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Neurophysiological mechanisms underlying the distinction between automatic and controlled processes

A Dissertation

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in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

by

Danko Nikolic

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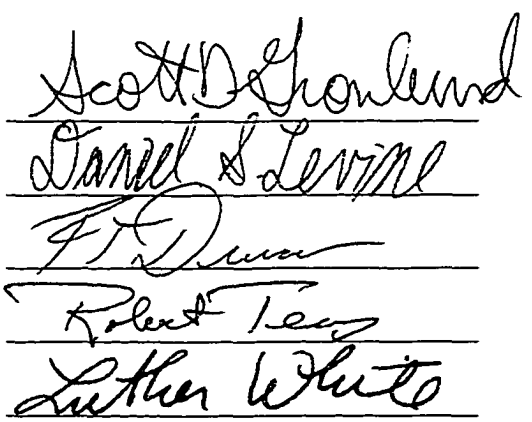
Neurophysiological mechanisms underlying the distinction between automatic and controlled processes

A dissertation APPROVED FOR THE

DEPARTMENT OF PSYCHOLOGY

BY



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Abstract

Automatic processes are fast, effortless, mostly unconscious, take very little capacity and are slowly changing. Controlled processes are much slower, require effort and attention, require capacity, are closely tied to consciousness but provide high behavioral adaptivity in unfamiliar situations. Because this distinction is fundamental for virtually all aspects of human cognition it is important to understand the difference in the neurophysiological mechanisms that underlie these two aspects of cognition. Through computer simulations we show that the neural computations that rely on oscillatory and synchronous neural activity share several fundamental properties with controlled processes. By accounting for several experiments that first established the distinction between automatic and controlled processes in visual perception, we show that synchrony-based computations observe limitations in capacity and that processing time depends on the task complexity. We also show that synchrony-based computations have an ability to handle new, not previously encountered computations. Finally, we show that a learning mechanism that employs synchrony-sensitive changes of synaptic efficacy provides a good tool for developing automaticity. In other words, the system learns to develop synchronous patterns faster and more reliably and thus increases the speed and accuracy and decrease the demands on limited attentional resources. In sum, controlled cognitive processes seem to rely heavily on synchronous neural activity while automatic processes seem to employ synchrony-based computations to a far lesser degree.

Neurophysiological mechanisms underlying the distinction between automatic and controlled processes

The different properties of automatic and controlled processes have been experimentally established in many domains in human cognition (e.g., perception, Treisman, 1982; memory, Sternberg, 1966; Schneider and Shiffrin, 1977; and social cognition, Devine, 1995). Automatic processes occur faster, do not appear to have limitations in processing capacity, and usually are not in the focus of awareness. They are closely related to skills, but not only behavioral skills such as driving a car, but also perceptive skills, memory skills and thinking skills. Controlled processes, on the other hand, occur slower, are very limited in their capacity and we seem to be aware of them to a much higher degree. We seem to have much better conscious control over controlled processes but subjectively they appear as requiring effort (hence the terms *voluntary* and *effortful* processes).

Automatic processes change relatively slowly and this makes them quite rigid in information processing. It usually takes a long time to develop a new automatic process and it also takes a long time to change or unlearn an automatic process. The main advantage of controlled processes over automatic ones is their adaptability. Controlled processes are those that allow the brain to process information in a novel previously never encountered situation. For example, if one responds to a light by pressing a button after being instructed to do so (i.e., no

conditioning has taken place) a controlled process mediates the behavior. The cost of the flexibility of controlled processes is the considerable limitation in processing capacity (see Schneider and Shiffrin, 1977 for a more thorough review of properties of automatic and controlled processes). These two processes, therefore, seem to complement each other and allow us to use an optimal combination of past experience and new information in each given task. Treisman (e.g., Treisman and Gelade, 1980) proposed a feature binding theory for the explanation of the controlled and automatic processes in visual perception. There is also evidence that the feature binding theory applies to visual working memory (Luck & Vogel, 1997). Here, we develop a model of spiking oscillatory neurons and study its behavior in order to understand the possible neurophysiological processes underlying the two different cognitive processes.

With extensive practice, some controlled processes become automatized. Learning has the effect that the brain changes its processing strategy in such a way that it automates controlled processes that are frequently used. The processing becomes faster and the capacity required by controlled processes is freed so other controlled processes can take place. As more and more information is processed by means of automatic processes due to practice, the overall processing capacity in the practiced task increases. There have been many experimental demonstrations that extensive practice produces superior processing of information. Some examples include: memory for numbers (Chase & Ericsson, 1981), restaurant orders (Ericsson & Polson, 1988), chess pieces (Chase & Simon, 1973), and serial search (Schneider

& Shiffrin, 1977). Spelke, Hirst and Neisser (1976) have shown that after 80 hours of training to simultaneously read a story and write down dictated words, people can achieve very good performance. However, not all controlled processes can automatic equally easily. Schneider and Shiffrin (1977) presented participants with consistent (targets and distractors consistently from different sets) and inconsistent, or varied mapping (targets and distractors selected from same sets) conditions for memory and visual search. In the consistent condition, the participants automated responses very quickly so the response time increased very little with the increase in set size. In the inconsistent condition, however, after about 2000 trials, the response time still increased considerably with the set size.

Controlled processes are also important and sometimes necessary for successful development of automatic processes. It has been shown that, for example, learning even a very simple form of automatic processes such as trace conditioning (where the unconditioned stimulus occurs after the conditioned stimulus) requires awareness of the contingency between the two stimuli, which is a controlled process (Clark & Squire, 1998). The simulations and theoretical discussion presented here also attempt to provide arguments for understanding the possible neurophysiological mechanisms that might underlie the changes that take place while automatic processes replace controlled ones.

The most fundamental presumption in the theoretical framework underlying the models discussed here is that *synchronized* neural firing of oscillatory spiking

neurons serves as a computational mechanism that underlies primarily controlled processes (Nikolic, in press). On the other hand, automatic processes are assumed to rely more on the traditional view of the computations in the brain where only the *firing rate* and the *synaptic efficacy* are important, not the *precise timing* of action potentials. In addition, the transfer from controlled to automatic processing with practice is assumed to take place through a learning mechanism that takes into account the synchronous patterns among neurons.

That neurons synchronize their oscillatory activity has been known for a long time. For example, the possibility of recording EEG signals from the scalp is due to the synchronous changes of the dendrite membrane potentials of a large number of nerve cells (Martin, 1991). However, many of today's researchers find the intensity of neural firing (i.e., inhibition and excitation) to be the only relevant mechanisms for the brain's computations, while synchronization in neural firing is largely considered to be a side effect that has no computational significance. Recently, however, synchronous neural firing has been studied in more details (e.g., Gray, 1993; Singer, 1993; Singer, 1998; MacLeod, Backer & Laurent, 1998; Rodriguez et al., 1999) and our knowledge about the conditions in which the neurons synchronize their firings has considerably improved. These conditions do not appear to be independent of the other computations in the brain. On the contrary, experimental results closely follow the theoretical framework used here.

Probably the most extensively studied phenomenon with respect to synchrony in neural firing is the so-called binding problem. The binding problem refers to the question of how the neurons that fire for different features of an object 'know' that they belong to the same object (Damasio, 1989; Stryker, 1989; Treisman, 1986). The question is what binds them together (e.g., yellowness and furriness of a tennis ball)? In the last decade, it has been well demonstrated that cortical neurons synchronize their firing according to the hypothesis that the features of objects are bound together by synchronizing the bursts of action potentials of neurons that code for those features (e.g., Singer, 1993). In other words, it has been shown that neurons in V1 with non-overlapping receptive fields synchronize only if the stimuli they receive belong to the same object (e.g., Gray, Konig, Engel, & Singer, 1989). It is also important to note that in many cases the intensity of neural firing does not change across the experimental conditions, only the synchronous patterns.

It has also been shown that synchronous neural patterns observe several laws of Gestalt (Singer, 1998). Furthermore, in strabismic cats, for example, the information from the winning eye in the competition is synchronized much more strongly (Fries et al., 1997). It appears, therefore, that the intensity of neural firing reflects more the objective properties of the stimulus (e.g., the intensity of the stimulus) while the patterns of synchrony reflect some aspects of our subjective experience of the stimulus (i.e., the subjective grouping of features).

How synchrony might contribute to computations in the brain?

Probably the major criticism of the idea that assigns a computational role to synchrony in neural firing is expressed in the question "Who reads the synchronous neural patterns in the brain?" To address this question, consider the simple neural network in Figure 1. Neurons A, B and C receive input and map it to neurons D and E. Neurons D and E compete through mutual inhibition. If all of the input neurons are stimulated, neuron E wins the competition because it receives more stimulation due to stronger connections from input neurons. This is a well-understood process within networks of neurons. However, let us assume that another neuron, X, that has mutual excitatory connections with A and B, synchronizes the action potentials of those two neurons without necessarily changing their firing rate. In this case neuron D will receive more synchronized input, i.e., a much larger proportion of action potentials from neurons A and B will arrive simultaneously.

Some neurons are highly sensitive to the simultaneous arrival of action potentials. For those neurons, the likelihood of firing an action potential increases significantly if the action potentials arrive at the same time. Those neurons, therefore, are not very sensitive to the firing rate, but to the timing of the action potentials that arrive from different sources, hence their name: coincidence detectors. If neurons D and E are coincidence detectors, only neuron D will receive synchronized input and will consequently undergo stronger depolarization and win

the competition with E in spite of having weaker connections. This is a simple example of how a synchronous pattern could affect the processing of a neural network.

[Insert Figure 1 about here]

Most automatic processes are not entirely automatic but have to be engaged and disengaged by controlled processes. Otherwise, well-trained activities would initiate regardless of their adaptive significance in a given situation (e.g., a skilled secretary does not automatically move fingers positioned on the keyboard when he or she reads a text - the typing activity is under conscious control).

It is assumed here that *coincidence detection* is the primary neural mechanism through which synchronous patterns affect the firing intensity of other neurons. The coincidence detectors do not necessarily need to be involved in oscillatory and synchronous activity. High sensitivity to coincidence in the arrival of two action potentials has been experimentally demonstrated for different types of neurons. For example, Usrey, Reppas and Reid (1998) found that neurons in the lateral geniculate nucleus that receive stimulation from ganglion cells in the retina are much more likely to fire an action potential if two action potentials arrive within 10 milliseconds. They also demonstrated that this property causes synchronous firing of neurons in the lateral geniculate nucleus in thalamus. The neurons that implement coincidence detection to the greatest extent are probably the neurons

that detect the interaural time delay for sound localization. These neurons are able to distinguish a time delay as small as 10 microseconds (e.g., Skottun, 1998). One of the few experiments that demonstrate that synchronous patterns have computational significance is one where it was found that when the synchrony among projection neurons is abolished, the discrimination of molecularly similar odorants in bees is impaired (Stopfer et al., 1997).

In the model proposed and studied here, coincidence-sensitive neurons were not modeled. The focus of consideration is on the patterns of synchronization that result from various neural network architectures and conditions of stimulation. All the conclusions about the meaning of the obtained patterns of synchronization will be made under the following assumption: Once neurons are synchronized to form a group, the effect on the next level of processing for this group depends solely on the intensity of firing and the strength of connections (the traditional approach to neural network conceptualization). Because the dynamics of these mapping processes is well explored in many neural networks, we concentrate our simulation and discussion efforts on understanding the processes and conditions that lead to various synchronous patterns. We are primarily interested in how the dynamics of forming synchronous patterns could account for some of the fundamental properties of controlled processes.

Theoretical framework and simulation goals

Several theoreticians have tried to understand the possible computational role of synchronous neural activity for the higher cognitive processes in the brain. For example, it has been proposed that the mechanism that allows us to deal with analogies and metaphors relies on synchrony in neural firing as a computational mechanism (Hummel & Holyoak, 1997; Shastri & Ajjanagadde, 1993). Synchrony in neural firing could also be a mechanism that accounts for our performance on text comprehension with different levels of relational complexity (Halford, Wilson, & Phillips, 1999).

Each of these theoretical efforts discusses the possible role of synchrony in neural firing for a relatively narrow set of phenomena. For example, the model by Shastri and Ajjanagadde (1993) assumes specific units that are applicable only for a very narrow purpose, and as Diederich (1993) points out, are not physiologically plausible. Consequently, the model that Shastri and Ajjanagadde propose demonstrates that synchrony in neural firing could in principle account for reflexive reasoning but the model is neither completely physiologically plausible nor general enough to apply to various aspects of human cognition. All the previously mentioned cognitive phenomena that are proposed to rely on synchrony as the underlying mechanism seem to fall in the more general category of controlled processes. Therefore, in order to provide a more general understanding of the computational role of synchronous neural activity we address the properties

of the synchrony-based computations from a more general perspective of controlled and automatic processes.

