Dynamic Binding of Visual Features by Neuronal/Stimulus Synchrony

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Abstract. When people see a visual scene, certain parts of the visual scene are treated as belonging together and we regard them as a perceptual unit, which is called a “figure”. People focus on figures, and the remaining parts of the scene are disregarded as “ground”. In Gestalt psychology this process is called “figure-ground segregation”. According to current perceptual psychology, a figure is formed by binding various visual features in a scene, and developments in neuroscience have revealed that there are many feature-encoding neurons, which respond to such features specifically. It is not known, however, how the brain binds different features of an object into a coherent visual object representation. Recently, the theory of binding by neuronal synchrony, which argues that feature binding is dynamically mediated by neuronal synchrony of feature-encoding neurons, has been proposed. This review article portrays the problem of figure-ground segregation and feature binding, summarizes neurophysiological and psychophysical experiments and theory relevant to feature binding by neuronal/stimulus synchrony, and suggests possible directions for future research on this topic.


Keywords: binding problem, neuronal synchrony, stimulus synchrony, temporal phase, flicker-induced depth

Introduction

When humans and other animals see an object, they receive many visual stimuli from the object onto their retinæ. On the retina, the outline of the object is not clear, and there is only a mosaic of stimuli from which their brain receives the necessary information to perceive the object. In the brain, features that are not needed for perceiving of an object are disregarded as noise, and only suitable features are regarded as signal and bound together into a coherent perceptual unity.

The process by which a perceiver binds many visual features together into coherently segregated figures is termed “figure-ground segregation” by Gestalt psychologists (e.g., Kofka, 1935; Köhler, 1947). According to Gestalt psychologists, “figures” tend to be complete, coherent and to have shape. While “ground”, all the remaining parts of the visual field, appear to be less distinct and to have no shape. Consider an example of a lion that must quickly locate a zebra, his prey, in a complex natural environment. If there is only one zebra and no other object in the visual field of the lion, it is very easy for the lion to see the zebra, because the clear discontinuity between the visual features of the zebra’s body and the environment helps to delineate the zebra. In most cases, however, it is not so easy to determine the boundary between the zebra and the surrounding environment, because a zebra has a pattern and colors that camouflage him in its natural environment (Fig. 1). As Figure 1 shows, it is generally difficult to conclusively determine which features should be bound together as figure and which features should be ignored as ground.

The theory of “binding by neuronal synchrony” (in

Fig. 1 A zebra in natural environment. It must be noted that the mosaic of retinal stimuli per se cannot determine which areas should be perceived as a zebra. Therefore the brain must segregate areas which will constitute a zebra from other areas which will be regarded as the surrounding environment.
this review, shortened to “synchro-binding theory”) argues that figures are organized through binding of various features in a visual scene and are represented in the brain by synchronization of neuronal firing (“neuronal synchrony”) of spatially separated neurons encoding different features. The synchro-binding theory has been proposed by a small number of theoretical researchers. One of the earliest studies on the synchro-binding theory appeared in 1974 (Milner, 1974). But the theory was not widely accepted until the end of the 1980’s. Around 1989, however, two independent laboratories in Germany conducted experimental studies that support the theory. The results of these experimental studies triggered various studies, which attempted to confirm what the theory predicted.

Although opinions regarding the synchro-binding theory are not unified, it attracts the attention of researchers in a wide variety of fields such as cognitive science, neuroscience and philosophy as well as perceptual psychology, because the theory helps to predict the representation of figures in the brain. In this review, I aim to summarize various studies on the synchro-binding theory, focusing on how figures are represented in the brain. Therefore, a review of the results of a great number of neurophysiological studies on invertebrates or computer simulations which have no direct relationship to psychology were omitted. Instead, most neurophysiological studies on vertebrates and psychophysical studies were reviewed in detail and controversial points arising from these studies were summarized, and possible directions for future research are suggested.

