

Cortical synchronization as a neural basis for visual perception

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Cortical synchronization has been suggested as a neural mechanism that is able to solve the feature binding problem. This idea has been intensively studied at neurophysiological, psychophysical and computational level. In this paper, arguments for and against the role of cortical synchronization in visual perception are critically examined. Initial neurophysiological findings of correlated neural activity in the primary visual cortex have been questioned by studies which reveal enhanced firing rate to the figure region compared to the background. Computational investigations reveal that synchronization has capacity limit. At the behavioural level, change blindness has been used as the evidence for capacity limit of visual perception. However, further examination of this issue showed that detailed visual representation exists but it is obscured by limitation of attention and visual working memory. Other behavioural phenomena, such as perceptual asynchrony, also point to the fact that there is dissociation between correlated neural activity and perception. Therefore, at present there is no sufficient evidence to support the conclusion that cortical synchronization plays a crucial role in visual perception.

Key words: change blindness; cortex; feature binding; neural mechanisms, vision

It is of fundamental importance to understand how sensory information is represented in the brain. In particular, what code is used between neurons to communicate relevant aspects of the environment. It is well established that electrical activity of neurons plays a central role in neural information processing but exactly what aspect of electric signaling is used to achieve perception is still an open question. Neurons, in response to stimulation, produce a sequence of very brief events known as action potential or spikes, which are transmitted along the axons to other neurons in the network. Spikes are separated by temporal gaps of variable duration ranging from few tenths of a second to a less than a hundredth of a second. Sequences of spikes are the only messages that neurons send to each other and we need to understand how to read these messages. One possibility is to count the number of spikes received in a certain time interval. This is known as a rate code (Shadlen, 2003). When

stimulus intensity is low, neuron will emit fewer spikes. On the other hand, when stimulus intensity is increased more spikes will be emitted in the same time interval. Therefore, varying the strength of stimulation will produce variation in spike density. However, this is not the complete answer because stimulus intensity is only one of many aspects of perceptual experience. For instance, in visual perception we would like to know how is information about different colors, shapes, and motions combined into unique representation of objects. The visual system processes different features in different modules. Color is processed in V4 and motion is processed in V5 or MT cortex (Zeki, 1993). Therefore, V4 could signal the presence of certain colors in the environment and V5 could signal the presence of certain motions. Now, consider a simple situation with two objects in the environment: one red object is moving in horizontal direction and one green object is moving in the vertical direction. V4 detects the presence of red and green colors while V5 detects the presence of vertical and horizontal motions. However, their neural activity could not distinguish which color belongs to which motion. This is known as a feature binding problem (Treisman, 1996, 1999). Another version of the binding problem is the question of how visual scenes are spatially segmented into different objects or how is perceptual segmentation achieved.

Feature binding problem could be solved using the firing rate model, assuming the existence of neurons which combine information from different feature maps. They

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would form a conjunctive representation because every neuron would respond to a particular combination of features. In the example given above it means that there would be separate neurons with sensitivity to horizontal and vertical motions of red object and horizontal and vertical motions of green object. This is consistent with the fact that higher visual centers have neurons with larger receptive fields responding to more complex features. However, such a coding scheme would lead to a combinatorial explosion because the number of potential conjunctions of visual features in the environment is infinite (Gray, 1999; von der Malsburg, 1981). As an alternative to the rate code, recently it has been proposed that temporal interval between spikes could solve the feature binding problem. In particular, it is suggested that neurons that code information about the same object in the environment should synchronize its firing of spikes. That is, they will fire spikes at the same time. The idea is that time is used as a code for signaling perceptual groups and this idea is termed temporal correlation hypothesis (TCH; Singer & Gray, 1995). It was independently proposed by Milner (1974) and von der Malsburg (1981). Later, the same idea was applied in modeling more complex functions such as object recognition, attention, memory formation, motor control, sensorimotor integration and sensory awareness (Engel & Singer, 2001).

