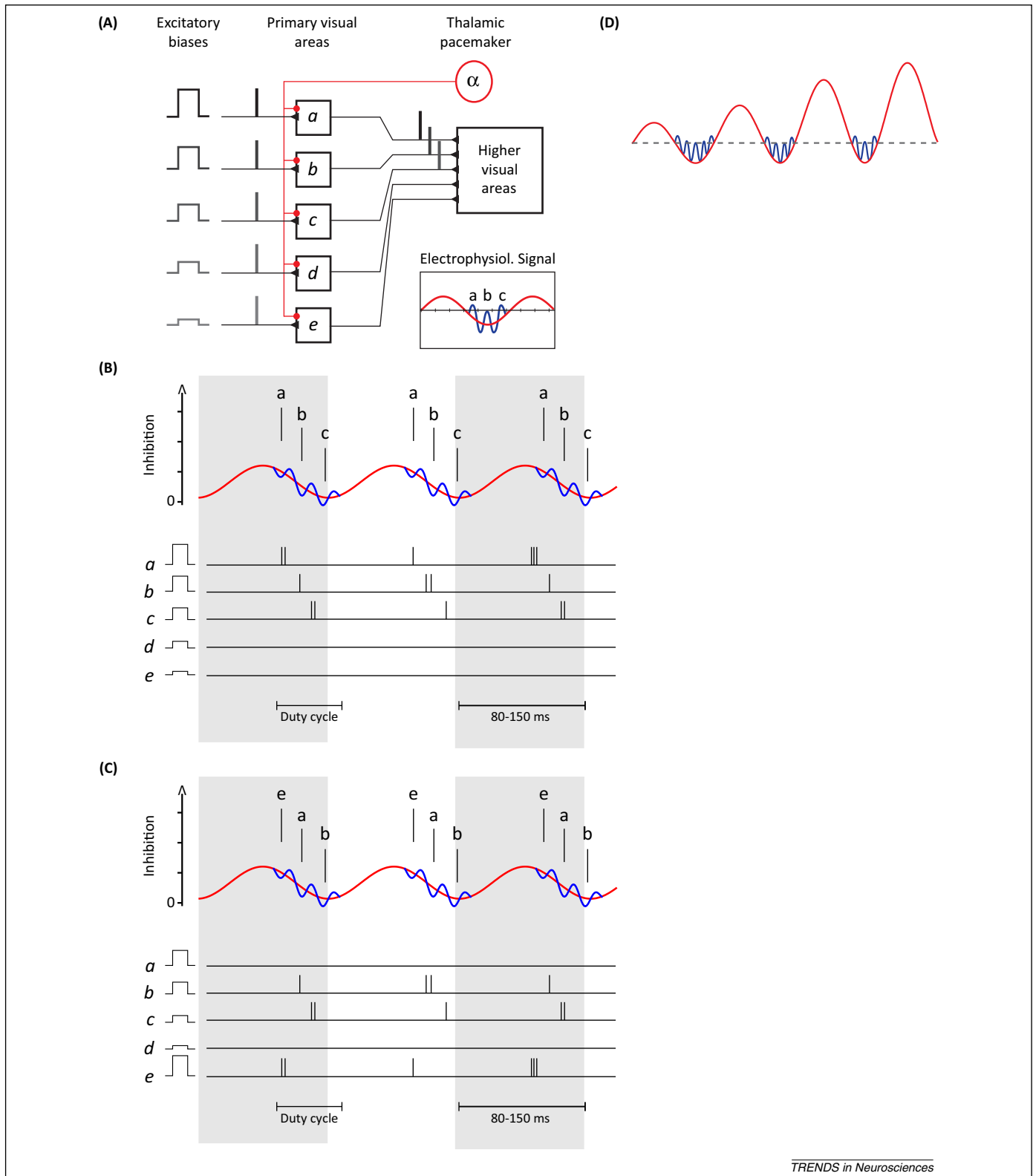
Figure 2. An oscillatory mechanism organizing sequential processing. **(A)** A network is receiving several inputs (*a*, *b*, *c*, *d*, and *e*). The inputs correspond to distributed neuronal representations of a visual scene organized retinotopically. These representations have different levels of excitability. Further, an inhibitory oscillatory alpha drive (8–13 Hz) is imposed on the network. **(B)** Assume that the inputs bias the excitability of the respective representations in the network (biased in strength from *a* to *e*). Initially the inhibition from the alpha oscillations prevents any neuronal firing; however, as the inhibition is reduced in the oscillatory cycle, the most excitable presentation, *a*, will discharge first. Then follows *b* and finally *c*. As the oscillatory inhibition increases again, it will prevent further activation of the other representations (*d* and *e*). The individual representations are kept apart in time owing to fast recurrent inhibition from an interneuronal network. The population activity from the sequential activation will produce power in the gamma band phase-locked to the alpha oscillations. As a consequence, the number of representations activating within a cycle are limited; furthermore, the order of activation is arranged according to excitability. **(C)** The order of activation changes according to the excitability of the individual representations. In this example, the elevated excitability of representation *e* will ensure that it discharges first and then *a* and *b*. **(D)** The number of presentations activating within an alpha cycle, and thus the duty cycle, depends on the level of the inhibitory alpha activity. A strong alpha inhibitory drive will reduce the number of gamma cycles per alpha cycle.

[30]. Interestingly, monkey recordings revealed that visual search was clocked by a 25 ms-period rhythm recorded in frontal eye-fields [31].

In the example in Figure 2C the representations have different levels of excitability and are re-ordered accordingly. In this case the cells representing *e* have the highest level of excitability, and this will result in *e* discharging first in the list. As a consequence, both the ordering and what enters the list are arranged according to the level of excitability. The proposed mechanism is similar to an observation made in monkey recordings [32]. This study reports that the phase of firing with respect to gamma oscillations was related to the level of neuronal excitation. Importantly, gamma phase in prefrontal cortex has also been related to neuronal coding during working memory maintenance [116]. In sensorimotor areas neuronal firing was found to be phase-locked to beta oscillations [33]. We propose that similar mechanisms apply to alpha band oscillations. We propose that a similar mechanism applies to alpha-band oscillations well. We later discuss in detail the various factors, such as attention, that determine the level of excitability.