Two Theories on the Representation of Figures in the Brain

It is known that there are many kinds of neuron in the brain, and information with different modalities (or regarding different features) is processed by different neurons. In the mammalian visual cortex, there are many neurons that seem to share different roles in visual processing and most of them respond only to “preferred features” in a visual scene. For example, neurons in the primary visual cortex increase their firing rate when a “light bar” of a certain angle is shown, and those in area V4 respond to stimuli of a certain color. Based on these facts, it is widely accepted that a visual feature is encoded by the firing of a neuron specific for the feature. In most cases, such feature-selective neurons respond to a feature only when it is presented in a limited area in a visual field that is called the “receptive field”.

Although most neuroscientists agree that visual features are encoded by feature-selective neurons, they have not reached a consensus on the encoding of figures. There are two kinds of major theory on the encoding of figures. One is the theory that figures as well as features are encoded by single neurons. The other is that the firing of a neuron encodes features that are constituent parts of figures, but it does not encode the figure itself. The latter theory hypothesizes that figures are represented by functional relationships between features encoded by feature-encoding neurons.

The former and the latter theories are reviewed below.

(1) Theory of Encoding of Figures by Firing of a Specific Neuron: “Theory of Grandmother Cell”

This theory emphasizes the idea that figures are encoded by specific neurons (e.g., see Barlow, 1972). Such a figure- (object-) encoding neuron is sometimes called a “grandmother cell”. The name came from the imaginary neuron that is supposed to fire during people see their grandmother’s face. Neurophysiologists who had succeeded in identifying many kinds of “feature-encoding neurons” believed that there should also be “figure-encoding neurons” somewhere in the higher visual areas in the brain. And in fact, several grandmother cell-like neurons were found. For example, neurons which respond to human faces were found in the superior temporal sulcus (STS) which is known to be one of the higher visual areas (Bruce et al., 1981; Perrett et al., 1982).

However, detailed examination of such neurons revealed that some of them responded to parts of a face (eyes, mouth, …) as well as the whole face, suggesting that these neurons do not encode and identify a face per se, but respond to certain features of a face. Because no convincing evidence of the existence of grandmother cells has been found, many researchers doubt the existence of such figure-encoding neurons.

Moreover, the theory of grandmother cells has several problems, even if such neurons exist. For instance, when people recognize faces, they can discriminate between numerous faces, and in an extreme case they can immediately recognize the unknown face of a person they meet for the first time. If every face is recognized by the firing of a specific neuron, vast numbers of neurons encoding unknown faces must be present in the brain before meeting an unknown person. It is unlikely, however, that vast numbers of such neurons encoding unknown faces are stored in the brain (see also discussion by Singer, 1994b). There is another difficulty in the theory of grandmother cells even in the case of recognition of well-known faces. Assume that a face consists of three parts, outline, eyes and nose, and that there are only two characteristics for each part, such as, round/square outline, sparkling/dull eyes and large/small nose. In this case, there are a total of eight possible faces \((2 \times 2 \times 2 = 8)\), so theoretically all eight faces can be recognized if there are eight kinds of grandmother cells.
specific for them. In reality, humans can discriminate between hundreds of characteristics for each part. If there are one hundred characteristics for each part, there must be 1,000,000 grandmother cells \((100 \times 100 \times 100 = 1,000,000)\) to recognize all of the faces.

Thus, the major problems of the theory of encoding by grandmother cells are that it cannot explain the vast numbers of neurons required, and it cannot deal with figures which are not present in the stock of figures with which a person is likely to come in contact.

(2) Theory of Encoding of Figures by Relationships between Features: Theory of Binding by Neuronal Synchrony