That synchronous firing might underlie controlled processes has been previously proposed (Nikolic, in press; Nikolic, 1998). Singer (1998) also has a proposal for distinguishing neural mechanisms underlying conscious and unconscious processing. According to this hypothesis, the automatic processes rely more on inhibition and excitation when the synchrony is not engaged to a large extent (i.e., the traditional neural network approach). Controlled processes, however, rely heavily on synchrony in neural firing. A new, never previously used, synchronous pattern could be formed very quickly, and this feature is assumed to underlie the high adaptivity of controlled processes (Nikolic, in press). This same synchrony-based mechanism is, however, limited in its processing capacity. If one needs to parse the visual scene into several different objects, the binding theory suggests that the neurons that code for features of the same object will fire in synchrony, but will not be synchronized with neurons firing for features of another object. In other words, several mutually-segregated groups of synchronized neurons will exist. If the neurons oscillate with a similar frequency, the only way to separate the neural assemblies seems to be the phase shift of oscillations (i.e., while one group is firing the others are more or less silent). As the number of independent assemblies increases, the distance between the oscillating phases decreases. Eventually the assemblies become so close to each other in the phase space that they cannot be distinguished one from another. Consequently, only a small number of separate

assemblies can exist simultaneously. Several independent estimates of the maximal number of synchronous neural groups that can exist simultaneously in the brain (e.g., Basar, Basar-Eroglu & Roschke, 1988; Lebedev, 1980) are very similar to the estimates of our perceptual span and working memory capacity (Luck & Vogel, 1997; Miller, 1953), namely, between four and nine. These findings, therefore, support our theoretical framework.

The hypothesis that a transfer in processing strategy occurs as automatic processes replace controlled has also experimental support. Processing that is relying on synchrony, according to the hypothesis, should be replaced by a processing style that relies more on intensity of firing (i.e., inhibition and excitation) and less on synchrony. Experimental data on the chaotic dimensionality of hand movements (Mitra, Riley, & Turvey, 1997; Mitra, Amazeen, & Turvey, in press) indirectly support this hypothesis by showing a decrease in the number of active variables, and therefore the number of synchronous groups, controlling the movement as the skill improves (see Nikolic, 1999, for discussion).

The example in Figure 1 could also be used to discuss a simple mechanism that might be involved in engaging automatic processes. Because computation through mapping only (i.e., intensity in firing and synaptic efficacy) is assumed to underlie automatic processes, and because different mapping (thus different automatic processes) results from different synchronous patterns, the synchronous patterns

set up by controlled processes might be the instrument of engagement and disengagement of automatic processes.

The goal of the models here is to test to what degree a neural network system that employs synchronous neural firing can account for the different properties of automatic and controlled processes. The models' behavior should be consistent with 1) neurophysiological findings on synchronous patterns and 2) findings of the cognitive phenomena essential for distinguishing between automatic and controlled processes:

1) Probably the most fundamental distinction between controlled or 'serial' and automatic or 'parallel' processing is processing time (e.g., Schneider, & Shiffrin, 1977; Treisman, 1986). In serial search, the processing is slower and one typically finds a linear increase in response time with an increase in the complexity (i.e, number of distractors) in the stimulus. In automatic processing (or "pre-attentive" or "non-attentional"), however, the response time does not increase with the complexity of the stimulus. Such phenomena have been studied extensively in the visual search domain (Kinchla, 1992; Schneider, & Shiffrin, 1977; Treisman, 1995) as well as memory search (Sternberg, 1966). A neural system based on synchronous neural firing should, according to the theory, provide a neurophysiological explanation for those findings.

2) Limited processing capacity for controlled processes. The estimates for the capacity for the number of simultaneously stored or processed items are between four or five (e.g., perceptual span) and nine (working memory capacity) (Miller, 1953; Luck & Vogel, 1997). The model should produce limitations in this range, but only for processes that rely on synchronous neural firing. In other words, the number of synchronous groups that can simultaneously exist should be limited.

3) Number of features that each memorized object possesses does not affect the maximal number of objects that could be remembered (Luck & Vogel, 1997). In other words, the capacity does not seem to be affected by the number of features that each object consists of. The only factor affecting the capacity is the number of objects. The model should show similar behavior so that different features of the object should be synchronized within one neural group. Therefore, the number of neurons belonging to one group should not affect the processing limitation due to the limited number of synchronous neural groups.

4) With practice, controlled processes become replaced by automatic ones accompanied by an increase in speed and overall capacity (e.g., Chase & Simon, 1973; Spelke, Hirst, & Neisser, 1976). The model should apply a learning mechanism that relies on synchrony in neural firing that allows restructuring of the network in such a way that repeated exposure to a stimulus results in faster processing time, and less demands on the limited synchrony-based resources.

Neuron model specification

It was necessary to develop a neural network model where neurons produce action potentials in bursts, e.g., an oscillatory fashion. There are at least three sources of oscillation in neural activity: 1) under certain conditions mutual delayed excitation of distant neurons can result in oscillatory activity, 2) coupling of an excitatory and inhibitory neuron also can result in oscillation (e.g., Grossberg & Somers, 1991; Grunewald & Grossberg, in press) and 3) some neurons have been shown to produce spontaneous endogenous oscillations (e.g., Volgushev, Chistiakova & Singer, 1998). The oscillatory activity in the brain is probably a result of all three sources of oscillations. In order to keep the model as simple as possible it is probably advantageous to model only one source of oscillation. Case 1) would probably result in a computationally demanding model. Simulations that compared sources 2) and 3) have shown that neurons driven by endogenous oscillations have very robust oscillation phases and are very slow in adapting them to exogenous input (simulations not shown here). In other words, because the endogenous oscillation is driven in large part by factors other than the dynamics of input and output, the neuron is very slow in changing its oscillatory phase - much slower than what is necessary for synchrony to attain its assumed computational role in information processing[1]. For that reason, a model that assumes that each neuron is coupled with one inhibitory neuron is adopted and described here.

[1] For example, a network with endogenous oscillating neurons would need 10 cycles to settle down to a stable synchronous pattern, whereas a similar exogenous oscillating network would require one or two.

Input (I) to any neuron (j) is defined as the sum of all inhibitory and excitatory inputs to the neuron:

$$I_i = K(T_{Fi}\sum_j (F_j w_{Fij}) + T_{Gi}\sum_j (G_j w_{Gij}))$$

Where F_j is the excitatory input and G_j is the inhibitory input from other neurons and have value 1 if the presynaptic neuron sends an action potential and 0 otherwise. w_{Fij} and w_{Gij} are the weights of excitatory and inhibitory synaptic connection between neurons i and j and also have value between 0 and 1 and negative values for inhibitory synapses. K is a constant that has value $.2$ in all simulations. T_{Fi} and T_{Gi} normalize input to each neuron separately for inhibition and excitation for the maximal possible value of input:

$$T_i = \frac{1}{\sum_j w_{ij}}$$

The oscillatory activity of the neuron is modeled by assuming that each neuron couples with an inhibitory neuron. In order to make simulations computationally more effective, the inhibitory feedback is modeled as self-inhibition with delay. The self-inhibition P is defined as:

$$P_i(t) = F_i(t-c)$$

where F is the neural activity for the same neuron at time t-c. c is a time constant set to 10 in all simulations.

The change in the depolarization, x, of neuron i is given by following equation:

$$\Delta x_i = AI_i - BP_i$$

where A and B are constants set to $.5$ in all simulations.

In order to simulate action potential generation it was necessary to model the membrane potential at the hillock, u:

$$\Delta u_i = Cx_i - D(1 - x_i)$$

The term $(1\text{-}x_i)$ additionally decreases delta u for low x_i. C and D were set to $.5$ and $.1$ respectively for all simulations.

If u exceeds the threshold value t_u, the neuron fires an action potential $(P_i = 1)$ and resets u to 0 ($t_u = .9$ in all simulations). The refractory period of the neuron is assured so if the neuron fired at time t, the next action potential can occur only at time $t+2$.

External input to neurons always had $F\ w = .5$ with probability of action potential equal to $.2$.

Some properties of the spiking model

Lateral and feedback excitatory connections synchronize firing activity

The basic and simplest premise under the hypothesis of the computational role of synchronized neural firing assumes that the system uses its 'natural' tendency to synchronize firing of neurons that have mutual excitatory connections. First, it is shown that neurons do not synchronize firing if they do not have mutual connections (Figure 2 A) and synchronize their firing if they are mutually connected by excitatory connections in small groups of two (Figure 2 B) or three (Figure 2 C). Note that Figure 2 C has three synchronograms, one for each pair of neurons. One can also see that the two neurons that are not directly connected (1 and 2) have a smaller degree of synchrony than the neurons that are directly connected. In addition to synchronograms in Figures 2 A and B, one can see a series of action potentials. From the series of action potentials, one can see that 1) the neurons fire in oscillatory fashion and 2) the neurons that are mutually connected have a tendency to fire simultaneously.

[Insert Figure 2 about here]

The most commonly used measure of synchrony among a pair of neurons is the synchronogram (there are also other, more advanced analyses of neural spike

activity such as Tam (in press)). The synchronogram shows the cross-correlation between the firing patterns of two neurons. Synchronograms can provide several pieces of information about the firing activity of two neurons: 1) the degree of synchrony, 2) if neurons oscillate 3) frequency of the underlying oscillation and 4) phase shift of oscillations. If the synchronogram is not flat, it means that the firing of one neuron is not independent from the firing of the other neuron. If the peak of the synchronogram falls to zero (the vertical line in the middle), it means that the two neurons have a strong tendency to fire at the same time. In other words, the neurons are synchronized with zero time-lag. The size of the peak provides information about the degree of synchrony. The larger the peak, the higher the degree of synchrony (for example, pairs 1 and 3 have larger synchrony than pairs 1 and 2). If the peak is shifted away from zero (one or the other direction), it means that the burst of activity of one neuron is shifted in time compared to another neuron. In other words, the neurons are shifted in phase. The shift in phase is more likely to be observed if the neurons oscillate with the same or nearly the same frequency. In oscillating neurons, synchronograms often have the shape of a spindle (interchange of high and low levels of cross-correlation with amplitudes decreasing with distance from zero, e.g., Figure 1 A). This type of synchronogram suggests that the two neurons oscillate regularly with similar frequency. The distance between two peaks equals the length of oscillation.

Figure 2 D shows how an oscillatory neuron is synchronized with itself. Because the maximum value for the auto-synchronogram is much larger compared to other

cases, the synchronogram in Figure 2 D is on a different vertical scale than other synchronograms in Figure 2.

Inhibition produces desynchronization

Simulations suggest that in addition to decreasing the firing rate of another neuron, inhibition can produce two different types of desynchronization: producing zero synchrony and pulling phases apart. Figure 3 shows activity and the synchronogram of two oscillatory neurons that are inhibiting each other. The firing pattern demonstrates that the neurons are quite independent in their firing. The synchronogram shows that there is not much synchrony between the neurons. The auto-synchronogram for one of the neurons (Figure 4) shows that the neurons do not produce regular oscillatory activity. The inhibition, therefore, did disturb the oscillatory activity of neurons.

[Insert Figure 3, 4 and 5 about here]

Figure 5 shows the effects of inhibition on neurons that are synchronized by other neurons. In this case the oscillation persists but the phases of the mutually inhibited neurons are shifted. When oscillatory neurons are shifted in phase, the inhibition between them has much less effect because it acts during the period when each

neuron is not very active and there is not much activity to be suppressed. These results have several theoretical implications:

1) Synchrony might serve as a factor for stabilizing and supporting the oscillatory activity of a neuron. The mutually synchronized neurons support each other to endure the desynchronizing and activity-attenuating effects of inhibition.

2) An activated neuron that cannot bind with other neurons in the system is not necessarily turned off by inhibition, but it can remain active with irregular oscillations. This neuron's activity in an irregular-oscillatory fashion still allows the neuron to contribute to computations in the brain, but probably only on the automatic non-synchronous level.

3) Another advantage of a non-oscillating neuron is that such a neuron has no ability to influence the phases of oscillation of other oscillating neurons. This is because it does not produce a consistent timing of inhibition. As a consequence, such a neuron should have a greatly diminished effect on the phase-shifting competition between different oscillatory groups. In other words, such a neuron should not take up the limited processing capacity posed by a limited number of simultaneously existing oscillatory groups (see simulations and discussion on limited processing capacity).

In conclusion, there are several effects that inhibition can have on the oscillatory and synchronous activity of neurons. First, a pair of an inhibitory and excitatory neuron can serve as an oscillation generator (this property is embedded here in the

neuron model). The mutual inhibition of oscillatory neurons can either suppress the regular oscillatory activity or shift phases of oscillation.

Collective neural activity

Synchronized neural activity has been studied at the level of group activity of a large number of neurons in a form of electroencephalogram (EEG), event related potentials (ERP), and magnetoencephalogram (MEG). Figure 6 demonstrates average depolarization of a group of 15 neurons. The obtained signal should be considered as roughly corresponding to the signal recorded by EEG. As a demonstration, an ERP was computed for 50 EEG signals as a response to the same stimulus. In Figure 7 one can see the superposition of 10 EEG signals and the average for 50 signals (ERP). The obtained ERP signal suggests that the network proposed here could be used to simulate EEG-based experimental data and the neural processes underlying various findings in EEG.