The magnitude of the alpha-band activity determines how many representations are processed
We assume that alpha oscillations are produced in the neocortex but are controlled by a pacemaker that synchronizes the rhythm over larger neocortical areas. Multi-site intracranial recordings and MEG have demonstrated that the pulvinar could have such a role [19,34,35]; however, the lateral geniculate nucleus (LGN) could be involved as well [36–38]. It should be emphasized that even though the alpha rhythm is attenuated by visual stimulation, the rhythm is still detectable when strong visual stimuli are presented [39–41]. As further required by our model framework, a strong case has been made that the alpha activity is inhibitory in a rhythmic manner [7,8,42–46]. Consistently it has also been demonstrated that the alpha oscillations rhythmically modulate perception [47–49].

One key parameter determining how many representations are discharging within one alpha cycle is the magnitude of the alpha drive. Figure 2D demonstrates what happens when the alpha drive is increased or decreased. If the drive increases, the duty cycle is shortened because fewer representations can discharge. If the drive is decreased, more representations can discharge and the duty cycle is prolonged. By way of this mechanism, the number of representations to be processed is adjusted by the magnitude of the alpha oscillation relative to the strength of the input. Because the alpha oscillations are under top-down control, the proposed mechanism allows for adjusting the number of active representations that have to be processed by execute control mechanisms. For instance, when attention is allocated to the left hemifield, the right hemisphere alpha activity decreases, whereas it increases in the left hemisphere [40,50–52]. The mechanism we proposed then allows for only a few representations to be processed in the unattended hemifield, whereas more representations can be processed in the attended hemifield. By this principle, the information flow is dynamically controlled by adjusting the level of the alpha-band activity [53]. Several pathways

are likely to be involved in the top-down control of the posterior alpha activity. For instance, based on studies combining EEG and transcranial magnetic stimulation (TMS), the frontal eye field has been suggested to control the posterior alpha activity via the intraparietal sulcus [54]. Another route is a subcortical possibly involving the pulvinar [19,55]. Future work disentangling the mechanism and contributions of these two pathways would be highly informative. In particular, it would be important to understand the physiological mechanisms exercising the inhibitory control. Acetylcholine might have an essential role (see [56]) because it has recently been demonstrated that a cholinergic agonist modulates the alpha-band activity in an attention task [57].

In short, the magnitude of the alpha-band activity relative to the level of excitability of the visual representations determines how many visual items can be represented in one alpha cycle.

Relation to temporal coding in the hippocampus
The mechanism proposed is strongly inspired by models accounting for phase precession in the rat. Hippocampal cells identified in behaving rats and mice discharge when the animal is at a specific place: the place field [58]. These place cells also fire in relation to 6–9 Hz theta oscillations identified in local field potentials (LFPs). As the rat enters the place field, the firing occurs relatively late in theta cycle. As the rat runs through the place field, the firing advances to earlier and earlier phases [59]. This phenomenon, termed phase precession, demonstrates the existence of a phase code in which firing with respect to the theta cycle carries spatial information [59–61]. A simple model for phase precession is based on a ramp of excitation that systematically increases as the rat runs through the place field. The excitation interacts with hippocampal theta oscillations and determines when a given cell fires [62]. The theta oscillations that are paced by the medial septum provide a rhythmic GABAergic inhibitory drive [63]. As the rat advances through the place field, the increase in excitation will allow the place cell to overcome the theta inhibition earlier, thus explaining the phase precession. It has been proposed that firing of the different representations is segmented in time by a local GABAergic feedback provided by inhibitory cells [20,23]. As a result, different spatial representations activate in different gamma cycles [15,64,65]. This mechanism provides a temporal code in which different spatial representations are represented in different phases of the theta cycle [17]. As such, the temporal code produces a list organized according to events that the rat will encounter in the immediate future [17,64,66]. This mechanism protects the hippocampus from information overload by ensuring that only a limited number (5–10; see [17]) of spatial representations are processed in a given theta cycle. We propose that the alpha oscillations serve as a related mechanism in the visual system for coordinating neuronal representations organized as temporal sequences. As such, theta and alpha oscillations are mechanistically related [15]. Note that covert attention necessarily is not necessarily moved in every gamma cycles as suggested by Graboi and Lisman [111]; rather we suggest that attention is allocated to the

first items in the list while the rest of the items are processed pre-attentively.

Temporal organization according to contrast
The level of neuronal excitability in early visual cortex is determined by bottom-up and top-down mechanisms. The bottom-up drive refers to the direct input from the LGN modulated by lateral interactions in the visual cortex. The top-down drive includes spatial attention and figure–ground segregation. We will first explain how visual contrast in part can help to prioritize processing. It is well established that visual contrast modulates firing rates in primary visual cortex [67] (Figure 3A). As such, the excitatory drive to V1 neurons must be strongly influenced by contrast. Consider a neuron in V1 when its receptive field is exposed to stimuli of various contrasts while it receives an oscillatory inhibitory drive at alpha frequency (Figure 3B). The stronger the excitatory drive, the earlier in the alpha cycle the neuron will overcome the inhibition. By this principle, visual contrast is converted to a phase code. We will now generalize this example to a natural visual scene. In Figure 3C the receptive fields overlapping the zebra clearly have a higher contrast than the receptive fields overlapping the horses. In the presence of the inhibitory alpha oscillation, the neurons coding for the zebra in early visual cortex will discharge earlier than the neurons coding for the horses. After-hyperpolarizing currents will

ensure that neurons mainly discharge once per alpha cycle. The firing of the neurons for the zebra will engage fast GABAergic inhibition, preventing the firing of the neurons representing the horses for 10–30 ms. As a consequence, a temporal code is created in which the firing in early visual areas is ordered according to contrast. This mechanism is one of several operations serving to segment the visual scene into parts that then can be processed sequentially in downstream areas.