Neurophysiological evidence

TCH has gain on importance when Gray, König, Engel and Singer (1989) and Engel, König, Gray and Singer (1990) found neurophysiological support for this type of coding. In cat's primary visual cortex it was found that groups of neurons synchronize their activity in response to appropriate visual stimulation. Degree of synchronization was dependent on the properties of stimulations. Gray et al. (1989) used two bars moving either in the same direction or in the different direction. When two bars moved in the same direction, neurons that respond to their movement synchronized its activity. When bars moved in the opposite direction there was no synchronization. This is closely related to our perceptual experience because we tend to see objects moving together as a single group. More precisely, Gestalt principle of common fate states that objects moving in the same direction and with the same speed will be perceived as a group (Palmer, 1999). Later it was found that synchronization occurs not only between the neurons in the same cortical column but also between different columns in the same cortical area and even between different cortical areas and hemispheres. Synchronization was more likely to occur between cells that are closer in cortical space and between cells that represent similar perceptual features. For instance, synchronization in primary visual cortex is more likely to occur between neurons that have similar orientation preference. These properties of synchronization suggest that it may be relevant for

perceptual organization because they correspond to Gestalt principles of perceptual organization. Principle of proximity states that objects that are closer together will be perceived as single group. Principle of similarity states that objects that have similar features will be perceived as a group (Palmer, 1999). Features could be color, orientation, shape, etc. Detailed reviews of evidence for neural synchrony were provided by Eckhorn (1999), Gray (1999), Singer (1999), Singer et al. (1997), and Singer and Gray (1995).

However, critics of the TCH point to the fact that neural synchronization is a widespread phenomenon and occurs in retina and lateral geniculate nucleus as well. Although these structures are a part of the visual system they do not take part in the processes of perceptual organization. Some researchers found synchronization but it was not related to the stimulus properties and others did not even detect any synchronization in primary visual cortex (Ghose & Freeman, 1992; Shadlen & Movshon, 1999). Moreover, several studies indicate that the rate code could represent perceptual grouping. Lamme (1995) studied neural activity in the primary visual cortex in response to stimuli where a figure is distinguished from a background based on the difference in a texture orientation or a motion direction. He observed a difference in the firing rate when neuron's receptive field was inside or outside a region belonging to the figure. Firing rate enhancement was uniform along the whole figure, irrespective of the location of the receptive field. It could be on the border or on the interior of the figure. In a subsequent study, Zipser, Lamme and Schiller (1996) found firing rate enhancement for the figures defined by difference in luminance, color or disparity. Furthermore, in both studies, the rate enhancement related to the figure-ground relationship had longer latency than initial response to the local image features. Also, texture boundaries are processed before a texture interior is enhanced suggesting different network mechanisms for surfaces and borders (Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999). Based on these studies, Lamme and Roelfsema (2000) proposed a model of sensory processing in the brain with two distinct modes. The first mode is a fast feedforward mode where cells respond to local image feature to which they are tuned. The second mode is a slower feedback mode, which represents a more abstract code related to figure-ground segregation and possibly to other aspects of visual perception.

It should be mentioned that study from another laboratory failed to find evidence for the enhanced activity in the interior of the texture in the texture segregation task (Rossi, Desimone, & Ungerleider, 2001). Enhanced activity was observed only at the texture borders. Rossi et al. (2001) argued that discrepancy in results could be accounted for by different behavioral paradigms employed in these studies. On the other hand, Albright and Stoner (2002) suggest that textured stimuli do not provide strong cues for segmentation and configurations with depth cues should be tested instead. Relevant

findings are summarized by Lee (2003) who also argued that enhanced firing rate in the interior of the surfaces reflects important information about figure-ground organization.

Two recent studies showed that neural synchronization might be more relevant for high-level cognitive processes such as selective attention. Steinmetz et al. (2000) found that neurons in monkey somatosensory cortex showed greater degree of synchronization when monkeys performed tactile discrimination task compared to visual discrimination task. Fries, Reynolds, Rorie and Desimone (2001) discovered that neurons in V4 cortex showed high frequency synchronization (in the range of 35 to 90 Hz) when attention was directed to the stimulus within their receptive fields. These studies indicate that synchronization increases neural responsiveness to behaviorally important stimuli in the environment and thus it may serve as a neural basis of visual selective attention (Fell, Fernandez, Klaver, Elger, & Fries 2003; Fries, 2005; Niebur, Hsiao, & Johnson, 2002; Salinas & Sejnowski, 2001). However, it should be noted that other neurophysiological studies of attention showed that changes in the focus of attention are accompanied by modulation in neuron's firing rate (reviewed by Reynolds & Chelazzi, 2004). Further research is needed in order to resolve these discrepant findings.