Next, I will examine another theory, which proposes that figures are encoded by relationships between features that are encoded by feature-encoding neurons. I have already mentioned that neurons that seem to directly encode figures have not been identified to date. At first glance, it seems that a figure can be represented, only if there are full sets of cortical neurons that respond to features composing a figure. However, this is not necessarily the case. To explain this, I will show an example of the recognition of a picture of a simple face (Fig. 2 (A)). When we see the picture, neurons in the primary visual area respond to bar stimuli originating from the contours of each part of the face. In higher visual areas, there may be neurons which respond only to an eye (or a mouth, a nose, etc.), as suggested by the results of neurophysiological studies. While a person perceives the face, full sets of feature-encoding neurons required to generate the figure of a face may fire. Then, imagine that the picture cut into pieces, thrown into a bag and shuffled well, then turned out and scattered onto a sheet. The rearranged parts do not look like a face anymore (Fig. 2 (B)). Imagine the neuronal activity in the brain on seeing this “shuffled face”. It is likely that the full set of feature-encoding neurons will fire, although this time you do not in fact perceive a face. This illustration suggests that the existence of a full set of visual features from the constituent parts of an object is the only condition necessary to construct a figure. Without suitable relationships among parts, a figure would not be organized in the brain, even if the brain has received visual features from the parts. Therefore, for representation of a figure in the brain, the problem is how the relationships between the parts are represented.

It is possible that the relationships between features are encoded by anatomical connections between neurons. For flexible recognition of figures, however, it is required that features, even those with large differences, can be quickly bound together. For this reason, anatomical connections between neurons seem to be insufficient for encoding the relationship between features, because they are static and cannot change in a short time.

The synchro-binding theory, which is one of the theories of feature encoding by the relationship between features, asserts that relationships between features are represented by the state of synchronous firing of feature-encoding neurons, not by anatomical connections between them. The basic concept of the synchro-binding theory is as follows. Firstly, individual feature-encoding neurons can participate at different times in the representation of different figures. And thirdly, representation of figures for objects, which a perceiver previously did not encounter, can be constructed by feature-encoding neurons which are present in the brain (e.g., Singer, 1994b, 1994c).

Binding Problem

Perceptual psychologists and neuroscientists have long been interested in the so-called “binding problem”, that is the problem regarding how features are bound together in the brain (e.g., Crick and Koch, 1990; Nelson, 1995; Sejnowski, 1986; von der Malsburg, 1981). One of the reasons the synchro-binding theory has been widely accepted is that it seems to solve the binding problem. In this section, the binding problem is introduced in relation to the synchro-binding theory.

To explain the binding problem, imagine the perception of a moving vehicle. Assume that a vehicle is perceived as a figure consisting of three features: color, shape and direction of movement (Fig. 3). Neurophysiological studies showed that neurons in area V4 and those in area MT (middle-temporal area) respond to color and motion, respectively. There are probably neurons that respond to
the shape of a vehicle in area IT (inferotemporal area). Therefore, if people see “a red car moving rightward” and “a blue trailer moving leftward” simultaneously in a visual field, V4 neurons specific to red and blue, MT neurons specific to rightward and leftward motion, and IT neurons specific to the shape of the car and trailer must fire simultaneously. If a feature binding mechanism does not exist and features are bound at random, people may see a figure that does not exist in reality such as “a red trailer”. In the brain, there must be mechanisms by which only features from the same object are bound together. The synchro-binding theory predicts that binding is achieved by neuronal synchrony of cortical neurons that respond to different features.

What is this mechanism? The synchro-binding theory can be used to predict the mechanism. As explained above, the theory asserts that feature binding is achieved by neuronal synchrony of feature-encoding neurons. In other words, the temporal coherence of the firing of feature-encoding neurons is an indication that features are dynamically related (e.g., Gray, 1994; Grossberg, 1980; Hebb, 1949; Shimizu and Yamaguchi, 1987; Singer, 1993; von der Malsburg, 1981). Let us try to apply the synchro-binding theory to the above example of the representation of vehicles. According to the theory, if firing of neurons responding to red and those responding to the form of the car is synchronized, it means that the color red and the form of the car are related and the red car is represented as a figure in the brain. This type of encoding makes it possible to bind a vast number of features flexibly and dynamically.