Another important factor is bottom-up saliency effects. As demonstrated in recent EEG and functional magnetic resonance imaging (fMRI) studies, a patch of bars produced a stronger neuronal response in V1 when these bars had a different orientation compared to the background [68]. The elevated event-related potential (ERP) response was detected ~70 ms after stimulus onset. The differences in neuronal responses are unlikely to be explained by a conscious top-down drive, because they were not perceived when backward masking was applied. On the basis of these findings, it has been argued that saliency biases the excitability in early visual regions owing to lateral interactions constituting a mechanism for pop-out [69].

In the context of this framework, we propose that V1 neurons representing salient stimuli will overcome the oscillatory alpha inhibition slightly earlier than neurons representing other components of the visual scene. In this
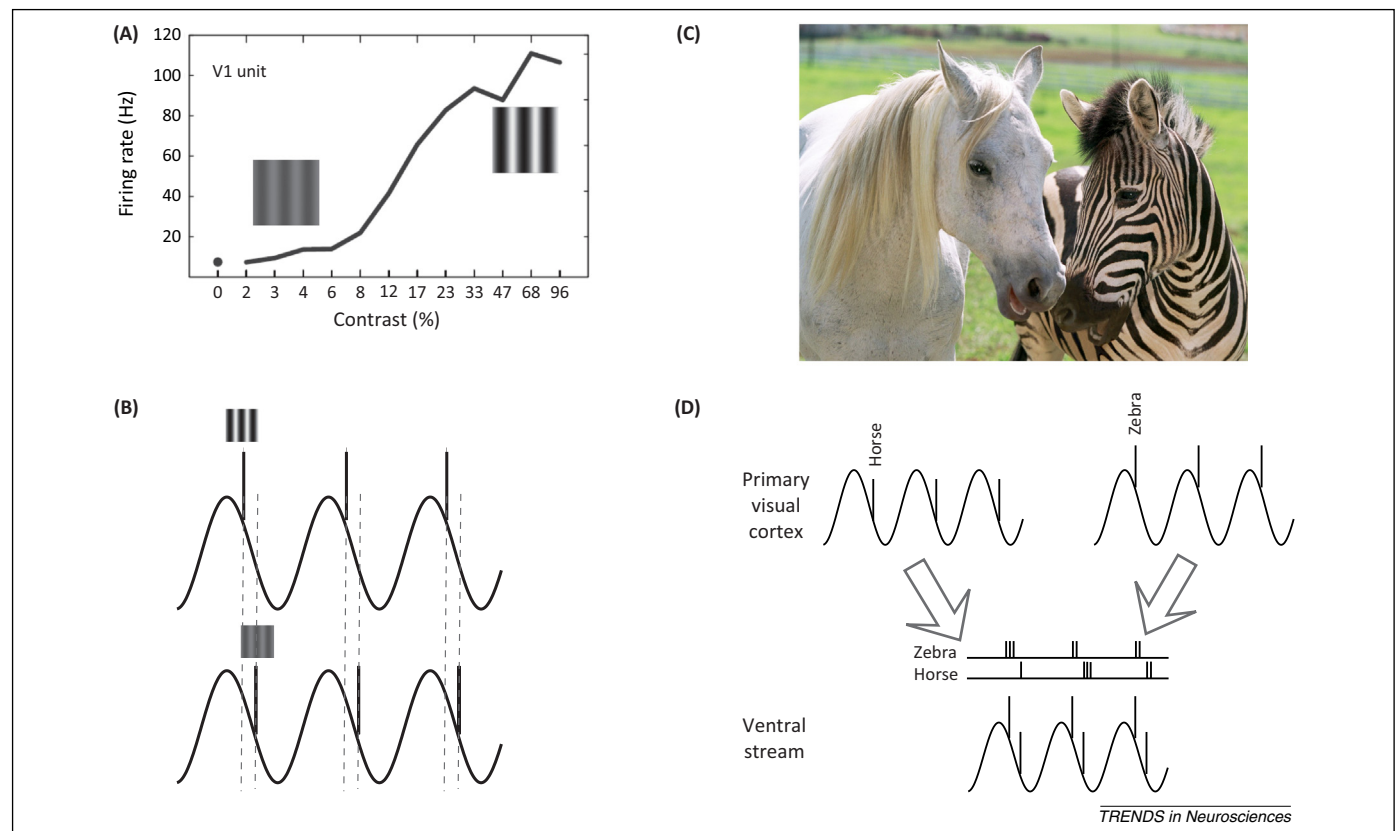