[Insert Figure 6 and 7 about here]

The two components of the simulated ERP are due to the initial synchronization of the neuronal oscillations whose onset starts with the stimulus presentation. Within nearly one cycle, however, the phases of oscillations shift due to the inhibitory and excitatory connections between neurons. This has the consequence that the

oscillations are not aligned with the stimulus onset any more and the ERP graph remains flat. The system does not produce later automatic components of ERP (such as N200 and P300) that are of significance for understanding working memory and learning process (i.e., Banquet et al., 1998). N200 and P300 are automatic responses that show increased ERP components for rare (i.e., unexpected and presumably novel) stimuli. N200 and P300 components are not simulated here because our simulations address only one step of processing (i.e., one layer), which would correspond to the earliest components of the ERP signal. Because an increase in the ERP component indicates an increase in the stimulus-onset-locked synchronization of neural activity, one could expect that the later steps of processing would show different intensities of ERP components depending on the familiarity of the incoming stimulus. A more familiar stimulus that has stronger connections between units and results in faster formation of synchronous patterns (see later discussion on automatic and controlled processes) forms synchronous patterns faster with a higher degree of synchrony that might have different effects on the ERP compared to a less familiar stimulus.

Feature binding

One of the most cited experimental findings that support the hypothesis that features of a perceived object bind through synchronization of neuronal discharges includes moving bars (Engel et al., 1992). They have shown that the degree of synchrony between two neurons with non-overlapping receptive fields depends on

the degree to which the features that the neurons detect belong to the same object. The highest degree of synchrony was found for the condition where one single object moves across the visual field and spreads over both receptive fields (Figure 8 C). If the object is split in two parts, the degree of synchrony decreases (Figure 8 B). It is important to note here that the gap between the objects cannot influence directly the activity of the two neurons because the gap between the objects does not fall on receptive fields of either of the neurons. Finally, if the two objects move in different directions, the synchrony between the two objects drops to zero (Figure 8 A).

[Insert Figure 8 about here]

In order to simulate these results, a set of small neural networks was developed for each condition (see Figure 8). The current understanding of the architecture of the primary visual cortex suggests the following architectures. The detection of only two features is modeled (e.g., line orientation and movement). In the case when two stimuli move in opposite directions, the neurons that fire for features of one object are either not connected or very weakly connected to the neurons firing for the other object. If the two objects move in the same direction, than the direction-detection neurons in the neighboring cortical columns are connected. The strength of connection is a function of the distance of two neurons. Finally, if one single object is presented, another line detector neuron that has a receptive field between the two neurons is stimulated and is more strongly connected to each of the

neurons. The resulting synchronograms are shown in Figure 8 together with the experimentally received synchronograms. The simulations support the hypothesis that the synchronization occurs as a result of the lateral excitatory connections between the neurons.

Separation of oscillating groups and limited processing capacity

As has been discussed previously, the limited processing capacity of synchrony-based processing is believed to stem from the limited number of oscillatory groups that can exist simultaneously. In order not to confuse the membership in a synchronous group, the oscillations of neurons that belong to different groups should not be perfectly synchronized, but shifted in phases. A shift in phase among oscillating groups allows neurons to send and receive stimulation only from the members of the group. We have already seen that inhibition could be a factor that shifts the phases of separate oscillating groups apart. The more different oscillating phases the system can maintain, the more separate oscillating groups can exist and, therefore, the larger will be the capacity of synchrony-based processing. According to our theoretical background an increase in the number of groups leads to larger capacity of controlled processes such as working memory capacity. That oscillating neural networks can produce a very limited number of separate oscillating groups has been reliably demonstrated (e.g., Horn & Opher, in press). Here we are interested in studying some additional properties of this phenomenon.

[Insert Figures 9 and 10 about here]

To demonstrate the limited processing capacity of the model proposed here the oscillatory patterns of three (Figure 9 A and B) and four (Figure 10) oscillatory groups are observed. When three groups compete for oscillating space the phases are shifted among all three groups so each group can oscillate on its own with minimal disturbance from the other groups. When four groups are competing, however, the synchronograms show that the groups are not well separated. Some neurons are separated in phases (i.e., 3-6, 3-9, and 6-9), while other seem to fire at the same time more often (i.e., 9-12 and 6 - 12). When the coincidence detectors react to activity from those groups (not simulated here), they do not have sufficient temporal information to distinguish the group from which the input comes. In cognitive terms, this should result in an increased likelihood to bind features of different objects in working memory and consequently making an error during retrieval. Luck and Vogel (1997) demonstrated that the participants do make error in memorizing features of objects when the number of objects is larger than four.

Another important finding by Luck and Vogel (1997) was that an increase in the number of features that belong to the same object does not impair the working memory capacity. The binding theory explains this finding by assuming that all the features that belong to one object are synchronized together and therefore the number of features does not have an effect on the limited capacity posed by the

limited number of separate oscillating groups. The simulation results in Figure 9 show the model has the same property. Figure 9 A has two features per object, while Figure 9 B has four features per object. The synchronograms show clear distinction of the phases of the three oscillating groups in both cases confirming therefore, that if the system is able to bind or chunk together many features, the working memory capacity can appear to increase. This could be, therefore, a mechanism underlying the chunking process proposed by Miller (1953).

This property of separation of oscillating groups combined with coincidence detectors in the next level of process could serve as a mechanism of early attentional filtering. First, the segregation of neural assemblies in separate groups might allow the system to use only one part for further processing (i.e., one assembly) of the stimulus and disregard the others. When subsequent input arrives into the system, only the input that easily synchronizes with the current activity in the system (the attended assembly) could easily enter the processing while the input that easily synchronizes with the disregarded groups (non-attended) will not receive further processing. An important stimulus that is connected with unusually strong connections (such as the listener's name) might even without synchrony produce stimulation in subsequent levels that is stronger than the stimulation from a synchronized (attended) group (i.e., the cocktail party phenomenon).

There are several reasons why a system's ability to maintain a larger number of separate synchronous groups would be advantageous. First, it would allow for a

larger working memory capacity. Second, it allows for a larger number of parallel processes to occur regardless of whether the parallel processes are used for different simultaneous tasks or are used for different subtasks of one major task (such as sentence comprehension). For example, in the task of occluded face recognition (e.g., Rodriguez et al., 1999) the input needs to be organized in such way that the object and the background neurons are appropriately grouped. Because the task is difficult, it is likely that the system has to try several binding 'hypothesis' before it finds the correct one. It is likely that the larger number of groups could allow for larger number of hypotheses simultaneously tested. However, from the proposed theoretical framework, it also follows that the large number of groups could be disadvantageous in a situation where a fast and simple (i.e., automatic) reaction is required, such as the flight or fight situation. In this case, a large number of groups that leads to more thorough information processing might slow down the responses and bring the organism into a life-endangering position. Because the optimal arousal for complex tasks is much lower for simple tasks (i.e., the Yerkes - Dodson's law) there is a reason to believe that the arousal associated with the flight or fight situation also decreases the processing capacity and that this is an adaptive feature of the brain important for survival.

It is important to note that one reason why clear separation in firing oscillations is rarely found experimentally is because the regular oscillations in the cortex seem to be very rare. Instead, the oscillations in the cortex have a very strong chaotic component that has been explored recently (e.g., Basar, Basar-Eroglu, & Roschke,

1988; DeMaris, in press; Freeman, 1983; 1994). Large proportion of this dynamic activity runs in the background of the computations of incoming stimuli (Arieli et al., 1996) and this is the reason why averaging is necessary to obtain evoked potentials.

Also, particular patterns of oscillation in the cortex, whether chaotic or not, are probably very short lived. There are at least three factors that prevent the system stay in an attractor: 1) constantly changing input from the environment, 2) parts of the brain are not isolated and they influence each other and 3) continuous, relatively fast biochemical changes that take place within cells and result in habituation (e.g. depleting resources) or sensitization (e.g., post-tetanic stimulation). In our simulations, however, the system is isolated from the rest of the brain and runs for a longer time. Enough time is therefore allowed for the system to reach the attractor to repeat itself in the attractor, so it could be observed. In a real experiment, the synchronograms, however, need to be obtained by averaging many trials. This difference has the consequence that only the zero-lag synchrony and a consistent shift in oscillating phase can be detected. In the system that is simulated here, however, the direction of shift is random and therefore averaging over many trials would result in a flat synchronogram.

Letter and color perception task

An experiment in which three letters of different colors presented for 200 milliseconds were followed by a mask demonstrated the difference between processing of individual features and conjunction of features (Treisman & Gelade, 1980). For example a blue R, red P and a green T are briefly presented and the participants are asked to report what they saw. The participants were successful in reporting the individual features, but made many mistakes in combining the features. They would be very likely to see a red R and blue P, for example. The conclusion from these studies is that the features are processed automatically or preattentively while attention and time is needed for the conjunction of features. This was one of the fundamental findings that led Treisman (1982) to develop the Feature Binding Theory.

Figure 11-novel combination shows a simplification of the neural network architecture that might underlie this experiment. Neurons 1 and 2 are assumed to code for one feature (e.g., letter) and neurons 4 and 5 for another feature (e.g., color). The neurons that fire for the same feature are assumed to be strongly connected ($w_{ij} = .8$ in all simulations). If the features occur in the same spatial location they are assumed to be weakly connected through a mediating neuron ($w_{ij} =$

.2). The features of the same type are also assumed to mutually compete through inhibition. The dashed areas in Figure 11 show the neurons that are mutually competing through inhibition ($w_{ij} = -.5$).

[Insert Figure 11 about here]

The experimental manipulation was the time allowed for processing. According to feature binding theory, participants failed to report the color and the letter correctly because there was not enough time to bind the features of the object. One can see that if enough time is provided for the neural network system to evolve, it produces appropriate patterns of synchrony (Figure 12). The neurons that belong to different objects are shifted in phases (i.e., 1-6, and 1-11) and neurons that belong to the same object seem to be in a much higher degree in phase (1-4, 6-9 and 11-14). In order to see how the system behaves when not enough time is provided for information processing, average synchronograms are computed for the system's reaction to the first 350 computational steps (Figure 13). For early stages of processing, the synchronograms were somehow different. The neurons that do not belong to the same object (1-6 and 1-11) observe a small peak at zero delay (the dashed line) indicating that those neurons observe a certain degree of synchrony. According to the hypothesis of the computational role of synchronous neural firing, this zero-delay synchrony of neurons belonging to the same object prevents the distinction between the objects and the correct conjunction of the features.

[Insert Figures 12 and 13 about here]

In another experiment participants were presented with randomly scattered S's and vertical lines. The participants were instructed to look for dollar signs ($). If presented for a brief period of time, participants often reported seeing dollar signs when the stimulus contained none (Treisman, 1986). The authors concluded that the detection of features in early processing is independent of their location. The behavior of the network reported here suggests that the same system would produce similar behavior. If not enough processing time is allocated to the system, two neurons that do not share the same location often synchronize together, which can lead to an incorrect representation of the input.

It is important to note that when the stimulus is presented (i.e., the simulation starts), all of the neurons start being stimulated at the same time and consequently they start firing at about the same time - they have the same phase. It takes time for the system to organize and pull apart the phases of the neurons that do not belong to the same group. The weaker the connections between the neurons, the longer it takes to synchronize them and the weaker will be the synchrony between them. On the other hand, if in one's past experience all the R's were always blue, and all the P's red and T's green, one would probably have different performance on this task. The connections between all the features would be strong and the mistakes in perception of conjunctions of features should result in many fewer mistakes. If only part of the features were presented (e.g., shape of a letter without the color), because

of the strong connections among the features, an expectation of the system would either activate (or bring very close to activation) the neurons coding for the not presented features. In this way, the system would observe a form of a top-down expectation.

The following experiment employed well-learned associations between the shape and color. Participants were presented with objects of different colors (e.g., orange triangle, blue oval and a black doughnut) followed by a mask (Treisman, 1986). Participants would make mistakes in associating the shape with a color even when they were told what combinations they would be presented with and that they would be asked to report the location only. However, if the same stimuli were described as familiar objects (i.e., a carrot, a lake, and a tire) the errors in perception would drop from 42% to 5%. It is important to note that the participants were presented with the same stimuli, but in the latter case they have used their knowledge that carrots are orange, lakes are blue, and tires are black.

Figure 11 - well-learned depicts a possible neural network architecture that might be engaged in such an experiment. The difference is that the features that were previously weakly connected just by appearing at the same location are now strongly connected by direct excitatory connections ($w_{ij} = .5$). When the system is allowed to process information for a long time, the distinction between and within group synchronous patterns is now much more emphasized (Figure 14). When the network is allowed to process information for only a short period of time, the

average synchronograms also show a peak at zero time-lag for the neurons that do not belong to the same group (Figure 15 compared to Figure 13). The degree of synchrony, however, is much smaller than the degree of synchrony of the neurons that belong to the same group. If coincidence detectors are receiving the information from this group of neurons, this large difference in the degree of synchrony could account for the significant drop in the error rates between the two conditions.

[Insert Figures 14 and 15 about here]

The results of these simulations show that synchrony in neural firing has the potential to provide an explanation of the neural processes that underlie the feature binding process. The less familiar a certain combination of features is, the more time it takes to acquire an adequate representation of the stimulus. In addition to time, the number of independent oscillatory groups seems to be a limiting factor for processing based on synchrony in firing. If one compares the synchronous patterns of the neurons that belong to the same groups (i.e., 1-4, 6-9 and 11-14) in Figures 12 and 13 to Figures 14 and 15, one can see that the peak of synchrony matches the zero lag hidden line much better for the well-learned network. The slight shift in phase for the novel combination network indicates that the oscillations of neurons in the network wander more within the phase space and neurons are therefore more likely to be mistakenly bound to an incorrect neuron. Consequently, in order to ensure a good level of performance, the novel combination network can maintain a relatively smaller number of separate oscillating groups as compared to the well-

learned network. Therefore, in addition to requiring more time to process information, the novel combination network also spends/requires more of the limited processing resources expressed in terms of number of oscillating groups. Slower processing and the need for more capacity are two salient properties of controlled processes.