To date, many studies on the synchro-binding theory have been published and there are several variations of the theory among researchers. Next, I will review the history of studies of the synchro-binding theory.
A Historical Outline of Studies on the Synchro-Binding Theory

As early as the 1940's, Sherrington (1941) and Hebb (1949) proposed the idea that sensory and motor patterns should be represented by cooperative firing of neuronal assemblies, not by the activity of individual neurons. Their hypothesis and the synchro-binding theory were similar in the sense that both of them asserted that the function of each region in the brain is integrated by dynamical binding of neuronal assemblies, although in Sherrington and Hebb's time there was no direct comment on the binding by neuronal synchrony. Since the 1960's, neurophysiological studies of the cerebral cortex of experimental animals were carried out and it was found that many cortical neurons respond to particular features, which was very important and led to the proposal of the synchro-binding theory. Although it is not widely known among neuroscientists, Milner proposed a theory very similar to the synchro-binding theory in Psychological Review in 1974, long before the results of neurophysiological studies supporting the synchro-binding theory were published (Milner, 1974).

A few reports also predicted the oscillatory process in the brain in the 1960's and the 1970's, although they did not refer to the process of neuronal synchrony. Harter (1967) studied the mechanism of time perception and considered that in the human brain, there are intrinsic clocks that order external events and relate them temporally. He thought that time perception might occur via certain oscillatory mechanisms in the brain. According to him, there are two kinds of oscillatory mechanisms. One is the “excitability model” which assumes the induction of oscillatory rhythm by an external stimulus and the other is the “scanning model” which assumes that oscillatory rhythm exists independently of an external stimulus and the stimulus cannot affect the oscillation. In both models, a cycle of oscillation is assumed to be a unit of temporal integration of events. Poppel's (1970) study is also notable. Using psychological experiments, he plotted the reaction time of experimental subjects on a histogram and found that the temporal difference between successive peaks of the histogram had a mode value of 30 ms. On the basis of this result, he hypothesized that in the brain there is an oscillatory process around 30 Hz which quantizes time and integrates sensory information discretely. The importance of his work is evident when one considers that after about 20 years, neurophysiologists found the 40 Hz oscillatory process using a neurophysiological recording technique (see also Poppel and Logothetis, 1986; Poppel, 1988; Poppel et al., 1990).

In the 1980's, the number of studies on the computational theory of the brain increased dramatically and theoretical studies on the synchro-binding theory began to appear. In particular, studies by von der Malsburg are among the most famous ones on the synchro-binding theory, and they have been cited widely (von der Malsburg, 1981; von der Malsburg and Schneider, 1986). He proposed solving the problem of figure-ground segregation with the concept of “binding by neuronal synchrony”. At nearly the same time, Shimizu et al. independently proposed a similar theory (Shimizu et al., 1985; Shimizu and Yamaguchi, 1987). They assumed that neurons in the primary visual cortex fire in an oscillatory pattern, and a figure is self-organized through entrainment of these neuronal oscillations. It is notable that based on their theory, they made a computational model of the brain in which a structure, the “hypercolumn”, in the primary visual cortex was implemented. In their model, it was assumed that entrained neuronal clusters represent a figure and the remaining unentrained neurons represent ground.

As I have mentioned, there were several theoretical studies on the synchro-binding theory in the middle of the 1980’s. However, until the end of the 1980’s, there were no neurophysiological studies carried out, because simultaneous recording of multiple neurons which was essential for examining the validity of the theory was very difficult for technical reasons and it was time-consuming to analyze the data.

In 1988-89, two experimental studies in Germany, which were independently conducted, broke the deadlock. Using anesthetized cats, Eckhorn et al. (1988) and Gray et al. (1989) found that firing of neurons in the primary visual cortex oscillates stimulus-dependently and the oscillatory firing is synchronized under certain stimulus conditions. The results of these two studies suggested the validity of the synchro-binding theory for the first time and had an impact on other studies. Because, many researchers were aware of the limits of the theory of grandmother cells and were interested in an alternative theory to explain the representation of figures in the brain (Abeles et al. 1993; Barinaga, 1990; Engel et al., 1992; Singer et al., 1990; Stryker, 1989).  