How is synchronization detected in neurophysiological recordings? Neuroscientists use cross-correlation histogram or cross-correlogram to study the joint activity of neurons (Salinas & Sejnowski, 2001). It is constructed from the spike trains of two neurons. Cross-correlogram shows the probability of one neuron firing a spike, τ milliseconds before or after a spike from another neuron. τ is called the time shift or time lag. When the two spike trains are independent, the cross-correlogram is flat; if there is any covariation in the spike trains, one or more peaks appear. For instance, a peak at zero time shift means that the two neurons tend to fire at the same time more often than expected by chance. Usually, cross-correlograms are corrected so that peaks caused by covariations in mean firing rate, computed over several tens or hundreds of milliseconds, are eliminated. Typically, cross-correlograms from experimental data have single peaks, although they can vary in width from a few to several hundred milliseconds. However, an important problem with cross-correlation method is that it requires large amounts of data in order to resolve significant deviations from independence and alternative techniques are being developed in order to overcome this and other limitations (Salinas & Sejnowski, 2001). Furthermore, several other factors could produce peaks in cross-correlograms that give the appearance of synchrony. These factors include slow response variability, correlated response latency and correlated visual responses associated with fixational eye movements (Shadlen & Movshon, 1999). All these phenomena can be quite prevalent in visual cortical recording experiments and their contribution to the observed synchrony is difficult to establish.

Mathematical models

Important criticism of TCH is that it lacks concrete algorithm on how synchronization is achieved. There are several attempts to solve this problem (Abeles, 1991; Eckhorn, Reitboeck, Arndt, & Dicke, 1990; Phillips & Singer, 1997; Wang & Terman, 1995, 1997; Watanabe, Aihara, & Kondo, 1998; Watanabe, Nakanishi, & Aihara, 2001). We will focus on one such formalization of TCH known as LEGION (Locally Excitatory Globally Inhibitory Oscillatory Network, Wang, & Terman, 1995). Building block of LEGION is a mutually connected excitatory and inhibitory neuron whose activity oscillates around certain mean value. Oscillation is not imposed externally but it is an emerging property of a dynamic interplay between excitation and inhibition. It is an example of a dynamical system known as a relaxation oscillator. Such system is characterized by alternation between periods of time during which little is changed and periods of abrupt change in dynamics.

Physical interpretation of relaxation oscillator is a seesaw with two buckets of water placed on its ends (named A and B). On one end of the seesaw is a water source that pours water in a bucket A. The bucket A is designed so as to contain the water only when it is in the upper position. When it is in the lower position, water is spilled out. On the other end of the seesaw is a bucket B which contains constant amount of water. When the bucket A is heavy enough to overweight the bucket B, bucket A will drop to the lower position and water will spill out. After the water spills, the bucket B will become heavier than the bucket A and it will force the seesaw to change the position. In other words, the bucket B will drop to the lower position and the bucket A is lifted to the upper position which is close to the water source. After a while, the bucket A will become heavy again due to the fact that new water is pouring in it. When it becomes heavier than the bucket B, the bucket A will induce another change of the seesaw, that is, it will drop to the lower position again and the bucket B will be lifted to the upper position. This process induces indefinite cycling of transition between the two positions of seesaw: one in which bucket A is on the lower position and another state where bucket B is on the lower position (Wang, 1999).

When two relaxation oscillators are connected via excitatory connections their oscillation will synchronize. That is, their initial phase difference of oscillation will disappear. When many oscillators are connected they will all synchronize together. In order to achieve temporal segregation of oscillation of groups of neurons, global inhibitor is introduced. Its function is to keep different groups of neurons from synchronizing its activity. In this way, synchronization is restricted to a group of neurons that represents the same object. Neurons that code different objects desynchronize its activity (Wang & Terman, 1995, 1997). Figure 1 illustrates how synchronization among groups of neurons is achieved. In this example a two-dimensional network of relaxation

oscillators is used. Input to the network is a visual scene containing three distinct objects: Mountain, Sun, and Tree. Figure shows neurons' activity as a function of time. At the beginning, all neurons oscillate asynchronously. However, group of neurons representing Sun starts to synchronize its activity and at the same time desynchronizes from other groups. When neurons that code Sun are inhibited neurons coding Tree start to synchronize. Note that transition to active state starts at different times for different groups which indicate desynchronizations. Global inhibition also shuts down background activity (4th row). Bottom row shows activity of global inhibitor which is essential for desynchronization.