Visual search

The experiments on visual search were probably the prime experimental tool for learning about the distinction between automatic and controlled processes in human perception. In these experiments the participant is asked to find a target in the set of distractors. Figure 16 demonstrates a typical stimulus. The participant needs to find the letter Q among O's and R's. The dependent variable of interest is the response time. In many experiments (Treisman, 1982; 1986), it has been demonstrated that the response time increases linearly with the number of distractors, if it is necessary to detect a conjunction of features in order to distinguish the target. On the other hand, if the detection of the target requires only one feature (e.g., different color or tilt), the detection time is slower and does not increase with the number of distractors. Because there is no one single feature that distinguishes the target in Figure 16 (i.e., the circle is an O distractor and the tilted line is a part of the R distractor), the detection time increases linearly with the number of distractors. If the target was of a different color, or if the target was the letter X, only one feature

would distinguish the target and the response time would not increase with number of distractors. On the basis of these experiments it was concluded that perception of conjunction of features requires attention while a single feature pops out. Because attention relies on resources limited in capacity, it is necessary to successively shift attention between different parts of the stimulus, which results in a serial search.

[Insert Figure 16 about here]

The neural network that might be activated in an early step of stimulus processing is built under following assumptions (Figure 17). Neurons that detect the same feature (e.g., line under the same angle) share excitatory connections. However, other neurons that feature detectors are connected to ($w_{ij} = .2$) share mutual inhibitory connections if their receptive fields do not overlap ($w_{ij} = -.5$) and excitatory connections if their receptive fields overlap ($w_{ij} = .5$, only for neurons 1 and 4 that detect features of the letter 'Q'). Finally, only the feature detector neurons are assumed to receive stimulation from input (i.e., 1, 4, 5, 8, 9, and 12).

[Insert Figures 17 and 18 about here]

The synchronous patterns obtained for such a network are shown in Figure 18. The network synchronizes its activity in such a way that all the features of one type cluster into one oscillatory group and the features of the other type form another group. The excitatory connections for the location neurons for letter Q do not lead

to synchronization of the features of the letter Q (1-4). Obviously, the network is not able to provide synchronous information necessary to detect the object that these features belong to. Even though neurons 1 and 4 have mutual excitation, they do not synchronize. In other words, the connection is not strong enough to bind the two features. Note that if there were no distractors, the indirect excitation would be sufficient to synchronize the neurons. So, the distractors prevent the neurons from synchronization. If the number of distractors increases, the behavior of the system does not change. Those simulation results are not shown here but they are similar to the effect of an increase in the number of features in Figure 9 A and B.

According to binding theory, attention is necessary to bind these two neurons. The actual attentional mechanism that might bind these two neurons is not proposed here. Such a mechanism would probably be quite complex compared to the network system here. This attentional mechanism might involve several different parts of cortex such as spatial processing in the parietal lobe and search control that might involve the frontal lobe (e.g., Passingham, 1993). However, we do not propose the neural network mechanisms that underlie the controlled processes emerging from the frontal lobe, but merely suggest what neurophysiological factors result in a need for higher-level controlled processes and what could be the mechanism of control - the change in synchronous patterns. Applying an algorithm-based procedural system in the fashion of the ACT* model, for example (Anderson, 1983), would be a trivial modeling solution. However, it would not provide any additional explanation of the neurophysiological mechanisms underlying controlled processes.

According to Horowitz and Wolfe's (1998) recent finding that the visual search does not have any memory, an algorithm that randomly picks certain locations for attentional binding might be even more appropriate. Either of those would result in an increased search time as the number of distractors increases.

[Insert Figure 19 about here]

The model proposed here, however, provides an explanation why this unspecified attentional mechanism that binds these two features cannot search for the conjunction of the features in parallel: the system needs to bind the features that are at the same location and unbind the features that are on different locations. Figure 19 show synchronograms for the same neural network architecture (Figure 17) with one change. The location neurons 2 and 3 receive strong stimulation from an unspecified top-down process. As a result, the neurons 1 and 4 observe a much stronger degree of synchrony. In addition, the synchronograms for pairs 1-2 and 1-5 show a slight shift of oscillating phases indicating a tendency of the neuron 1 to separate from the rest of the oscillating group. Fries et al. (1997) reported experimental results that supporting these findings. In strabismic cats, they found that if attention is taken by another stimulus, the degree of synchrony between stimulated neurons decreases.

By no means is it suggested here that this non-oscillatory top-down process is the mechanism by which attention binds features. It seems that attention needs to

accomplish more. First, such excitatory input does not seem to provide changes in the synchronous patterns that are sufficient for appropriate binding of features. For example, the degree of synchrony also increases for neurons that are on other locations and are not features of letter Q (neurons 5 and 8, Figure 19). Even more problematic is the fact that such excitation could increase synchrony only for neurons that are already connected by excitatory connections. If the neurons share inhibitory connections, such stimulation would strengthen the shift in oscillating phases, which produces opposite effect. Finally, this mechanism violates the most fundamental principle underlying the theory of the computational role of synchrony in neural firing: the attentional mechanisms should be an emergent property of synchronous neural activity.

It is much more likely that the actual detection of the letter Q and binding of the features actually occurs in a subsequent level of processing. First, experimental evidence by Lamme and Spekreijse (1998) demonstrates that the contours of an object that result solely from texture segregation are not reflected in the binding of feature detectors in the primary visual area (V1). In the first level of feature detection only the features that are common for all or a vast majority of possible perceived objects should be detected. Otherwise, the processing of visual information would not be very efficient. For example, if the feature detector for letter Q was detected without any attentional control, the response time in the visual search task would not increase with the number of distractors but would attract attention even when the shape of the letter was embedded in a more complex object

such as a circle stroked by a tilted line. In addition, only one form of letter Q would be detectable and it would not reflect our ability to readily recognize the letter printed in different fonts. Finally, all the Q letters on one page would synchronize together which would have a catastrophic effect on the reading process.

It seems, therefore, that the detector of letter Q, in a subsequent level of processing, should be controlled by attention, and the simulation results support this notion. The information about features of the target stimulus that the first level of processing supplies arrives with shifted phases. In addition, the information about features of the target stimulus arrives simultaneously with the information from distractors. Consequently, a coincidence detector will not be able to detect the presence of these features unless some attentional process narrows down the input region for further processing. The most important point that we want to make here is that the necessity for attentional process has as a consequence that the attentional spotlight must move in a serial fashion. Hence, the average search time must increase linearly with the size of the search set.

On the other hand, if the target has at least one feature that is different from features that distractors consist of, the neuron(s) will separate its oscillation phase and will unbind from the rest of the stimulus. In this case information sufficient to detect the target will enter the later stages of processing without a need for the attentional spotlight. Consequently, the time for detecting the target will be shorter and will not depend on the number of other features (i.e., distractors).

Horowitz and Wolfe's (1998) finding that the visual search does not involve memory for previously searched parts of the stimulus might help understanding some properties of the searching mechanism. Because the neurons in this model are neither perfectly synchronized nor perfectly desynchronized, and because the oscillatory patterns of neurons show either chaotic or random fluctuations, it is conceivable that the neurons that are mutually desynchronized fire simultaneously by chance for a very brief period of time. A mechanism that would use this random coherent firing of non-synchronized neurons to attract attention would probably be the simplest solution to visual search. The advantage for the brain by using such an approach for visual search is that most of the process relies on the computations in the visual cortex and the demand on other systems such as frontal lobe or memory system is minimal. The only control that would be required from the frontal lobe would be to prevent other activities from taking place (i.e., redirect attention) during the search. The only requirement on memory would be the current content of the attended part of the stimulus in visual working memory. This strategy would, therefore, post minimal requirements on the limited resources of controlled processes.

The learning mechanism

Long term potentiation (LTP) and long term depression (LTD) have been recognized as the most likely mechanisms involved in neural learning (e.g., Bear 1996; Singer & Artola, 1994). The biochemical mechanisms underlying the synaptic changes on both the presynaptic and postsynaptic sides have also been well studied (e.g., Morris, Andersong, Lynch, & Baudry, 1986; Castro, Silbert, McNaughton, & Barnes, 1989). The learning rules behind the LTP and LTD do not follow completely the basic principle underlying Hebb's (1949) learning rule: if the presynaptic and postsynaptic neurons are both active at the same time, the strength of the connection between them will increase. We know today that the rules of synaptic change observe some significant deviations from Hebb's rule. For example, Hebb did not postulate that synaptic efficiency could decrease.

Decades of development in neural network modeling have lead to the development of many mathematical models of synaptic learning mechanisms, some of which follow more or less Hebb's principle. Most models (e.g., Grossberg, 1987) allow synapses to increase and decrease their weights. The increase typically occurs according to Hebb's rule while the decay in synaptic efficacy is assumed to take place gradually if there is no correlation in activity between the two neurons.

Neurophysiological research has, however, recently shown that the behavior of synapses is more adaptive than was initially assumed (e.g., Singer & Artola, 1994).

It has been shown that synapses increase their efficacy (LTP) only if a certain degree of correlation between the activity of the two neurons is reached (i.e., there is a threshold value for LTP). More surprising was the finding that for the subthreshold correlation in activity, the synaptic efficacy decreases (LTD). In other words, even though the two neurons are correlated in their activity, the strength of the connection between them decreases if the degree of correlation is low. Equally surprising was the finding that the synapse does not change if the correlation between the two activities is zero.

It seems therefore that the biological neurons have a slightly different philosophy of weakening their synapses than what was previously assumed. The forgetting takes place if two neurons are weakly correlated, not if they are not correlated. Such a rule provides different forgetting patterns. If either of the two neurons is not used, there will be no forgetting (in this way, the information is ensured to remain even if it is not used). But forgetting will take place if the two neurons have a connection, but the connection does not seem to be useful. The criterion of non-usefulness of the synapse occurs if the two cells are active but poorly correlated.

Finally, it is important to mention that the LTP process has been shown to depend highly on the precise timing of the incoming action potentials (Markam et al., 1997). It is the degree of synchrony in firing of neurons that determines the speed and direction of changes in synaptic efficacy.

Therefore, in order to successfully implement a learning mechanism in an oscillatory neural network that employs action potentials and their synchronization, it was necessary to develop a learning mechanism that mimics the experimentally obtained knowledge on LTP and LTD mechanisms.

Specification of the synaptic model

The correlation in activity, C, between two neurons is defined in the following way:

$$C_{ij} = P_i x_j$$

where P_i denotes activity of the presynaptic neuron and is 1 if the neurons fired an action potential and 0 otherwise. x_j is the level of depolarization of the membrane potential of the postsynaptic neuron. Synaptic efficacy changes according to the following formula:

$$w_{t+1} = w_t + K \cdot C \cdot r \cdot (1 - w)$$

where w denotes the synaptic weight, r denotes the learning constant $(r << 1)$, and K is determined in the following way:

$$K = \begin{cases} 1, & \text{if } C \geq Pt \\ 0, & \text{if } C < Dt \\ -1, & \text{otherwise} \end{cases}$$

where *Pt* represents the potentiation threshold and *Dt* represents the depression threshold.

Depression threshold, *Dt*, is computed as:

$$Dt = Pt / 10$$

Figure 20 summarizes the mathematical model of the synapse. If an action potential arrives when the post-synaptic cell is well depolarized, the synapse will increase its efficacy. If an action potential arrives when a cell is weakly depolarized, the synapse will change in the opposite direction. Finally, if there is no action potential or if there is a very weak depolarization, the synaptic strength will not change. The range of the possible values of the potentiation threshold is also shown.

[Insert Figure 20 about here]

Because there are no nonlinear terms in the model, the model is computationally efficient but still encompasses the basic properties of the learning processes on synapses.

Learning and development of automaticity

The most interesting question about the learning process in oscillatory neural network is its effect on controlled processes. As previously discussed, extensive practice leads to automaticity, that is, a change in processing strategy from controlled to automatic. Here we are interested in whether the learning process discussed above could underlie the development of automaticity.

We apply the learning mechanism to the neural network in Figure 11. It was shown that the *novel-stimulus* network has more properties of controlled processes than a *well-learned* network does. In Table 1 it is shown that after 13000 computational steps, the *novel-stimulus* network architecture restructured in such a way that it more resembles the well-learned network. The synapses that significantly changed were only those that connected neurons that belonged to the same oscillating group. In other words, only if the neurons were synchronized with near to zero time-lag does the synapse learn. The synapses among neurons that belonged to different oscillatory groups changed very little, indicating that learning between non-synchronized neurons could still take place, but it was much slower.

The network after learning is more similar to the *well-learned* network in Figure 11 and it should share more similar processing characteristics: faster, more accurate and less capacity-demanding processing. In other words, automaticity has

developed. In psychological terms it could be that the system learned to associate each letter with its corresponding color (i.e., R is always blue). This learning is on the automatic level because the association relies on strength of connections without intermediating synchronous patterns.

It is important to note that even though all the neurons in the network have approximately equal firing rates, the learning took place only among the neurons that synchronized their action potentials. The classical approach to neural network conceptualization and simulation, where only the firing rate of neurons is considered, would necessarily result in all the synapses among activated neurons being strengthened. The result would be catastrophic for a network's performance because the network could not distinguish between the letters and colors any more. We conclude therefore, that the system has an ability to change its architecture so the synchronous patterns that are slow to form and weak at the beginning form faster and become more robust after learning. And the demand for the limited processing capacity decreases at the same time.