As an example of an experimental paradigm for examining the synchro-binding theory, I will review the excellent experimental study of Singer and his colleagues (Gray et al., 1989) (Fig. 4). Assume that there are two moving light bars in a visual field. If each bar moves randomly, these two light bars seem to be independent of each other. If they always move together keeping a constant configuration, however, it seems that they are components of an object (a figure). Gray et al. (1989) recorded activity of neurons responding to these bar stimuli in the primary visual cortex using multiple electrodes. They examined the correlation of the timing of firing, where one of three methods of presentation of stimuli was used: (1) two light bars move in opposite
directions (Fig. 4 (A)); (2) two light bars move in the same direction (Fig. 4 (C)); and (3) a long light bar moves instead of two short light bars (Fig. 4 (E)). When two light bars move in opposite directions, they are perceived as two independent objects, whereas when they move in the same direction, it seems as if one large light bar consisting of two short parts is moving. Cross correlation analysis showed that in the former case firing of the neurons was not synchronized (Fig. 4 (B)), while in the latter case neurons fired synchronously (Fig. 4 (D)). Furthermore, the experiments of Gray et al. showed that when a long light bar crossed (Fig. 4 (E)), neuronal synchrony occurred to a higher degree than when two light bars stimulated the two receptive fields (Fig. 4 (F)). Following this study, Singer and his colleagues further accumulated neurophysiological data supporting the synchro-binding theory (e.g., Engel et al., 1991a, 1991b; Gray and Singer, 1989).

Inspired by these experimental studies, computational studies were also carried out and a vast number of computational studies suggested a significant role for the neuronal oscillation or neuronal synchrony in the brain (Eckhorn et al., 1990; Kazanovich and Borisyuk, 1994; König and Schillen, 1991; Neven and Aertsen, 1992; Schillen and König, 1991; Schuster and Wagner, 1990a, 1990b; von der Malsburg, 1988; Yamaguchi and Shimizu, 1994).

Following the pioneering experimental studies by Singer et al. (Engel et al., 1991a; Engel et al., 1991b; Gray and Singer, 1989; Gray et al., 1992) and Reitböck et al. (Eckhorn et al., 1988; Eckhorn et al., 1989; Eckhorn and Schanze, 1991), many neurophysiological studies on the synchro-binding theory have been published. In the experimental studies using anesthetized cats, it was reported that neuronal synchrony could be found in many visual areas of the cerebral cortex, that is in area 17 (primary visual area), area 18, area 19 and PMLS (Eckhorn et al., 1990, 1992; Engel et al., 1990, 1991a, 1991b; Gray et al., 1990). It was found that neuronal synchrony occurred between spatially separated neurons not only within a visual area, but also between two or more different visual areas: for instance, between area 17, area 18 and area 19 (Eckhorn et al., 1988; Kruse et al., 1990; Nelson et al., 1992), between area 17 and PMLS (Engel et al., 1991b), and between area 17 in the left and right hemispheres of the cerebral cortex (Engel et al., 1991a). Among studies in which neuronal oscillation and/or neuronal synchrony were found, there were some differences in the state of oscillation or synchrony. Frequency of neuronal oscillation was 40-50 Hz for cats (Eckhorn et al., 1988, 1990; Engel et al., 1991a, 1991b; Gray et al., 1989; Gray and Singer, 1989), 30 ± 4 Hz for V1 of awake monkeys (Freeman and van Dijk, 1987) and 46 ± 9 Hz for MT of awake monkeys (Kreiter and Singer, 1992). In the V1 (Freeman and van Dijk, 1987) and MT (Kreiter and Singer, 1992) in the brains of awake monkeys, neuronal oscillation could be found only when the signal/noise ratio was high. Later, in the primary visual area of awake monkeys, Eckhorn et al. (1993) recorded faster neuronal oscillation (60-90 Hz) than those recorded in the earlier experiments using cats. They argued that the reason that it was difficult to find neuronal oscillation in awake monkeys was because...
Researchers who had sought to record oscillation focused only on the 40 Hz frequency range, while in monkey brain, neuronal oscillation at a frequency of 60-90 Hz played a role in feature binding.