Wang and Terman (1997) provide a detailed mathematical analysis of the synchronization properties of the LEGION. They proved several theorems that specify conditions under which synchronization is achieved. One condition is that all inputs must arrive at the same time in order to achieve synchronization. When small temporal differences were introduced, LEGION could not synchronize its activity (Fox, Jayaprakash, Wang, & Campbell, 2001). Another problem for LEGION is that it cannot represent hierarchical structure of the objects. However, humans are flexible at representing parts of the objects. We may think of a human body as a single object. But we can partition it into smaller objects like head, body, arms and legs. Furthermore, head could be further divided into eyes, nose, mouth, etc. We may easily change the focus of attention to different level of abstraction which implies that perceptual representation requires more sophisticated mechanisms. On the other hand, LEGION could represent only one level of perceptual analysis. When some nodes are synchronized they could not be desynchro-

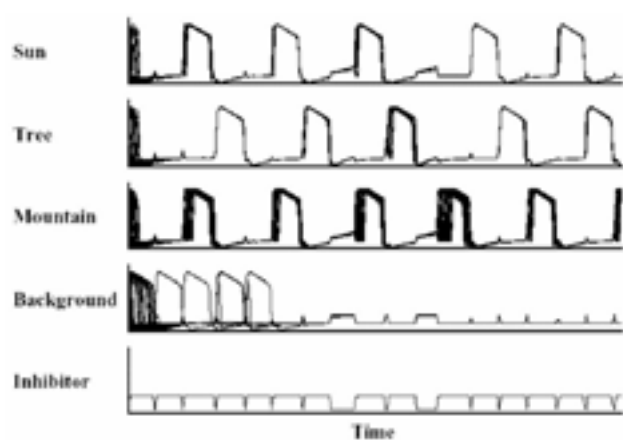


Figure 1. Synchronization of activity of groups of neurons coding different object in LEGION. From "Image segmentation based on oscillatory correlation" by D.L. Wang and D. Terman, 1997, *Neural Computation*, 9. Copyright 1997 by MIT Press. Reprinted with permission.

nized latter for different purpose. For instance, when nodes coding the human body are synchronized they could not, at the same time, be desynchronized in order to represent different parts such as head, arms and so on.

LEGION was also applied to the image segmentation problem. The task was to partition digital image into regions corresponding to objects. Wang and Terman (1997) found that LEGION could not represent more than 5 objects at the same time. Reason is that relaxation oscillator could not be in a passive state for an arbitrary long time and it needs to switch between states in a short, finite amount of time. This observation led Domijan (2004) to propose a different model of visual segmentation based on the rate code. His model also includes a recurrent network of mutually connected excitatory and inhibitory neurons. However, the standard model of a neuron is extended with the dendritic inhibition. The mechanism of dendritic inhibition assumes that dendrites operate as independent computational devices with their own input-output relationships (Häusser & Mel, 2003; London & Häusser, 2005; Poirazi, Brannon, & Mel, 2003). Output of dendritic computation is passed to the neuron, which integrates signals from different dendrites. Dendritic inhibition allows separation of activity amplitude for different groups of neurons. Therefore, different objects are represented by different rate of activity of neurons. On the other hand, neurons that represent the same object have the same activity level.

The segmentation network operates by spreading activation among excitatory neurons until activation hits an in-

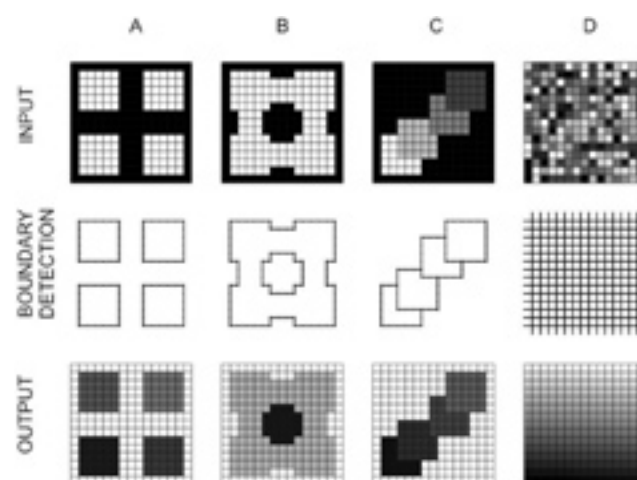


Figure 2. Computer simulations of the network for visual segmentation which uses firing rate or activity amplitude to label objects in the visual field. Simulations showed that the network does not have capacity limitations for representing surfaces. From "Recurrent network with large representational capacity" by D. Domijan, 2004, *Neural Computation*, 16. Copyright 2004 by MIT Press. Reprinted with permission.