Figure 3. Organization of a temporal according to visual contrast. **(A)** Several experiments have demonstrated that neurons in the primary visual cortex respond with increasing firing rate as patches with stronger contrast are presented in their respective receptive fields. This demonstrates that neuronal excitability increases with visual contrasts. Reproduced, with permission, from [67]. **(B)** In the presence of oscillatory alpha activity, neuronal firing will be prevented at the peaks of the inhibitory cycle. We hypothesize that as the inhibition decreases over a cycle, V1 neurons will start firing. Neurons stimulated by a high contrast stimulus will fire earlier in the alpha cycle because they will overcome the inhibition earlier in time. **(C)** In this visual scene the zebra has a higher contrast compared to the horse. **(D)** The neurons whose receptive fields overlap with the zebra will fire earlier in alpha cycle compared to the neurons coding for parts of the visual scene overlapping with the horse. This produces a temporal sequence organized according to visual contrast.
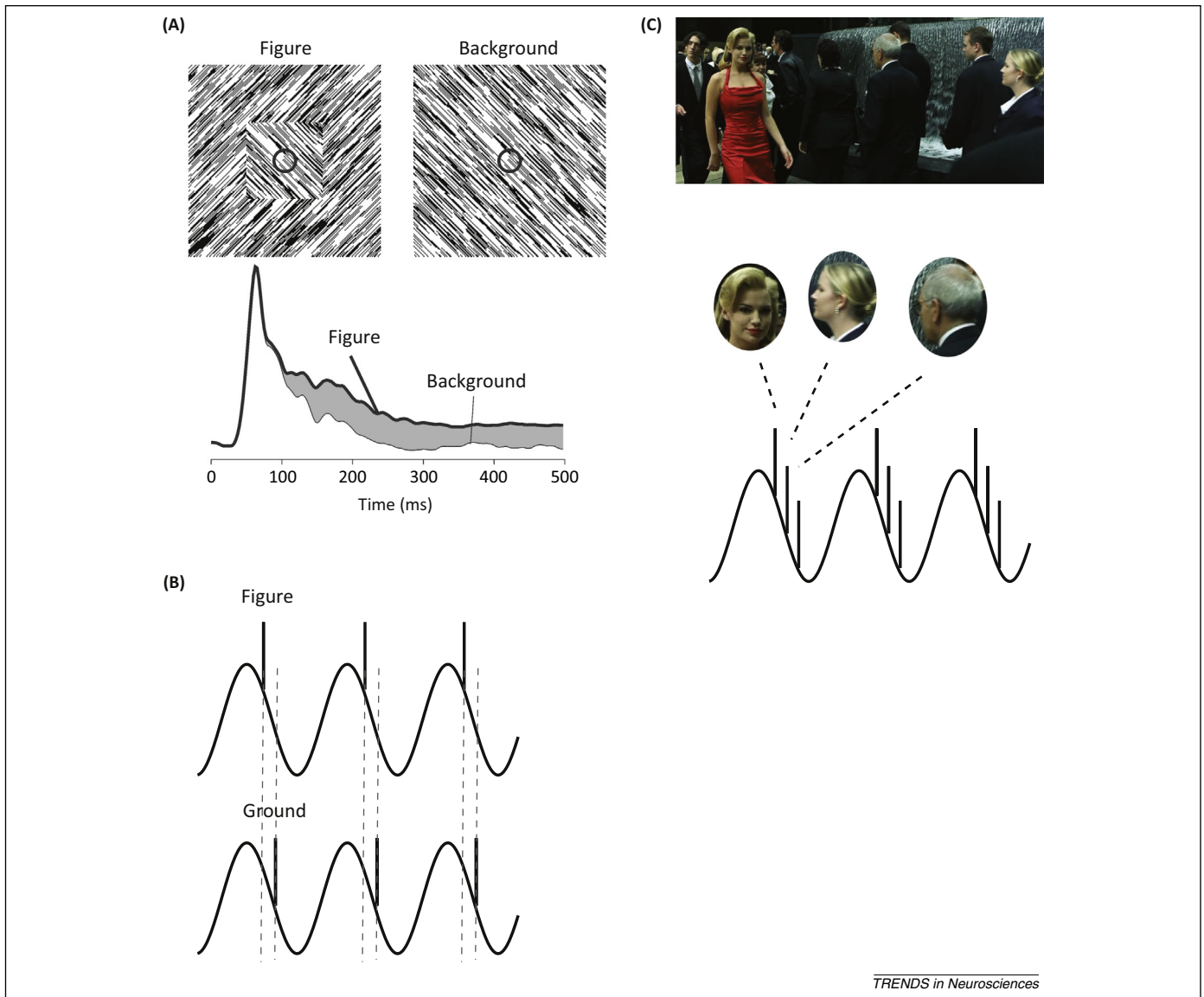
Figure 4. Organization of the temporal code arranged according to figure–ground segregation. **(A)** In the picture to the left, figure–ground segregation occurs because the central figure has a different orientation from the ground ('figure condition'). In the picture to the right, the central patch is similar to the ground ('background condition'). The black ring denotes the receptive field. Note that the figure exceeds the size of the receptive field. The firing rate of V1 neurons with a receptive field at the center of the figure is higher when figure–ground segregation occurs. Similar figure–ground effects have been demonstrated to occur with respect to color, luminance, and disparity [73]. The figure–ground segregation has been demonstrated to be a consequence of top-down modulation. Adapted with permission, from [70]. **(B)** In the presence of oscillatory alpha activity, we hypothesize that V1 neurons coding for the figure stimulus will fire earlier in the alpha cycle when figure–ground segregation occurs. **(C)** The principle of figure–ground segregation applied to a natural visual scene. Some of the individual objects, for instance, the lady in the red dress, will have a higher level of excitability. Saliency effects produce the figure–ground segregation and determine the levels of excitability. During an alpha cycle, this will result in a sequential activation of the objects in the visual scene.

case, a temporal code is formed that prioritizes not only visual contrast but also bottom-up saliency.

Temporal organization according to figure–ground segregation
It is well established that top-down influences bias the excitability in early visual cortex. These mechanisms include figure–ground segregation, spatial attention and pre-attentive emotional effects. We will here discuss the consequences of these mechanisms for the proposed coding scheme.

It has been demonstrated that figure–ground segregation modulates firing in early visual regions. This is thought of as a mechanism for segmenting and perceiving

objects in complex visual scenes. Figure–ground segregation has been investigated by means of single-unit recordings in V1 of monkeys [70] (Figure 4A). When a figure was presented that stood out from the background, the firing rate of neurons having overlapping receptive fields increased. The increase was observable as early as 30–40 ms after stimulus onset. This effect has been shown to be a consequence of top-down modulation: the figure–ground modulation is reduced by visual masking interrupting the feedback from extrastriate areas to V1 [71]. Further laminar recordings recently demonstrated that firing in particular increased in superficial and deeper layers of V1 during figure–ground segregation [72]. These layers receive top-down input from higher level visual

regions. Various features can create the figure–ground segregation. Beyond orientation difference in the stimuli, V1 neurons also respond to segregation according to color, luminance and disparity [73]. Consistent with this, a recent study using voltage sensitive dyes characterized the population activity in monkey V1 in which a monkey was presented with pictures of complete or scrambled faces [74]. Decoding algorithms applied to the distributed neuronal response demonstrated that local low-level features could be decoded in the early response, whereas high-level features such as faces could be decoded ∼150 ms after picture onset. These findings suggest that even though objects are represented in downstream regions, these representations bias the excitability in early visual regions.