The fact that the experimental animal was anesthetized raised concerns regarding whether an anesthetized animal can recognize figures (Kulli and Koch, 1991). If such an animal cannot recognize figures, it means that neuronal synchrony during the anesthetized state has no relationship to the cognitive process of figure-ground segregation. To clarify that neuronal synchrony is not an artifact arising from the effects of anesthesia, awake animals were used in experiments. Neuronal synchrony was detected in visual areas of the brain of an awake cat (Raether et al., 1989) and an awake monkey (Kreiter and Singer, 1992).

Not only visual areas, but also other cortical areas such as the somatosensory cortex (Ahissar and Vaadia, 1990), sensorimotor cortex (Murthy and Fetz, 1992), prefrontal cortex (Vaadia et al., 1995) and LGN (Ghose and Freeman, 1992; Podvigin et al., 1992; Neuenschwander and Singer, 1996; Sillito et al., 1994; Singer, 1994a) were examined, and neuronal oscillation and/or neuronal synchrony was shown to occur in many areas in the brain. Recently, it has shown that neuronal synchrony occurs between areas of the visual and parietal cortex, and between areas of the parietal and motor cortex, in the awake cat with zero time-lag (Roelfsema et al., 1997).

Although some studies failed to confirm the existence of neuronal synchrony (Tovée and Rolls, 1992; Young et al., 1992), vast evidence of neuronal synchrony has been accumulated. At present, it is necessary for us to make clear how the neuronal synchrony plays a role in feature binding or other neuronal process.

Functions of Neuronal Synchrony Other Than Figure-Ground Segregation

There are several studies which assert that neuronal synchrony has a function other than figure-ground segregation.

For instance, Pöppel and Logothetis (1986) conducted a psychophysical study and recorded the reaction time of human subjects during a task involving pursuit eye movements. They found that peaks in the histogram of the distribution of reaction times occurred every 30 ms. Although they did not record brain activity, they suggested the existence of an oscillatory process in the brain before neurophysiological studies on the synchro-binding theory were carried out. According to them, oscillation of reaction times at about 30 Hz in the brain, probably, reflecting neuronal oscillation, may play a role similar to that of a clock giving a temporal structure to events. Linás and Ribary (1993, 1994) considered that neuronal synchrony was related to cognitive experience. By magnetic recording of the brain activity of human adults, they observed large 40 Hz magnetic oscillation in the awake and in rapid-eye-movement (REM) sleep states. The 40 Hz magnetic oscillation was reset by sensory stimuli in the awake state but such resetting was not observed in the REM state. Madler et al. (1991) measured the auditory evoked potential (AEP) from human scalps in the awake and anesthetized states. They found stimulus-induced oscillatory components at a frequency of 30-40 Hz in the middle latency range of the AEP in the awake state. The oscillation frequency decreased as the dose of anesthetic was increased and sometimes the oscillatory components of the AEP completely diminished. They speculated that the oscillatory components reflect the state of consciousness. In this respect, Kulli and Koch (1991) also discussed the possibility of monitoring neuronal oscillation at around 40 Hz as a means of monitoring the state of consciousness of patients. Other than the above-mentioned hypotheses, the functional role of the neuronal synchrony is also hypothesized to be multimodal integration (Damasio, 1990), discrimination of tactile texture (Ahissar and Vaadia, 1990), selective attention (Crick, 1984) or state of consciousness (Crick and Koch, 1990).

Psychophysical Studies Related to Stimulus Synchrony

For investigating the validity of the synchro-binding theory, it is necessary to record activities of the brain. However, current non-invasive neurophysiological techniques used for recording human brain activity do not fully satisfy researchers’ needs, because spatial and temporal resolution of the experimental data is not as high as that obtained by spike recording for which only experimental animals can be used as subjects. Therefore it is difficult to obtain data pertaining to human subjects with spatial and temporal resolution sufficiently high to be able to judge whether neuronal firing is synchronized.