hibitory obstacle provided by a separate network which is sensitive to object's boundary. Network for boundary detection simulates the properties of simple and complex neurons observed in monkey's primary visual cortex which are sensitive to object's boundaries. Interaction between the network for boundary detection and the segmentation network achieves proper object's representation because all neurons which participate in the representation of the same object will obtain the same level of activity. Therefore, all spatial locations occupied by the object will be bounded together in visual representation by the same level of firing rate. Computer simulations of the proposed network architecture for visual perception showed that it is able to segment visual scene into arbitrary number of visual objects. This is illustrated in Figure 2 where four different input configurations are supplied to the network. Network for boundary computation detects object's edges (middle row) and disable activity propagation in the output network layer (bottom row). When there are four different surfaces present in the input (Figure 2a), the output layer assigns different amplitude level to every surface. Different activity amplitudes are depicted by different shades of grey with white as maximal amplitude and black as minimal amplitude. When surfaces are connected as in the Figure 2b they all receive the same activity amplitude because they are now a part of the same surface. Network does not have a problem in segmenting even overlapping surfaces (Figure 2c). The most difficult test for the network is the noisy pattern where every patch or pixel is its own object (Figure 2d). However, network assigns different activity amplitude to all patches which illustrate the network's ability to represent visual environment without capacity limitations. The new model is also applied on digital images of real scenes where it shows good segmentation results (Domijan, 2004).

The central issue is whether there are any limitations for representation of visual scenes in the visual system. In other words, are there any limitations to the number of objects that humans could process? Answer to this question will allow us to distinguish the merits of the proposed models of visual segmentation. Our experience of rich and detailed representation of visual scene suggests that we do not have a problem with visual processing of arbitrary many entities. However, recently discovered phenomenon of change blindness indicates that our intuition might be wrong.

Change blindness

Change blindness refers to our inability to detect large changes in visual environment when they are not in the focus of attention (Simons & Levin, 1997; Simons & Rensink, 2005). It is usually demonstrated by a pair of pictures that are presented in rapid succession separated by a brief blank display. Both pictures depict the same visual scene but in one picture certain object is deleted. The task of the observers is to discover differences in pictures. It is surprising to

find how difficult it is to solve this task. Most people believe that they would easily notice such large changes and they are surprised when confronted with this task. When attention is directed to a part of image where deleted object is, the task is easily solved, which implies that attention is necessary to detect the change. This is consistent with the fact that the most dramatic examples of change blindness occur in situations where the change is unexpected. For instance, during a movie watching, if an actor in a scene is changed during a shift in a camera position, most observers do not notice that the actor is replaced by another person. In a real-life situation, when a conversation partner is replaced by a different person, many observers report that they do not notice anything unusual. These findings of change blindness in natural conditions suggest that it is not a by-product of artificial interruptions between two successive displays. Rather, it is a general failure to retain and/or compare information across successive views of the same visual scene (Simons & Ambinder, 2005; Simons & Rensink, 2005).

Some theorists argue that change blindness provides the evidence for a sparse visual representation (Rensink, 2000, 2002) and other even goes so far to suggest that there are no representations in vision at all (O'Regan & Noe, 2001). According to these claims construction of detailed representation would be a wasting of processing resources and it is easier to construct dynamic representation of just a part of the scene that is currently relevant. Instead of using neural tissue, external world is used as a representational medium from which only small part is extracted as needed. This is in accordance with LEGION limitations for visual segmentation. But not everyone agrees on the implications of change blindness (Lamme, 2003; Simons, 2000). It is possible to have a detailed representation that is simply overwritten every time a new scene or image is encountered. Another possibility is that when two different pictures are presented both are represented in detail but the process of comparison between them is limited in capacity. Evidence for these explanations has been found in several behavioral studies (Hollingworth, 2003; Hollingworth & Henderson, 2002; Landman, Spekreijse, & Lamme, 2003; Simons, Chabris, Schnur, & Levin, 2002). Therefore, change blindness could not be taken as an evidence for sparse representation (Simons & Ambinder, 2005; Simons & Rensink, 2005), and consequently as a confirmation of the LEGION model, or more generally as a confirmation of neural synchronization as a mechanism of visual perception.