How might the biasing in excitability by figure–ground segregation operate together with the alpha activity? Consider a neuron firing in response to a patch of lines presented in its receptive field (Figure 4B). In the presence of oscillatory alpha activity, neuronal firing is prevented at the peaks of the inhibition. As the inhibition reduces over a cycle, the neurons responding to the figure patch will discharge. When figure–ground segregation occurs, the neurons will overcome the inhibition slightly earlier within the alpha cycle. As a consequence, the figure–ground segregation will be reflected in the phase of firing with respect to the alpha oscillations, as illustrated in Figure 4B.

We will now generalize these ideas to the visual processing of more complex visual scenes. The visual scene in Figure 4C shows several people. We hypothesize that the segregation of these people will be reflected by the excitability of neurons in V1 as a consequence of top-down modulation from extrastriate regions. For instance, the neurons whose receptive fields have overlap with the woman in the red dress will have the highest level of excitability. This is because she will be associated with the strongest figure–ground segregation in the visual scene, owing to the difference in color. Thus the neurons of the woman in red will discharge first because they will be the first to overcome the inhibition within an alpha cycle. As the inhibition is reduced further within a cycle, the second-most-excitable representations will discharge, and so forth. The individual representations are kept apart by fast GABAergic inhibition, resulting in activation at the gamma frequency. As a consequence, the visual scene is decomposed into a temporal code that can be processed by downstream regions. This temporal segregation serves to reduce the problem of information overload because the visual object now can be processed serially.

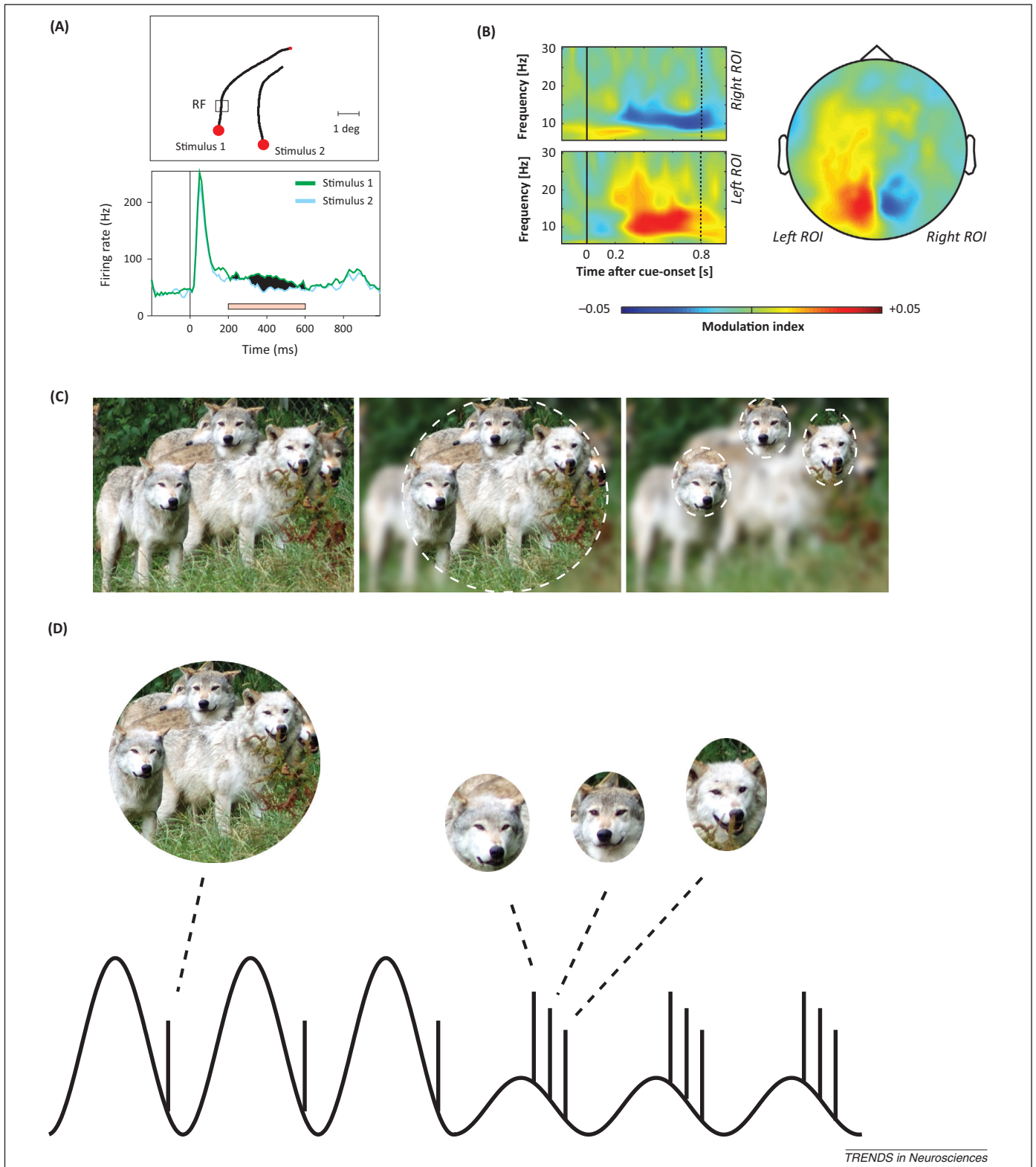*Temporal organization according to spatial attention*
The allocation of spatial attention is also expected to have a strong influence on the organization of the temporal code. When spatial attention is allocated, several mechanisms are at play. First it has been demonstrated that the activity of V1 neurons increases when spatial attention is allocated to the respective spatial fields. This has been demonstrated by intracranial monkey recordings [75] (Figure 5A), but it is also supported by, for instance, fMRI recordings in humans (see [76], for example). A complementary effect is a decrease in the power of alpha oscillations with the