It is also important to note that the network was continuously stimulated by consistent pairing of letters and colors. An inconsistent pairing would not produce the same result. In a case of inconsistent pairing, two neurons that would strengthen mutual synapses in one trial, would weaken them in the next trial. This property of the network is in agreement with the finding by Shiffrin and Schneider (1977) that consistent mapping results in a relatively fast development of automaticity, while

automaticity develops much slower, if at all, for inconsistent mapping. However, there is no evidence that development of automaticity cannot take place for inconsistent mapping. On the contrary, it has been shown that in some conditions inconsistent mapping can result in automaticity (Durso et al., 1987). We do not know if an extended practice in the Shiffrin and Schneider's task would lead to a higher degree of automaticity. On the other hand, we also know that a neural network architecture that employs (automatic) detection of inconsistently combined features could be easily implemented with several layers of neurons. Finally, the same type of learning might take place in the cortex and in the hippocampus. The need for more rapid learning in hippocampus (e.g., Banquet, et al., 1998) might be fulfilled through a faster learning rate with the same underlying mechanism. The only conclusion, therefore, that could be made from the simulations reported here is that synchrony-based neural networks learn to automate consistently mapped input much easier than inconsistently mapped.

Because of the ability to provide selective update of synapses it is possible that this learning mechanism could provide a protection from the stability-plasticity dilemma (Grossberg, 1987) also known as catastrophic interference (Lewandowsky & Li, 1995); that is, when network learns new material, it forgets what it previously learned. The Adaptive Resonance Theory by Grossberg (1987) is widely considered to be today the best solution to this problem. The mechanism is, however, quite complex. A learning process that is sensitive to synchrony in neural activity might be a more elegant solution to the problem. Because the synapse will learn only if the

neurons are synchronized, the system allows for many neurons to be simultaneously active without changing their connection strength. Therefore, if the stimulus activates a neuron but the neuron does not synchronize with other neurons, there might be no significant changes to this neuron's connectivity. In addition, this system seems to perform a matching test 'naturally' by desynchronizing the neurons that do not belong to the same category. This same matching test might play a similar role to that of the 2/3 rule proposed by Grossberg (1987). A solution to the stability-plasticity dilemma could therefore be an emergent property of the system (i.e., no additional mechanisms need to be assumed), but more research needs to be done to answer this question.

Discussion

That the brain processes information by performing mathematical mapping is well known. This mechanism has been widely explored both experimentally (e.g., receptive fields) and theoretically (most neural network models). What is new is that there seems to be another, slower process for information processing that gives rise to attention and consciousness. With learning and practice the brain seems to learn new mappings so that in a familiar situation, it reduces the need for this slower, attention-based process.

Our primary conclusion is that synchronized neural firing could have two relatively independent effects on the processing in the brain. 1) On the shorter time scale it seems to be able to provide mechanisms related to controlled processes such as binding, attentional filtering, engagement of automatic processes and limited capacity. 2) On the longer time scale, the learning process might benefit from selectively strengthening the synapses connecting only well synchronized neurons.

Two or three decades of connectionist modeling research that employed only inhibition and excitation have produced numerous models that provide explanations for many phenomena in human cognition. Assuming a computational role of synchronous firing does not necessarily exclude those models. On the contrary, it might improve them and provide an understanding of how the brain puts many of

these, previously studied, subsystems together and how it decides which subnetworks will be engaged in a particular situation. Because the distinction between automatic and controlled processes applies to a wide range of cognitive phenomena (i.e., from the perception of simple patterns to social cognition), a consideration of synchronous neural activity has a significant potential to bridge many aspects of the mind/brain barrier.

We believe that the behavior and possible computational mechanisms of the synchronous neural activity modeled here are quite likely to produce similar effects in the brain. We also believe that the computer simulations and the discussion presented here makes a strong case that the controlled processes in human cognition emerge from the interaction of oscillatory and synchronous activity of nerve cells in the cortex. Therefore, we argue that it is necessary to consider the role of synchronous neural activity whenever neurophysiological mechanisms of cognitive phenomena (including controlled processes) are studied. Because most cognitive phenomena involve controlled processes to some degree, synchronous neural activity might be a significant factor in bridging the brain-mind barrier and help provide additional physiological understanding of many psychologically observed phenomena for which the traditional neural network conceptualization as inadequate.

Another attractive property of a synchrony-based model for a possible explanation of cognitive phenomena is that many computational phenomena 'emerge'. In other

words, if a certain behavior of the model, such as early filtering or limited capacity, emerges from the most fundamental assumptions (i.e., the model of the neuron) without a need for introducing new assumptions, the model should be seriously considered for further exploration and experimental testing. Please note that the model used here has very few assumptions, most of which are included in the equations for the neuron and the synapse. The neural network architectures used to demonstrate the behavior of synchronous neural networks is only one example and many other architectures would provide similar synchronous behavior (as it is the case with synchronization and limited processing capacity that have been shown in other oscillatory models). For this reason, the theoretical work shown here might not be considered to be a proposal for a model in the strict sense but rather a study of the behavior of oscillatory/spiking sorts of systems that demonstrates that their general properties might underlie some general cognitive phenomena. Another set of differential equations that produces synchronous and spiking activity organized into different neural network architectures is quite likely to demonstrate similar behavior (synchronization, phase shift, limited capacity, etc.). The purpose of this study was not to propose a model that explains particular experimental data, but to provide arguments for more serious consideration of the synchrony in neural firing (presumably with more advanced models than the one studied here).

The theoretical framework proposed here is not necessarily a competition to other theoretical approaches addressing similar issues. First, the model discussed here is an attempt to provide a better understanding of the neurophysiological foundation

for the feature binding theory (Treisman 1982; 1986; 1995). We also believe that it is consistent with Logan's exemplar theory of automaticity (Logan, 1988) that proposes that automaticity is developed gradually by acquiring a new memory trace with each episode. The approach discussed here suggests, however, what kind of effect each exemplar might have on the neurophysiological level. It is clear that the process of acquiring automaticity in many circumstances might be more complex than in the models discussed here.

Meyer and Kieras (1997), for example, emphasize the possibility that changes in information processing strategy rather than automaticity might decrease some limitations in processing capacity. In a follow up study, Schumacher et al. (1998) clearly demonstrated how an instruction to give the same priority to two simultaneous tasks allow people to perform time sharing that results in no interference among tasks. In other words, a change in strategy in the psychological refractory period paradigm can overcome the apparent limitation in processing capacity. Therefore, the processing strategy that one uses for information processing undoubtedly plays an important role in the speed and accuracy of information processing. However, our belief is that Meyer and Kieras' model addresses different aspects of cognitive limitation than the work presented here. In order to accept a view of the mind that does not assume any limitation in working memory capacity, as Meyer and Kieras propose, it would be necessary to demonstrate that a change in strategy could overcome a wide range of cognitive limitations that have been observed through years of research of cognitive phenomena. As it stands now,

however, it seems that the strategy can account for only a minor part of effects caused by automaticity. It is our belief that an appropriate strategy for information processing could somewhat improve processing capacity initially and hence help faster development of automaticity. Practice and learning that causes restructuring of neural networks, however, is probably necessary for the development of skilled performance. In terms of everyday practice, instructions for appropriate strategy might be provided by a coach or instructor, but practice is still essential for a skill to be developed.

Collapse of computational complexity

One cannot emphasize enough the superior adaptability of the brain as compared to any information-processing device created by humans. Consequently, an interesting and important question pertains to understanding the differences in information processing between the brain and the von Neumann computer architecture (e.g., Dreyfus, 1992). We close with a discussion of the implications that the brain mechanisms proposed here have on the issue of computational complexity.

There are two major approaches to defining and measuring computational complexity. The Solomonoff-Kolmogorov-Chaitin measure of algorithmic complexity, simply put, uses the length of the shortest computational algorithm (or program) necessary to accomplish certain computations as a measure of the

computational complexity (Chaitin, 1977). Therefore, the larger number of more fundamental operations the system has, the shorter the algorithm could be and the smaller the degree of complexity. Bennett's approach, called computational depth, defines computational complexity as the number of computational steps necessary to complete the computation (Bennett, 1985). Similarly to Halford's et al. (1999) proposal, we suggest that the one-directional mapping through several layers of neurons should be considered the simplest possible way to process information for the brain - that is, one computational step. The longer it takes to form appropriate synchronous patterns, and the more capacity from the limited resources is taken in order to accomplish the task, the larger the processing complexity is.

Mapping in a neural network, therefore, could be compared to a single machine instruction or to a look-up table. On the other hand, attentional and working memory processes that employ synchrony are analogous to several steps of CPU processing. The results and the theory provided here show how a decrease in complexity on both measures of computational complexity occurs with learning. By growing new connections (i.e., new mappings) the brain develops new 'functions or operations' and processing becomes much faster. Eventually, any computational process (or at least many) could be ultimately implemented in one single computational step. Even though this analogy with the computational science is rather rudimentary, we believe is sufficient to make the point that the computational changes resulting from automaticity in the brain could be referred to as a minimization or a *collapse of computational complexity*.

We believe that this ability to minimize its computational complexity is an important adaptive feature that distinguishes the brain from today's computers. If a computer would build look-up tables (or new machine instructions) for all functions that it repeatedly uses, the execution of programs would become faster and faster with time. There would also be less and less computational demands posted on the CPU and more and more of its capacity could be devoted to additional tasks. A slow processor paired with a huge and fast memory for look-up tables would probably be the most optimal architecture for such a device. According to the synchrony-based theory and simulations provided here, this is exactly what kind of computer the brain is.

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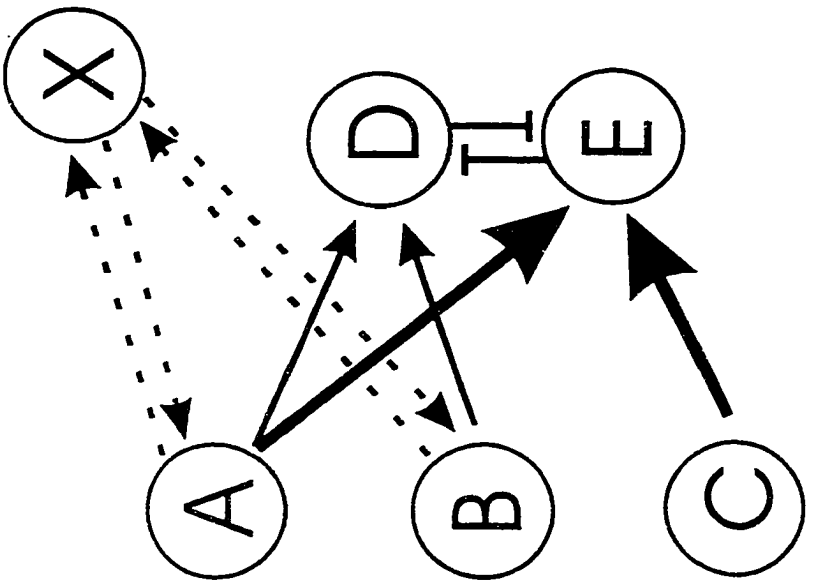
Before learning:

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1		0.8	0.2	0	0	-0.5	-0.5	0	0	0	-0.5	-0.5	0	0	0
2	0.8		0.2	0	0	-0.5	-0.5	0	0	0	-0.5	-0.5	0	0	0
3	0.2	0.2		0.2	0.2	0	0	-0.5	0	0	0	0	-0.5	0	0
4	0	0	0.2		0.8	0	0	0	-0.5	-0.5	0	0	0	-0.5	-0.5
5	0	0	0.2	0.8		0	0	0	-0.5	-0.5	0	0	0	-0.5	-0.5
6	-0.5	-0.5	0	0	0		0.8	0.2	0	0	-0.5	-0.5	0	0	0
7	-0.5	-0.5	0	0	0	0.8		0.2	0	0	-0.5	-0.5	0	0	0
8	0	0	-0.5	0	0	0.2	0.2		0.2	0.2	0	0	-0.5	0	0
9	0	0	0	-0.5	-0.5	0	0	0.2		0.8	0	0	0	-0.5	-0.5
10	0	0	0	-0.5	-0.5	0	0	0.2	0.8		0	0	0	-0.5	-0.5
11	-0.5	-0.5	0	0	0	-0.5	-0.5	0	0	0		0.8	0.2	0	0
12	-0.5	-0.5	0	0	0	-0.5	-0.5	0	0	0	0.8		0.2	0	0
13	0	0	-0.5	0	0	0	0	-0.5	0	0	0.2	0.2		0.2	0.2
14	0	0	0	-0.5	-0.5	0	0	0	-0.5	-0.5	0	0	0.2		0.8
15	0	0	0	-0.5	-0.5	0	0	0	-0.5	-0.5	0	0	0.2	0.8	

After learning:

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1		0.91	***0.64***	***0.57***	***0.59***	-0.5	-0.5	0.02	0.03	0.04	-0.5	-0.5	0	0.01	0
2	0.91		***0.67***	***0.57***	***0.59***	-0.5	-0.5	0.03	0.05	0.05	-0.5	-0.5	0	0	0
3	***0.67***	***0.66***		***0.64***	***0.64***	0.03	0.05	-0.5	0.05	0.04	0	0	-0.5	0.01	0
4	***0.57***	***0.58***	***0.65***		0.9	0.03	0.05	0.04	-0.5	-0.5	0	0	0	-0.5	-0.5
5	***0.58***	***0.59***	***0.66***	0.91		0.02	0.05	0.03	-0.5	-0.5	0	0	0	-0.5	-0.5
6	-0.5	-0.5	0.03	0.03	0.04		0.91	***0.65***	***0.54***	***0.55***	-0.5	-0.5	0	0	0
7	-0.5	-0.5	0.05	0.05	0.05	0.91		***0.64***	***0.57***	***0.56***	-0.5	-0.5	0	0	0
8	0.05	0.03	-0.5	0.04	0.05	***0.67***	***0.64***		***0.65***	***0.66***	0	0	-0.5	0.01	0
9	0.01	0.02	0.04	-0.5	-0.5	***0.52***	***0.55***	***0.65***		0.92	0.01	0	0.01	-0.5	-0.5
10	0.03	0.03	0.01	-0.5	-0.5	***0.53***	***0.53***	***0.63***	0.91		0.02	0	0.02	-0.5	-0.5
11	-0.5	-0.5	0.03	0	0	-0.5	-0.5	0.01	0.02	0.02		0.92	***0.66***	***0.58***	***0.6***
12	-0.5	-0.5	0.01	0.01	0	-0.5	-0.5	0.01	0.01	0	0.91		***0.65***	***0.59***	***0.61***
13	0.03	0.03	-0.5	0.01	0	0.03	0.04	-0.5	0	0.01	***0.64***	***0.65***		***0.65***	***0.64***
14	0.04	0.01	0	-0.5	-0.5	0.01	0.01	0.01	-0.5	-0.5	***0.59***	***0.56***	***0.6***		0.91
15	0.02	0.01	0.02	-0.5	-0.5	0.03	0.03	0.03	-0.5	-0.5	***0.57***	***0.58***	***0.64***	0.91	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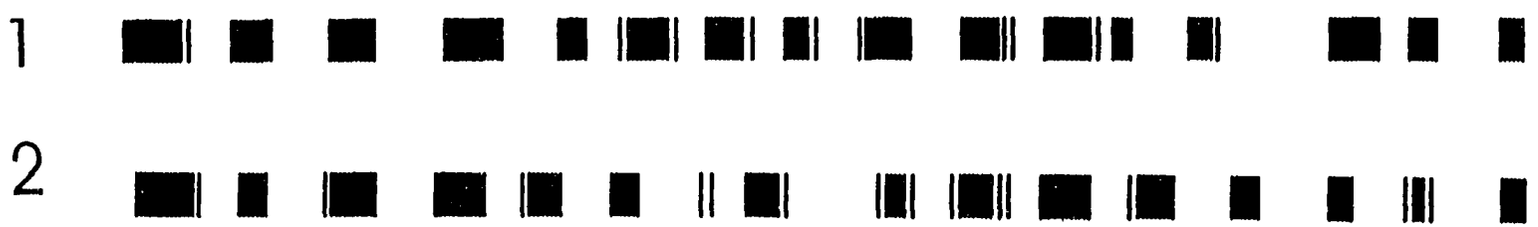

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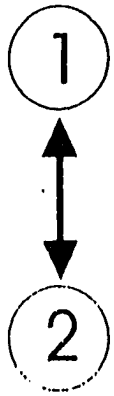

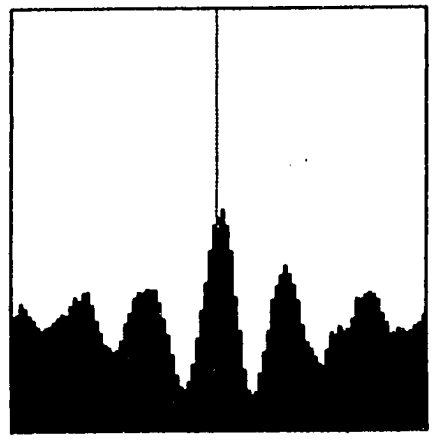

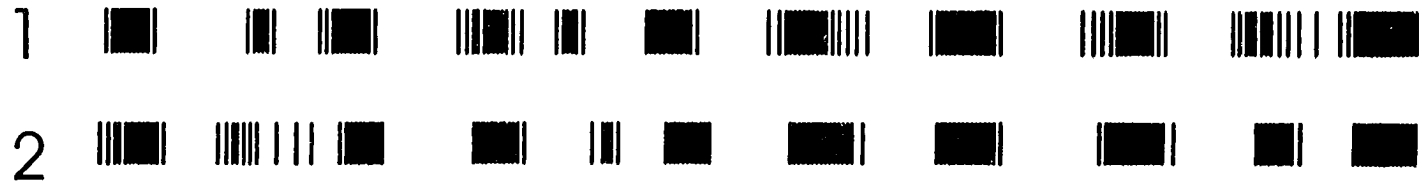

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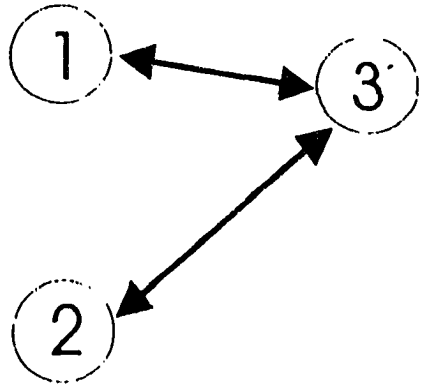

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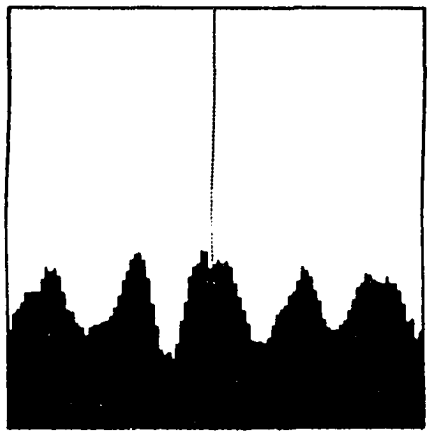

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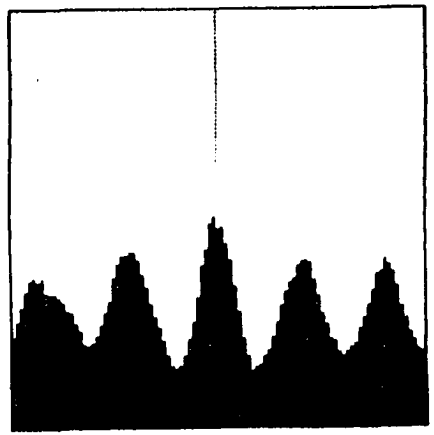

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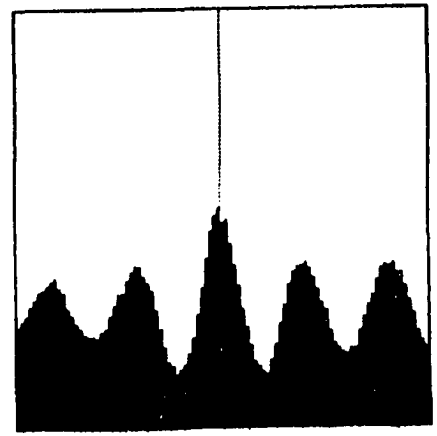

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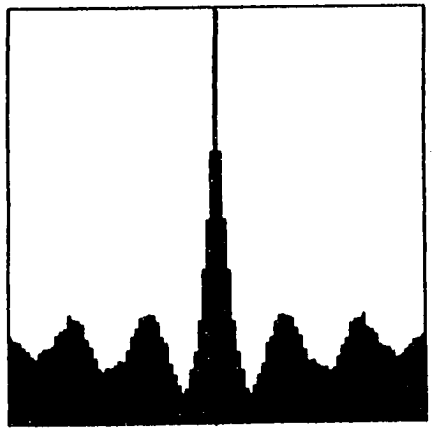

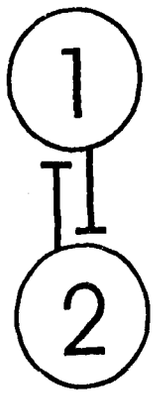
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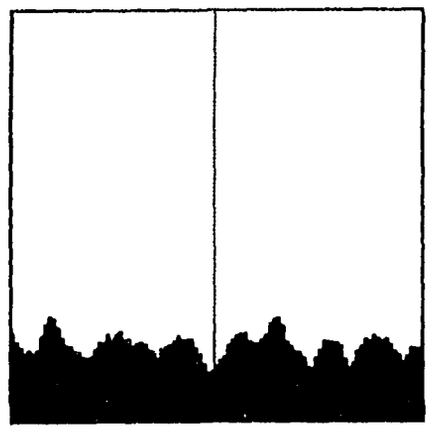

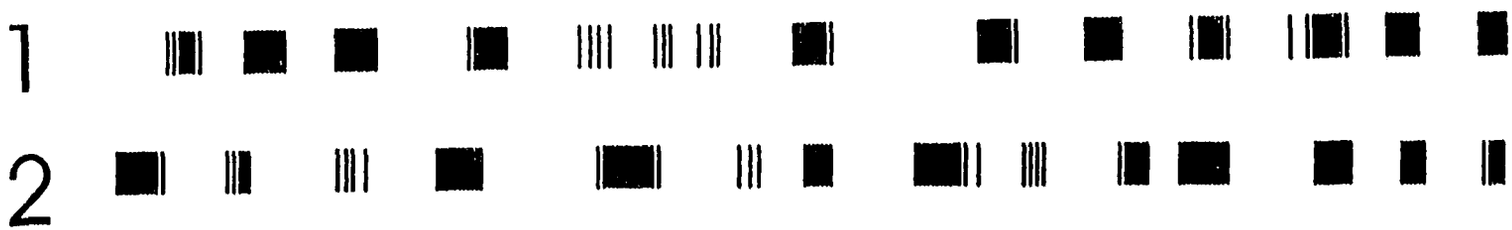
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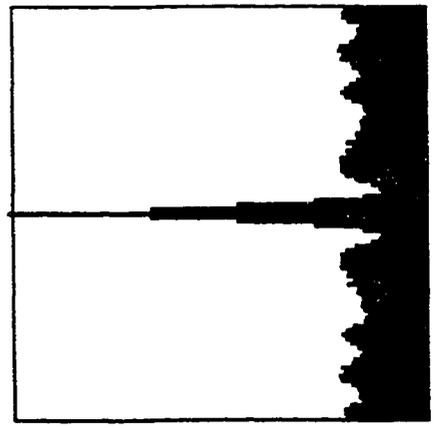

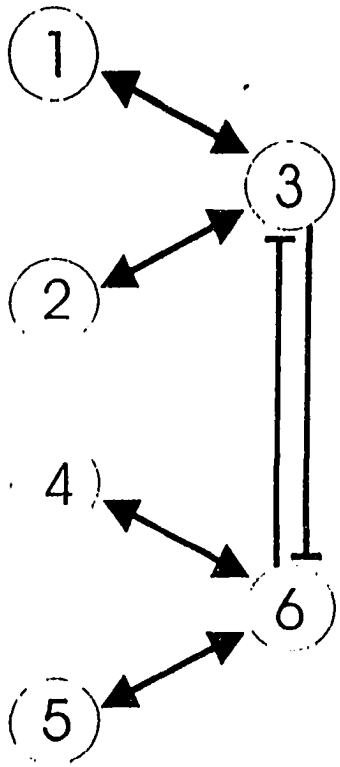

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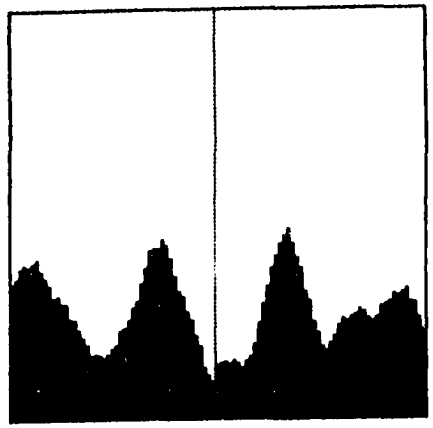

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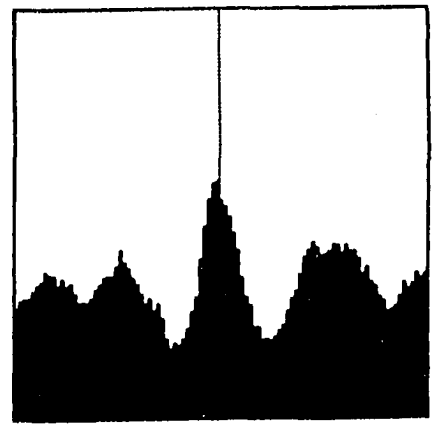

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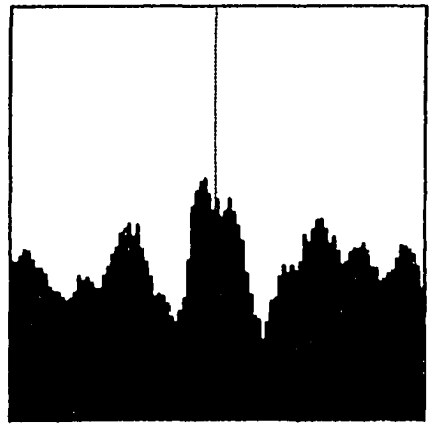