Other behavioral evidence

Irrespective of the discussion on representational capacity of the visual system, it is an interesting research question whether there is any behavioral evidence for neural synchronization as a mechanism of visual perception. If visual perception depends on the synchronization, visual system should be sensitive to temporal modulation of input. Fahle (1993) tested this idea by presenting two alter-

nating pictures containing figure or background. Figure was created by cutting small central patch from a field of randomly (or regularly) spaced dots. Therefore, if figure and background would be presented simultaneously they would be indistinguishable. However, two pictures alternate with different temporal asynchrony and observers were able to discern figure region even for temporal difference of 7 ms. In a similar vein, Roger-Ramachandran and Ramachandran (1998) used two pictures containing black and white dots. In the first picture, white dots occupied the upper portion of the display and black dots occupied the lower portion. In the second picture, contrast of the dots is reversed and white dots occupied the lower portion of the display and black dots occupied the upper portion. In both pictures there is a clear textural border between the dots. When two pictures alternate in rapid succession, black and white dots could not be distinguished. They merged in a uniform grey field. However, observers still report that they see a border, separating the upper from the lower portion of the display. Rogers-Ramachandran and Ramachandran (1998) termed this effect the 'phantom contour'.

Both studies point to the fact that perceptual system is sensitive to small temporal differences in the input arrival. On the other hand, Kiper, Gegenfurtner and Movshon (1996) showed that in texture discrimination task, temporal asynchrony does not play any role because performance was the same irrespective of the temporal modulation of the figure and background region. They found that the only relevant variable is the spatial orientation difference between texture elements. Fahle and Koch (1995) also failed to find support for the utility of temporal cues in perceptual organization.

Problem with previous studies is that they contain, in isolation, an obvious form cue. Namely, one of the pictures contains a figure element. Therefore, it is possible that visual system is sensitive to the onset of the figure element and not to the temporal difference between the figure and ground. In order to remove spatial cues present in previous research and to find unambiguous support for sensitivity to temporal synchrony, Lee and Blake (1999) created a new display containing a set of randomly spaced elliptical (Gabor) patches. These patches contain contrast borders, which move perpendicular to the shorter axis of the ellipse. The border moves back and forth and changes direction of the movement randomly. Exception is a set of central patches, whose contrast borders change the direction of the movement simultaneously. In this display there is no static form cue, but observers still perceive central patches as a figure. Lee and Blake (1999) claim that their display produces figure solely by temporal signals and that it is a strong evidence for temporal sensitivity of the visual system. However, Farid and Adelson (2001) questioned their conclusion. They showed that the display of Lee and Blake (1999) contained a subtle spatio-temporal cue that promotes grouping. It becomes evident when the display is filtered by the spatio-temporal filter used in a model of motion perception. Therefore, at the

moment it is not clear whether a visual system could process fine grained temporal differences in the input or it just relies on the mechanisms of motion perception. For recent reviews of relevant experiments and their interpretations see Blake and Lee (2000) and Farid (2002).

There is another interesting perceptual phenomenon relevant for the discussion of the status of neural synchronization. Moutoussis and Zeki (1997) discovered that different perceptual attributes such as color, form and motion are processed at different speed. They showed that color is processed faster than orientation for 60 ms, color is processed faster than motion for 118 ms and orientation is processed faster than motion for 50 ms. This phenomenon is termed perceptual asynchrony and it could be illustrated by a stimulus which changes two attributes with a certain temporal asynchrony. For instance, a rotating disk could change the direction of rotation and change the color. When color is changed before the direction of rotation, observers report that changes occurred simultaneously. The existence of perceptual asynchrony suggests that neural synchronization could not underlie the binding of perceptual features because we perceive them as simultaneous events occurring at different times.

Summary

Arguments for and against neural synchronization as a mechanism of visual perception could be summarized as follows (see Table 1):

As it can be seen from the preceding summary, TCH is still a controversial hypothesis, which deserves further investigations. There are many investigations that document the existence of synchronization of oscillatory neuronal activity in the nervous system (Usrey & Reid, 1999). However, its relation to behavior and to visual perception in particular, is still unclear. Central problem is that a direct test could not be made because neurophysiological investigations are not performed on humans, and animals could not tell us what they are experiencing when they receive stimulation. Evidence obtained thus far is contradictory at the neurophysiological and behavioral level. There are many methodological problems that remain to be resolved (Shadlen & Movshon, 1999). For instance, it is not entirely clear which is an appropriate statistical test for the detection of synchronization in multi-unit recordings (Breakspear, Williams, & Stam, 2004). Techniques for recording electromagnetic brain activity, such as EEG and MEG, may offer new insights into the feature binding problem because they can bridge the gap between the behavioral and neural level of analysis (Ward, 2003). For instance, Tallon-Baudry and Bertrand (1999) suggested that induced gamma activity is relevant for the construction of object representation. Induced gamma activity shows a high degree of spatial and temporal flexibility that depends on the experimental tasks involved. It seems to reflect interactions between different