allocation of attention. This has been demonstrated in numerous EEG and MEG experiments in which attention is allocated to either the left or right hemifield. As a consequence, the alpha activity contralateral to the attended hemifield decreases [40,52,77] (Figure 5B). These studies demonstrate that alpha activity is allocated according to spatial attention to the left and right hemifield. However, it might also operate on a finer spatial scale in a retinotopic sense. Recent electrocorticography (ECoG) recordings do indeed suggest that the alpha activity is modulated by attention on a finer spatial scale within one hemifield [78]. The mechanism we suggest is compatible with other theories that have been developed to account for the competition between items in a visual scene. For instance, according to the framework of biased competition [79,80], the firing rate to a given object will be reduced when a second object is presented in the same receptive field. The allocation of spatial attention to the first object will restore its firing rate. In our model, such competitive interactions would modulate the excitability in early visual regions and affect the order in which a set of visual stimuli is activated. The difference in excitability of two items when attention is allocated to one would serve to further augment the temporal segmentation.

How might the changes in excitability and the modulations in alpha activity work together with respect to spatial attention? Here, we suggest a somewhat speculative, but testable, hypothesis. Imagine a person walking in the forest listening to the birds singing. In this case the allocation of auditory attention will result in an increase in visual alpha power [81,82]. The increase in alpha power has been suggested to reduce the visual processing capabilities. Suddenly the person spots three animals (Figure 5C). As a result, spatial attention it allocated to the animals. Consequently, the excitability of the neurons in the attended field will increase. The joint neuronal representation of the wolves will overcome the inhibition at the trough of the inhibitory alpha cycle (Figure 5D). Furthermore, the magnitude of the alpha activity decreases allowing for a heightened information flow; that is, more representations can discharge per alpha cycle. In downstream ventral regions, the individual wolves will be identified. This allows for top-down mechanisms to bias the excitability of the individual representations in the primary visual cortex. As a consequence, the initial large receptive field is decomposed into smaller elements that will be processed sequentially.

Note that mechanisms other than figure–ground segregation and spatial attention might contribute to the top-down biasing. Emotional components are likely to contribute as well. Based on various investigations, it has been shown that fast subcortical pathways, including the amygdala, are involved in top-down biasing [83,84].

In summary, we propose a mechanism for how natural images can be decomposed to a temporal code determined by neuronal excitability and the inhibitory alpha oscillations. The excitability of the neurons in the early visual cortex is determined by feed-forward drives reflecting the local visual features, such as contrast and saliency. Subsequently, top-down drives, including figure–ground segregation, spatial attention and emotion, further bias the

Figure 5. Organization of a temporal code arranged according to attention. **(A)** In this study, a monkey was fixating on the red dot in the upper right corner. The monkey was then instructed to saccade to the stimulus connected to the dot via the line. Prior to the saccade, the neuronal firing in V1 was elevated for receptive fields (RFs) overlapping with the line. This demonstrates that spatial visual attention increases excitability. Reproduced, with permission, from [75]. **(B)** The human alpha activity in early visual areas is strongly modulated by spatial attention in a region-specific manner. In this example, moving dot kinematograms were presented in both hemifields. The magnetoencephalography (MEG) data demonstrated that when subjects were asked to covertly attend to the left, the alpha activity in the contralateral hemisphere decreased. Further, it relatively increased in the ipsilateral hemisphere. Abbreviation: ROI, region of interest. Reproduced, with permission, from [41]. **(C)** In this hypothesized example, visual attention is initially low (left panel). Then an attentional field is formed overlapping with the three wolves (middle panel). As attentional resources are further allocated, this field breaks into three subfields representing each of the animals (right panel). **(D)** A hypothetical mechanism supporting the allocation of attention. As the visual attention is initially low, the alpha activity is high; however, the excitability of the neurons representing the field of the three wolves is sufficiently strong to overcome the alpha inhibition. The allocation of spatial attention causes both an increase in excitability and a decrease in alpha activity. This allows for several representations to discharge within one alpha cycle. As a consequence, the representations of the three wolves will activate in a sequence such that they can be processed individually by downstream regions.

excitability. These mechanisms together set the neuronal excitability in the primary visual cortex. The levels of excitability in return determine the order of activation.

Further, the magnitude of the alpha-band activity is modulated by spatial attention. When the oscillatory inhibition is strong in the alpha band, fewer representations can discharge in a cycle. As a result, a temporal code is generated in which the number of elements is determined by the magnitude of the alpha activity, and the order of activation is determined by the excitability of the individual representations.

Predictions and future perspectives

We have presented a general mechanism that limits and prioritizes the visual representations to be processed. The mechanism is based on an inhibitory oscillatory drive in the alpha band allowing only the most excitable representations to discharge. Further, these representations are arranged as a temporal code organized according to neuronal excitability. The population dynamics arising from this mechanism will produce oscillations in the alpha band. Gamma activity phase-locked to the alpha oscillations serves to segment the representations in time. The proposed framework results in a set of predictions that we address below.