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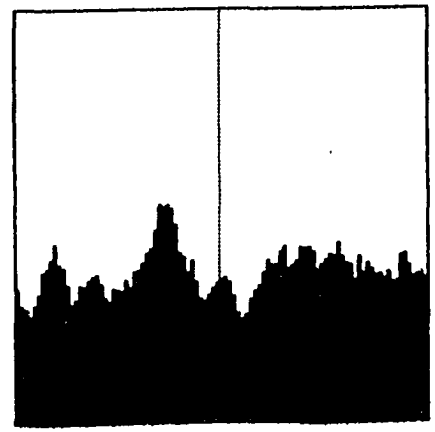

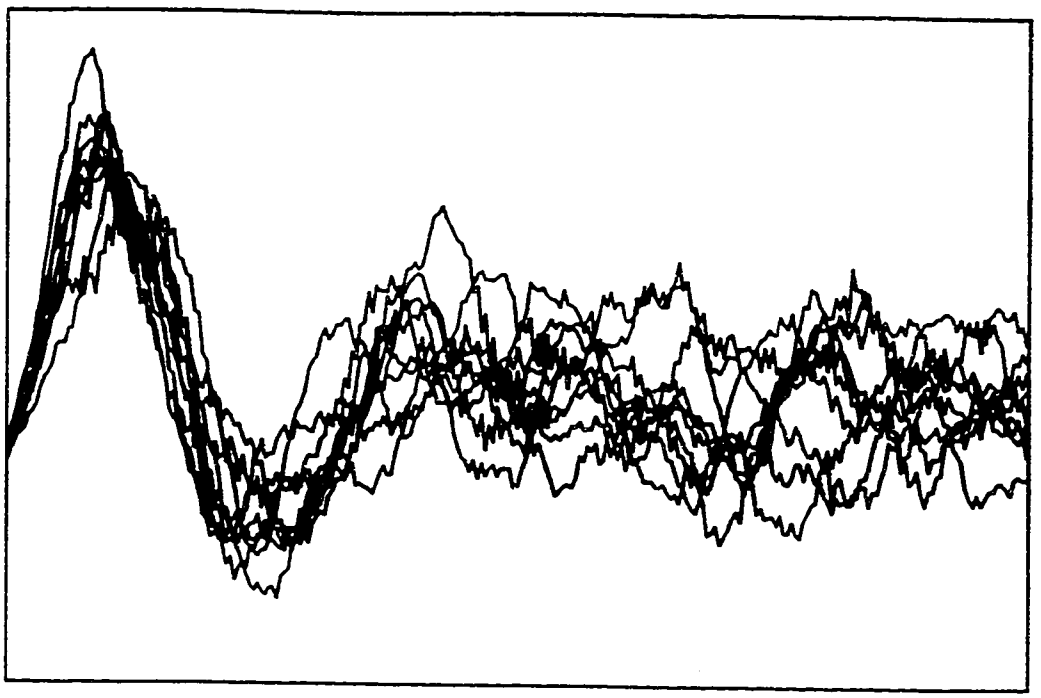

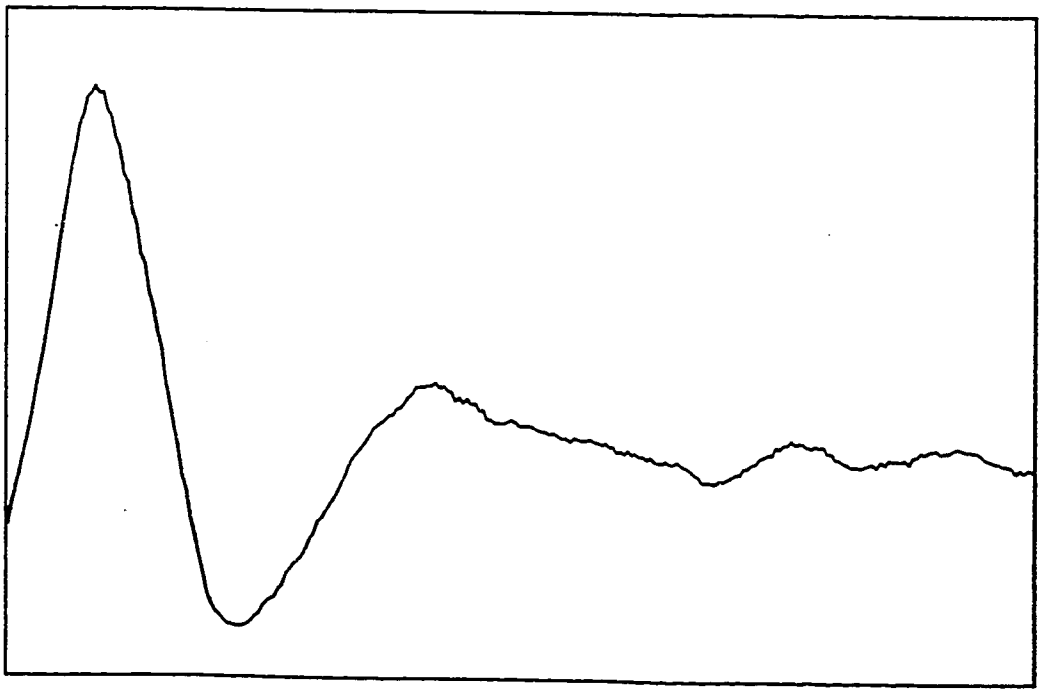

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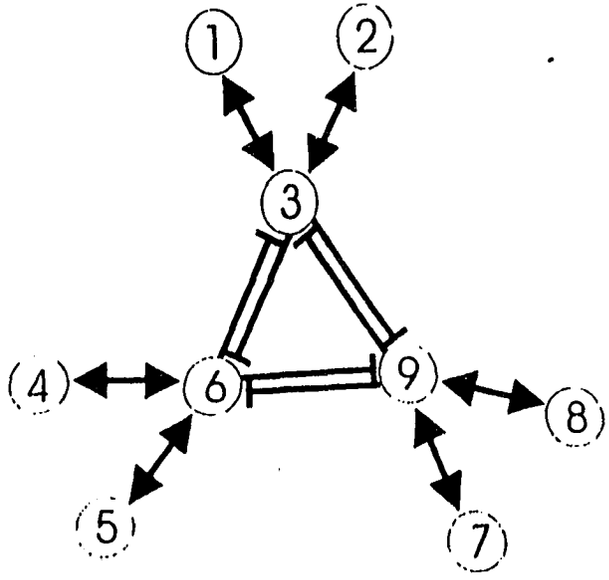

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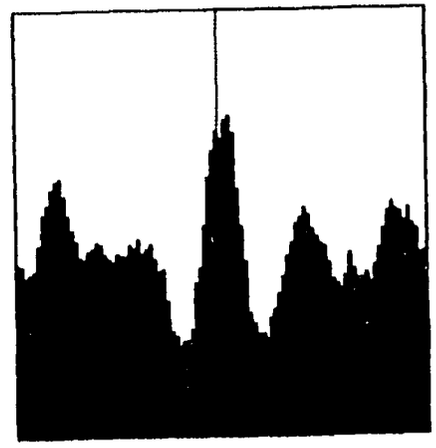

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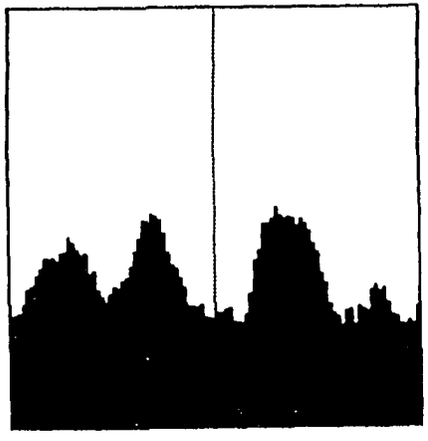

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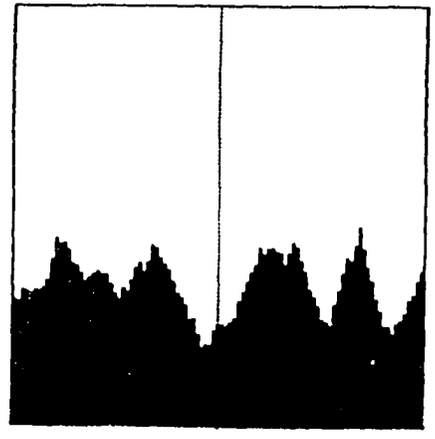

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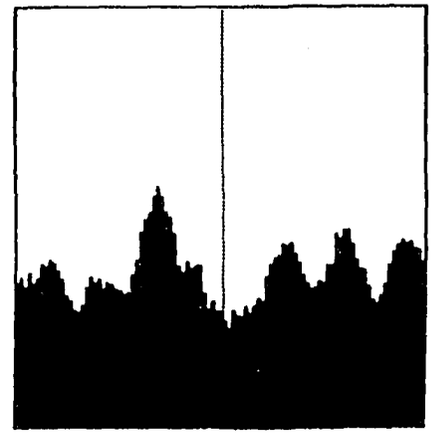

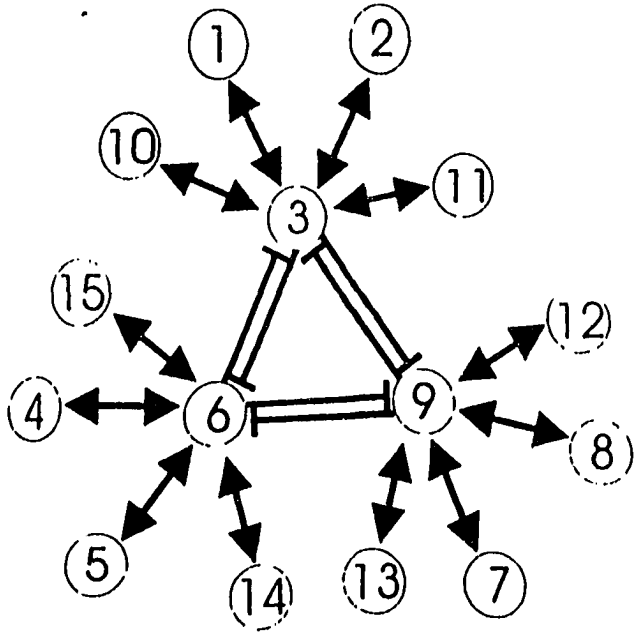

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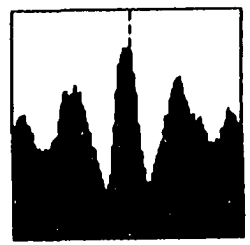

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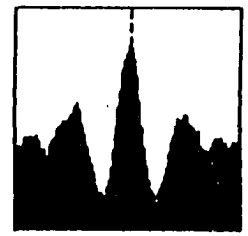

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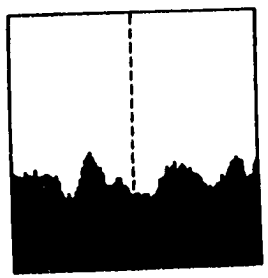

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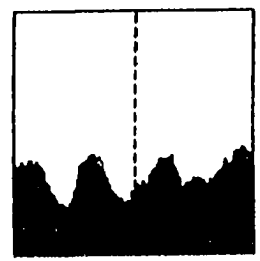

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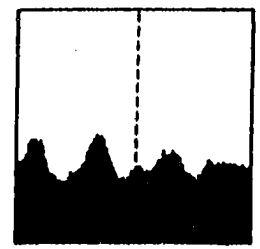

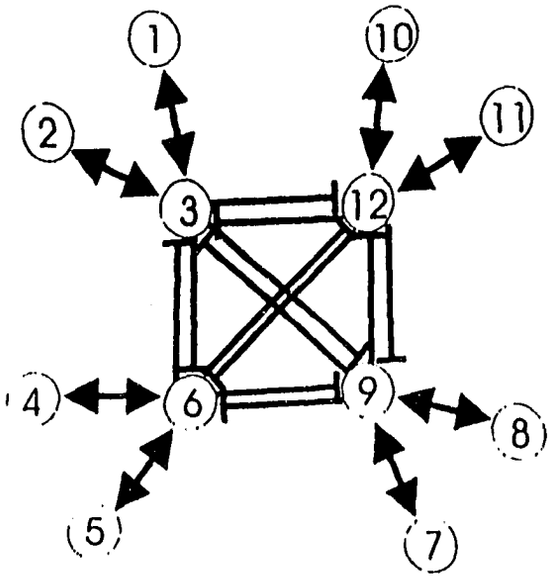

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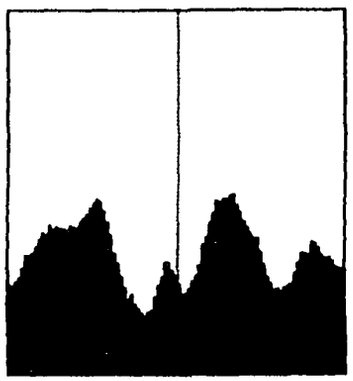