Table 1

Summary of arguments for and against cortical synchronization as a neural mechanism for visual perception

	PRO	CONTRA
NEUROPHYSIOLOGY	<ul style="list-style-type: none"> • Stimulus dependence of neural synchronization • Greater amount of synchronization among cells that are closer together or that are sensitive to similar features which is reminiscent of the Gestalt grouping of proximity and similarity 	<ul style="list-style-type: none"> • Neural synchronization in retina and LGN which indicates that this is not restricted to cortical areas where perceptual integration took place (Ghose & Freeman, 1992) • Figure-ground separation is signaled by firing rate modulation in monkey's primary visual cortex (Lamme, 1995) • Methodological problems which prevent direct test to be made (Shadlen & Movshon, 1999)
MATHEMATICAL MODELING	<ul style="list-style-type: none"> • Precise formulation • Detailed analysis (theorems) • Oscillatory dynamics 	<ul style="list-style-type: none"> • Limited capacity • Inability to represent hierarchical patterns • Inability to process temporal variations in the input
BEHAVIORAL INVESTIGATIONS	<ul style="list-style-type: none"> • Change blindness (implies sparse representation) • Perceptual grouping based on temporal cues (implies sensitivity to small temporal difference) 	<ul style="list-style-type: none"> • Change blindness could be the consequence of overwriting detailed representation • Temporal grouping could be the consequence of the mechanisms of motion perception (Farid, 2002; Farid & Adelson, 2001) • Perceptual asynchrony (Moutoussiss & Zeki, 1997)

brain areas that encode the different features of an object and have their own specific function in relation to the task performed. Tallon-Baudry and Bertrand (1999) reviewed the evidence that the strength of the gamma signal increases when participants passively view coherent moving patterns. Increase in gamma activity is also observed in the response to coherent versus incoherent static stimuli when participants were engaged in active tasks.

At the theoretical level, it is an open research problem whether it is possible to construct a model based on the synchronization of oscillatory activity which would not show limitations described above. On the other hand, capacity limitations could be considered as an advantage when modeling cognitive processes such as attention and short-term memory. Therefore, it may be the case that initially proposed solution to the problem of perceptual segmentation is better suited for modeling more complex cognitive functions while the problem of perceptual integration requires a different coding scheme. Another task is to try to find out whether it is possible to construct a model based on the firing rate code which would be able to perform perceptual grouping. Preliminary work done by Domijan (2004) showed that this is possible if a model of neural information processing is augmented with the mechanism of dendritic computation. In the model, perceptual groups are labeled with different

amplitude of neural activity and kept segregated by the dendritic inhibition. The same mechanism could also be applied in the feature binding of information from different sensory maps using the firing rate code (Domijan, 2003). The problem of combinatorial explosion discussed for conjunctive representation is avoided by using attention as a signal to combine different levels of neural activity in feature maps into a unique object representation. This representation is dynamically formed depending on the task demands and does not require special neurons for coding of all possible feature conjunctions.

One interesting possibility is that synchronization and rate code are not mutually exclusive representational formats and they could simultaneously support different types of computations. For instance, Lu, Liang and Wang (2001) identified two distinct populations of neurons in a primate auditory cortex. One population use neural synchronization to represent slowly varying sound sequences, and another population use the rate code to represent rapidly occurring sound events. Moreover, synchronization could coexist with the rate code in the same neuron. Evidence for this proposal is obtained in studies of rat hippocampus. Huxter, Burgess and O'Keefe (2003) showed that hippocampal pyramidal neurons use temporal and rate coding to represent different aspects of the animal's environment or behavior. Firing rate

represents the rat's speed of movement in space, and independently synchronization of spikes signals the rat's location in space. Masuda and Aihara (2003) proposed a model of neural network which is able to simultaneously utilize rate code and temporal code. Further research should explore how general is this dual coding strategy.

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