In this situation, psychophysical studies with human subjects, in which experimental paradigms were designed on the assumption that manipulation of external timing of stimulus to be synchronized by the experimenter ("stimulus synchrony") will affect internal (neuronal) synchrony. Psychophysical studies are useful to check the validity of predictions of the synchro-binding theory, although the results of these studies can only support (or reject) the synchro-binding theory indirectly.

In general, when carrying out psychophysical studies on the synchro-binding theory it is assumed that if a light spot stimulated “neuron A” and another light spot stimulated “neuron B” in synchrony in the retina, the timing of firing of a cortical neuron which was evoked by inputs originating from neuron A and that of another cortical neuron which was evoked by inputs originating...
from neuron B is coincident. If the assumption that synchronous stimuli in the retina induce neuronal synchrony in the cortex is valid, and the prediction of the synchro-binding theory that a figure is represented by neuronal synchrony of cortical neurons is also assumed, it is natural to think that synchronously presented visual features will be perceived as a figure more easily than asynchronously presented ones. So far only a small number of psychophysical studies on the synchro-binding theory have been carried out and I will review them below.

If the difference between representation of figure and ground in the cortex lies in the difference of timing of firing of neurons encoding figure and ground, imposed differences of timing of presentation of visual features might induce figure-ground segregation. Fahle (1993) examined the ability of human subjects to discriminate between figure and ground based only on asynchrony of onset of presentation of stimuli which will become a figure and those which will become ground. He used visual stimuli consisting of dots forming two shapes: a central rectangle and a surrounding square. These shapes were flickered at a frequency range of 1.3-30 Hz with differences in temporal phase, and there were no differences in features such as luminance, color, texture and motion between these two shapes. Therefore these two shapes were defined only by differences in temporal phase. In each trial, the central rectangle was presented either vertically or horizontally and the subject had to indicate the orientation of the rectangle in a forced choice task. Because differences in temporal phase were the only means of discriminating the central rectangle from the surrounding square, subjects could not perceive the central rectangle when the difference in temporal phase was zero. Fahle (1993) found that the time difference required for subjects to separate figure and ground was around 5 ms in the frequency range used.

Kiper et al. (1996) measured the psychophysical performance of human subjects in a texture segregation task and in a perceptual grouping task and in both tasks the elements comprising the stimuli were flickered and presented under a variety of flicker conditions. The results of Kiper et al. (1996) suggested that neuronal synchrony was unrelated to the processes underlying visual segregation and perceptual grouping.

Fahle and Koch (1995) also studied the relationship between synchrony of stimulus presentation and figure-ground segregation, although the stimuli used were very different from those used in the above psychophysical studies. Fahle and Koch (1995) used a “Kanizsa triangle” which consists of three “packmen” (Fig. 5). If visual information is processed as predicted by the synchro-binding theory, it is expected that the illusory triangle would be perceived more easily when three packmen are presented in synchrony than when they are presented in asynchrony. They examined the effect of synchrony of presentation of packmen on the perception of a Kanizsa triangle. For stimuli, two identical and partially overlapping Kanizsa triangles were used: one triangle consisted of three packmen presented in synchrony and the other consisted of those presented in asynchrony.

**Fig. 5** Effect of synchrony of presentation of visual features on figure binding. Using two identical partially overlapping Kanizsa triangles, Fahle and Koch (1995) examined the effect of stimulus synchrony on figure binding. In the figure of the two overlapping Kanizsa triangles (A), subjects can perceive either the upper or lower triangle predominantly, because the overlap of the two triangles disturbs the ability to perceive the two triangles simultaneously. The method of flickered stimulus presentation is shown schematically (C). The three “packmen” which constitute the upper triangle were presented almost synchronously (B1; C1), whereas the other three packmen which constitute the lower triangle were presented asynchronously (B2-B4; C2-C4). If stimulus synchrony can affect the binding of figures, the upper triangle will be perceived more often than the lower one. In some trials the upper triangle was presented almost synchronously and the lower triangle was presented asynchronously as shown in the figure, while in the other trials the upper triangle was presented asynchronously and the lower triangle was presented almost synchronously. Which of the two triangles was presented almost synchronously was randomized from trial to trial. In each trial, the subjects had to answer which triangle seemed more salient. The authors concluded that stimulus synchrony did not affect figure binding. (Modified from Fahle and Koch, 1995).
Subjects were instructed to answer which of the two seemed more salient. Each packman was flickered at a frequency in the range of 5-75 Hz. Contrary to the prediction of the synchro-binding theory, Fahle and Koch (1995) could not find any effect of synchronous presentation of visual features on perceptual grouping. They concluded that in figure-ground segregation the internal code used by the cortex for “binding” bears no direct relationship to the timing of external events.