Electrophysiological evidence for phase coding in the visual system

A key prediction of the mechanism is the existence of an alpha phase code: the higher the excitability of a given representation, the earlier it will activate in an oscillatory alpha cycle. Although there is ample evidence for theta phase coding in the rat hippocampus, the case is less clear for the sensory alpha oscillations. Nevertheless, it has been shown that neuronal firing is strongly modulated by alpha phase both in visual and sensorimotor regions [85–87]. When considering firing in the superior temporal sulcus (STS), some cells fired in response to both faces and objects. Importantly, the phase of firing was different for faces and objects with respect to the LFP in the alpha and gamma band [88]. In the auditory system, multi-unit recordings identified neuronal firing organized in 100–200 ms packages. Within a package, a set of cells typically activated in the same sequence. Importantly, although these packages were not activating rhythmically *per se*, the activation was coupled to the phase of LFP activity in the alpha band [89]. By multi-unit recordings in the monkey, it has been shown that different movie clips could be decoded by considering neuronal spiking in relation to the phase of LFP activity in the 1–4 Hz band [90,91]. However, the dominating oscillatory power in the LFP was not identified in these studies. Although these studies indicate the existence of phase coding in sensory regions, direct investigations are required to determine whether phase coding operates in the alpha band in the primary visual cortex. As also pointed out earlier, we argue that the alpha activity would still exercise a phasic modulation of neuronal firing, despite the fact that the alpha activity is attenuated by visual stimuli. Indeed there are several studies demonstrating that a decrease in alpha power is associated with an increase in interregional coherence (see, for

instance, [92,93]). We suggest that the increase in the duty cycle will produce less oscillatory modulations at the population activity [42]; this will be detected as a decrease in alpha power. Intracranial recordings linking single unit firing to the phase of ongoing oscillations are required to further investigate this issue.

One obvious criticism of the proposed mechanism is that the predicted sparse firing patterns (Figures 2–4) seems to be in contradiction to firing rate increases reported for stimulated V1 neurons [94]. However, the actual statistical properties of neurons in the primary visual system is debated [95]. One impact factor is that neuronal firing is often strongly reduced when stimuli larger than the visual receptive field are presented. An example is shown in Figure 6A, in which the firing rate is ∼45 Hz when only the relevant receptive field is stimulated. Importantly, when a texture much larger than the receptive field is presented, the response is typically drastically reduced [96]. The suppression is likely to be a consequence of center-surround suppression. The neuronal firing in V1 when presenting a natural stimulus equal in size to the neuron's classical receptive field has been compared to the firing activity when the stimulus has a diameter that is four times as large [97] (Figure 6B). The large stimuli reduced the neuronal response, resulting in much sparser firing patterns. Another aspect is that the reporting of neuronal recordings in the visual system is strongly biased towards characterizing neurons with strong firing-rate modulations [95]. As an example, neuronal activity is typically recorded in the more superficial cortical layers. When considering the firing in deeper layers, the firing properties might change considerably. A recent study relating local field potentials to neuronal firing found that in superficial layers, spiking was phase-locked to gamma band activity. However, in the deeper layers of V1, the firing was strongly phase-modulated by alpha oscillations [86] (Figure 6C). As a final point, the proposed mechanism would be robust to sporadic firing. The case has been made that burst and spike onset carry the neuronal code more so than later spiking [26]. As such, single spikes occurring in isolation would not posit a large problem.

We conclude that when natural visual scenes are presented, firing in early visual regions could be sufficiently sparse to support phase coding the alpha band. To further investigate alpha phase coding, it would be of great interest to investigate neuronal spiking in relation to ongoing oscillations while natural scenes are presented (Box 1). When visual properties or top-down biases of visual stimuli are manipulated, we predict a change in the alpha phase of firing. Such studies are best done in animals in which single units and LFPs are recorded. When several visual objects are presented simultaneously, it should be feasible to identify sequential neuronal activation patterns in relation to the phase of ongoing alpha oscillations.

Gamma power phase-locked to theta/alpha oscillation: a fingerprint of a neuronal to-do list?