The above-mentioned studies were concerned with how dots or shapes are bound into coherent figures. It is also interesting to consider other aspects of the binding problem, for example, how features of the same object are bound together rather than mistakenly assembled with features of another simultaneously presented object. Keele et al. (1988) investigated this problem. Keele et al. hypothesized that the synchrony of presentation imposed on the features serves as the binding cue but having conducted experiments, however, they found that stimulus synchrony did not result in binding.

Thus, several psychophysical studies failed to confirm the assumption that manipulation of stimulus synchrony by the experimenter will affect perceptual grouping. A psychophysical study by Iwabuchi and Shimizu (1997), however, suggested that this assumption might be true. Below, their study is introduced and implication of their study on future research on binding by synchrony is discussed.

**Depth Segregation Induced by Stimulus Synchrony: Possible Direction for Future Research on Binding by Synchrony**

Iwabuchi and Shimizu (1997) divided random dots filling a square into left and right rectangles (Fig. 6 (A)) and they presented these two alternately. In each trial, one of three combinations of sizes was used: (left rectangle : right rectangle) = (1:3), (1:1), or (3:1). They were each flickered at one of ten flicker frequencies in the range of 5-125 Hz. The ten flicker frequencies and three combinations of sizes gave a total of 30 stimuli, and each subject had to indicate the perceived depth between the two shapes by manipulating a joystick. In this study, Iwabuchi and Shimizu (1997) found that either the left or right rectangle seemed to be in front of the other one at flicker frequencies below 31.3 Hz (flicker-induced depth segregation), even when the rectangles were the same size (Fig. 6 (B)). In case of the configuration illustrated in Fig. 6, there were no luminance, spatial frequency or size differences between the left and right rectangles. It is interesting that subjects can perceive depth monocularly without pictorial depth cues.

This study suggested that stimulus synchrony is a critical factor of depth segregation. Iwabuchi and Shimizu (1997) speculate that neuronal synchrony is organized depending on the timing of presented visual stimuli, and hypothesize that information on random-dot stimuli from the in-phase flickering region is carried to the depth-related area of the cerebral cortex where dot information is grouped into perceptual units within the same depth plane.

It is likely that the brain assigns different depth planes to features presented at slightly different times. In other words, features presented at different times are bound into two different figures in different depth planes. Thus, flicker-induced depth perception seems to be a phenomenon which supports the synchro-binding theory.
predicting that synchronously presented stimuli are bound together and grouped into a figure in the brain.

Although psychophysical studies cannot show direct evidence of a relationship between stimulus synchrony and neuronal synchrony, they can suggest ideas on neurophysiological study that confirm the mechanism and role of neuronal synchrony. So far, neurophysiological studies on the binding by synchrony have been carried out from the viewpoint of perceptual grouping such as figure-ground segregation. However, none of them examined depth segregation, because there has been no data suggesting the close relationship between depth segregation and stimulus synchrony. The binding problem is typically concerned with an object whose features lie within a single depth plane. Sometimes, features of the single object lie in different depth planes, and the brain must bind only features within the same depth plane. It is speculated that, in this case, stimulus synchrony is utilized as a cue to separate features in one depth plane from those in other depth planes.

I suggest that depth segregation is a crucial perceptual phenomenon that links neuronal synchrony and stimulus synchrony. Here, I propose that neurophysiological studies that examine neuronal synchrony during depth segregation should be conducted for further understanding of binding by synchrony.

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