Population activity of multiple neurons operating together can be detected in electrophysiological data from LFP, ECoG, EEG, and MEG recordings [33,98,99]. The proposed framework predicts that gamma-band activity will be
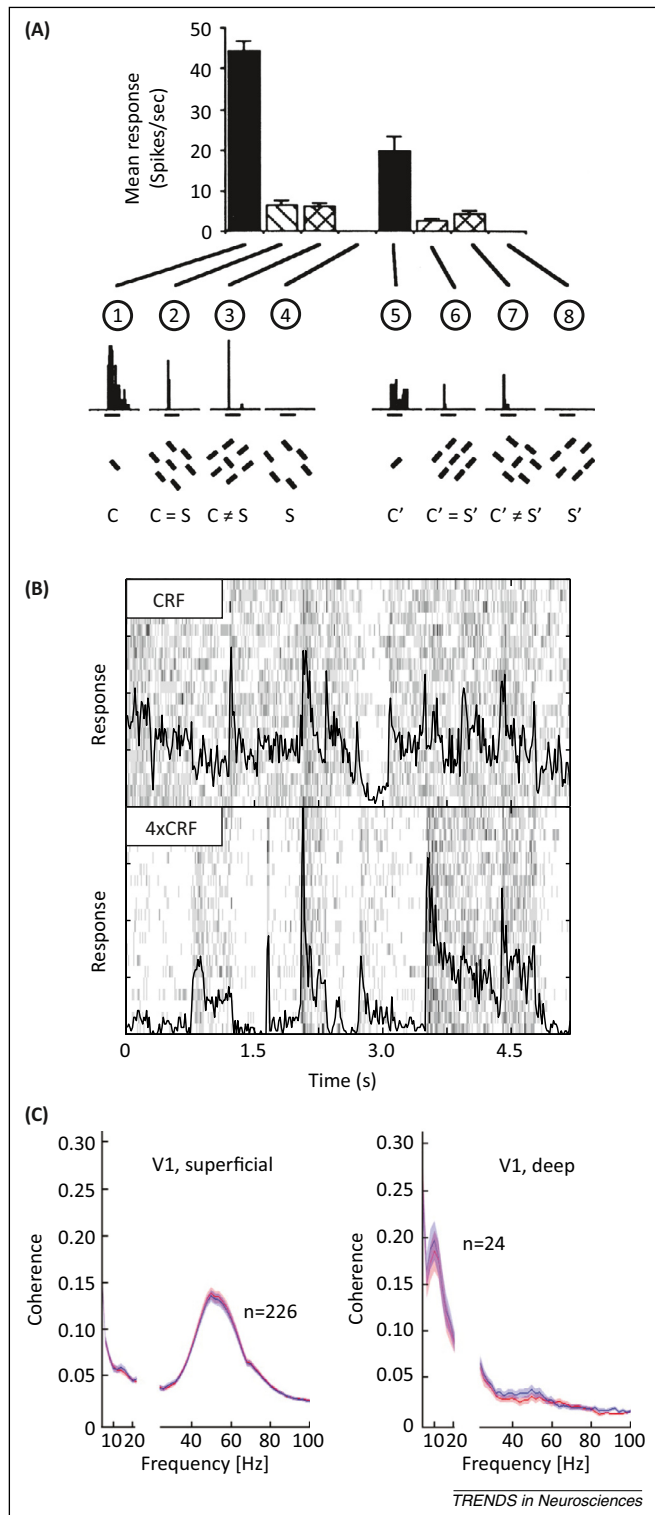
Figure 6. The neuronal code in early visual regions is relatively sparse in response to complex visual scenes. **(A)** The response of a complex V1 neuron when stimulated by a bar in its receptive field, (1) and (5). When patterns with surrounding bars are presented outside the classical receptive field (CRF), the firing rate is dramatically reduced (2, 3, 6, and 7). This pattern was observed for ~80% of the investigated cells. Reproduced, with permission, from [96]. **(B)** The response of a V1 neuron when a movie with natural images is shown. Upper panel: when only the receptive field of the cell is stimulated, the firing rate is relatively high. Lower panel: when a movie with a diameter four times that of the receptive field is shown, the firing rate is dramatically reduced. Furthermore, the sparseness is increased as the stimuli are increased in size. Reproduced, with permission, from [97]. **(C)** Spike-field coherence of V1 neurons in response to attended (red) and unattended stimuli (blue). In superficial cortical layers, the neuronal firing is phase-locked to oscillatory gamma-band activity of the local field potential. V1 neurons in deeper layers fire phase-locked to alpha oscillations. Reproduced, with permission, from [86].

Box 1. Outstanding questions

- Do neurons in early visual regions fire with a specific relationship to the alpha rhythm? In particular, our framework predicts that an increase in contrast, figure–ground segregation, or spatial attention for a given visual object should advance the firing within an alpha cycle.
- Do neuronal representations of different visual objects fire at different phases of the alpha cycle?
- What is the spatial extent of synchronization of alpha and gamma oscillations across early visual regions? Synchronization over a somewhat larger scale is required for coordinating neuronal processing associated with a complex visual scene.
- Does the duty cycle within an alpha cycle increase as alpha power decreases, as predicted in Figure 2D in the main text?
- Is neuronal firing still phasically modulated in the alpha band when the alpha power is reduced by visual stimuli?
- Is the exchange of phase-coded presentations reflected by inter-regional phase-synchronization in the alpha band, as suggested by [34]?
- Which mechanisms serve to control the modulation of alpha power and phase? Both neocortical and thalamic pathways are likely to be implicated.
- Which physiological mechanisms are responsible for generating the alpha rhythm, and is the thalamus involved, as suggested by [19,34,37]?

phase-locked to theta or alpha oscillations. Recently it has been proposed that theta and alpha oscillations serve very similar purposes in terms of organizing the neuronal code [15]. The gamma-band activity serves to segment the representations in time and also limits the number of representations that can be processed in each oscillatory cycle. Although there is a strong case for such phase–amplitude coupling in visual and hippocampal regions [8,9,11,12, 35,100–103], it has also been identified in many other regions: ECoG recordings in humans have revealed phase–amplitude coupling in numerous neocortical areas [10]. In the striatum of both rats and humans, robust phase–amplitude couplings have been reported [104,105]. In the auditory system, gamma-band activity was phase-locked to theta activity driven by the temporal structure of speech [106–108]. We propose that theta and alpha oscillations serve similar purposes for the temporal organization of neuronal codes. The stage is now set to investigate whether the alpha phase to gamma power coupling reflects a mechanism for organizing phase-coded information in the visual system.

A link to predictive coding

Several theories based on predictive coding have suggested that top-down mechanisms serve to prioritize processing in early visual regions. The core of the framework is that predictions about incoming stimuli are compared to sensory input. A large discrepancy between input and prediction will result in a stronger feed-forward drive [109,110]. This mechanism has also been considered in the context of visual attention. The idea is that attention in particular is allocated to process unexpected or uncertain input [111,112]. According to this model, one could propose that top-down mechanisms serve to upregulate the excitability of sensory inputs that do not match predictions. As a consequence, they will activate earlier within the alpha cycle: that is, they will be processed earlier in the to-do list.

Is a breakdown in the oscillatory code linked to attention disorders?

What happens if our ability to limit the information flow by inhibitory mechanisms is impaired? The resulting information overload would lead to suboptimal performance. Certainly, attention disorders could be considered in this context. In support of this notion, it has been demonstrated that patients with attention deficit hyperactivity disorder are impaired in their ability to control posterior alpha oscillations [41,113]. It would be of great interest to investigate whether similar relations can be drawn between oscillatory brain activity and other psychiatric or neurological disorders.

Concluding remarks

In conclusion, we have presented a mechanism for how complex visual information can be represented as a temporal code. Basically, a visual scene is decomposed to a sequence, allowing processing to be prioritized. By a gradual release of inhibition in each alpha cycle, this mechanism produces 'to-do lists' that can be processed sequentially in downstream regions. The framework can be tested by relating single unit firing to LFP oscillations in early visual regions while various parameters, such as contrast, visual attention, and segregation, are manipulated.

Acknowledgments

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