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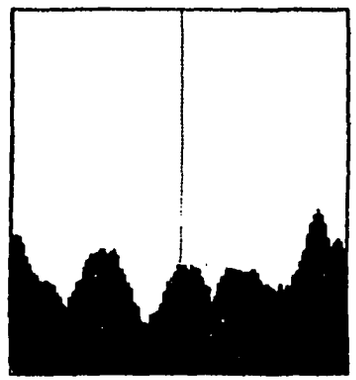

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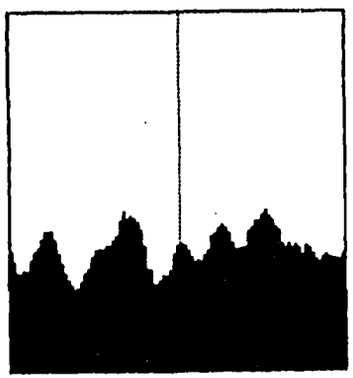

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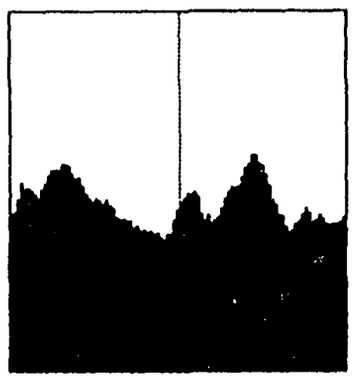

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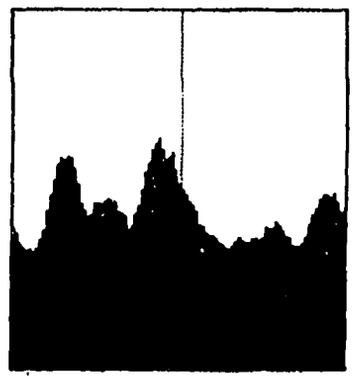

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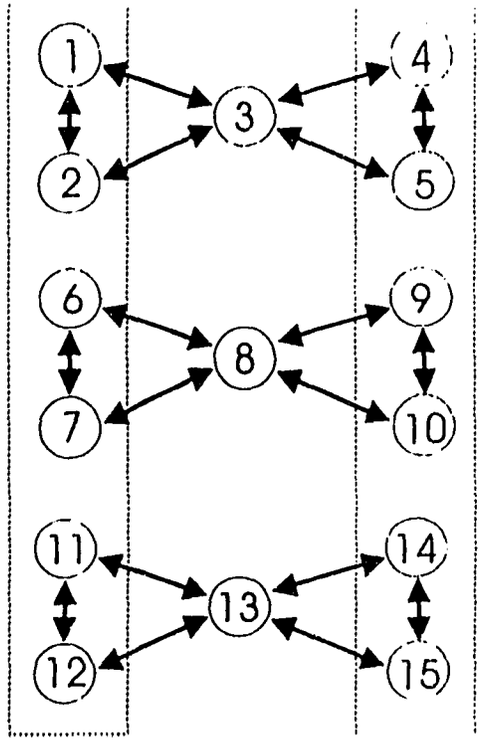

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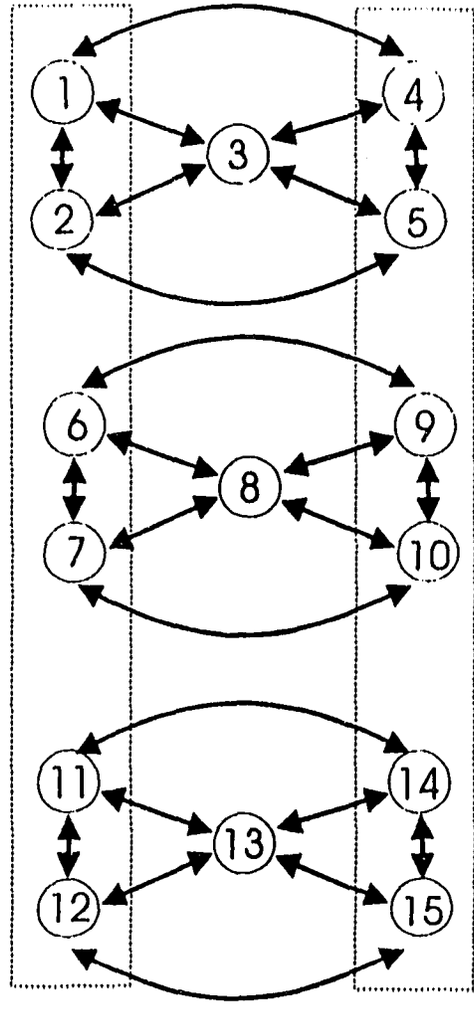

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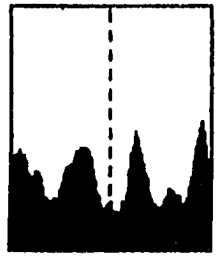

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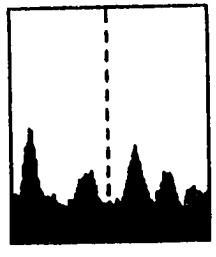

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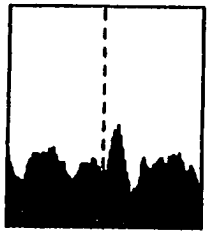

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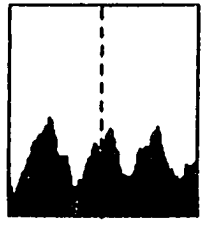

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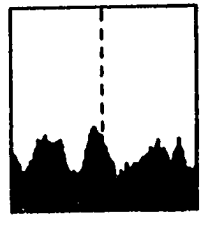

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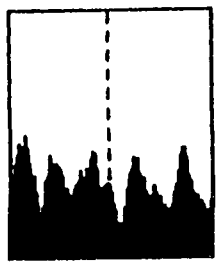

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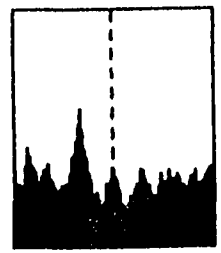

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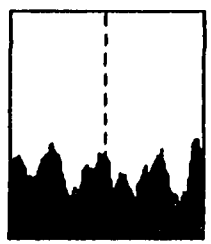

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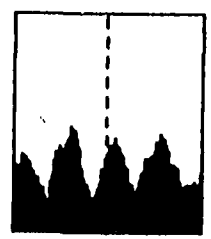

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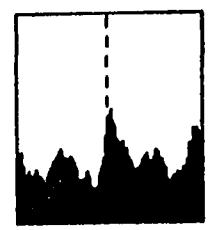

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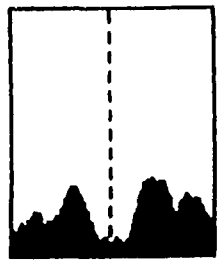

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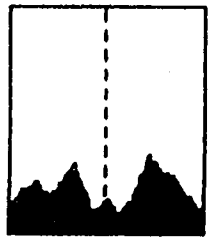

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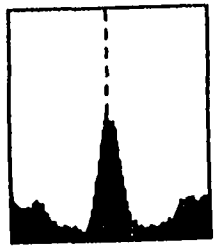

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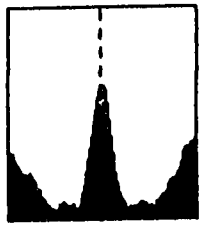

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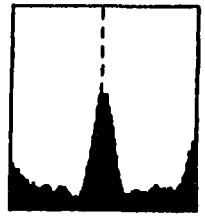

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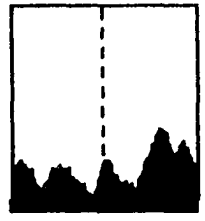

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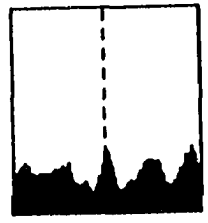

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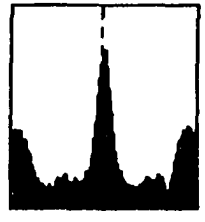

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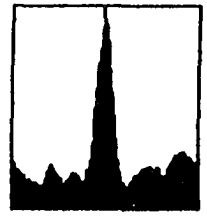

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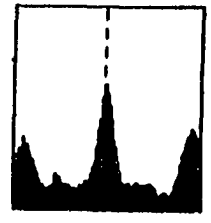

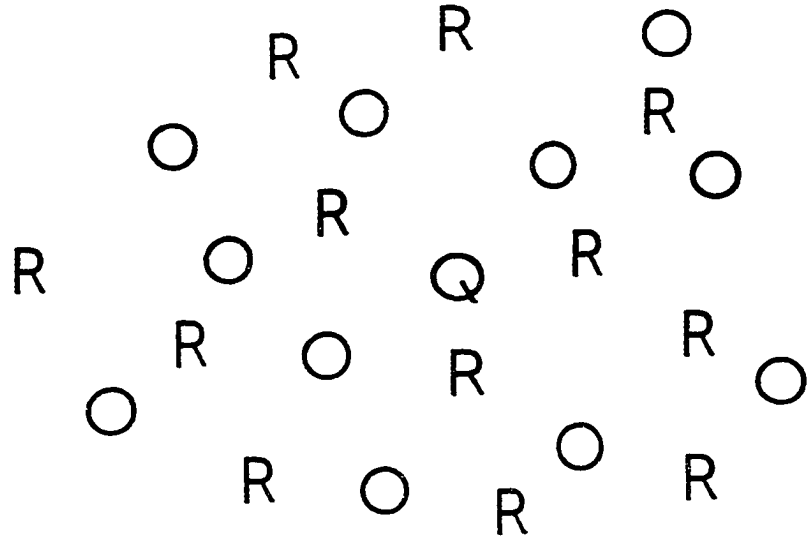
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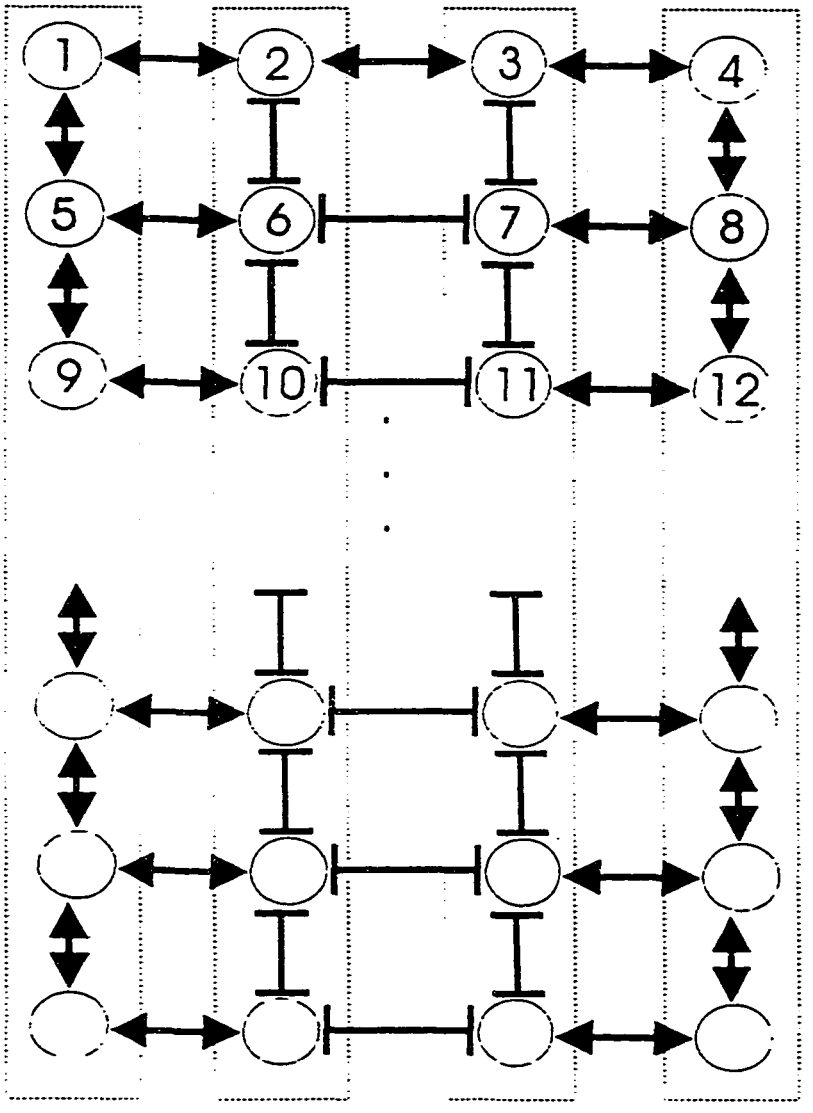
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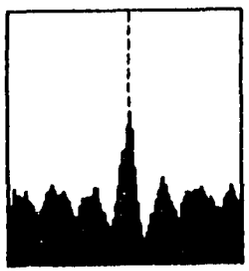

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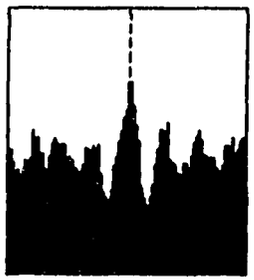

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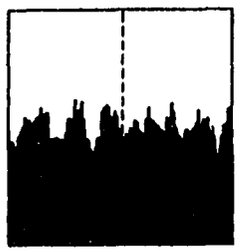

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5-8
9-12

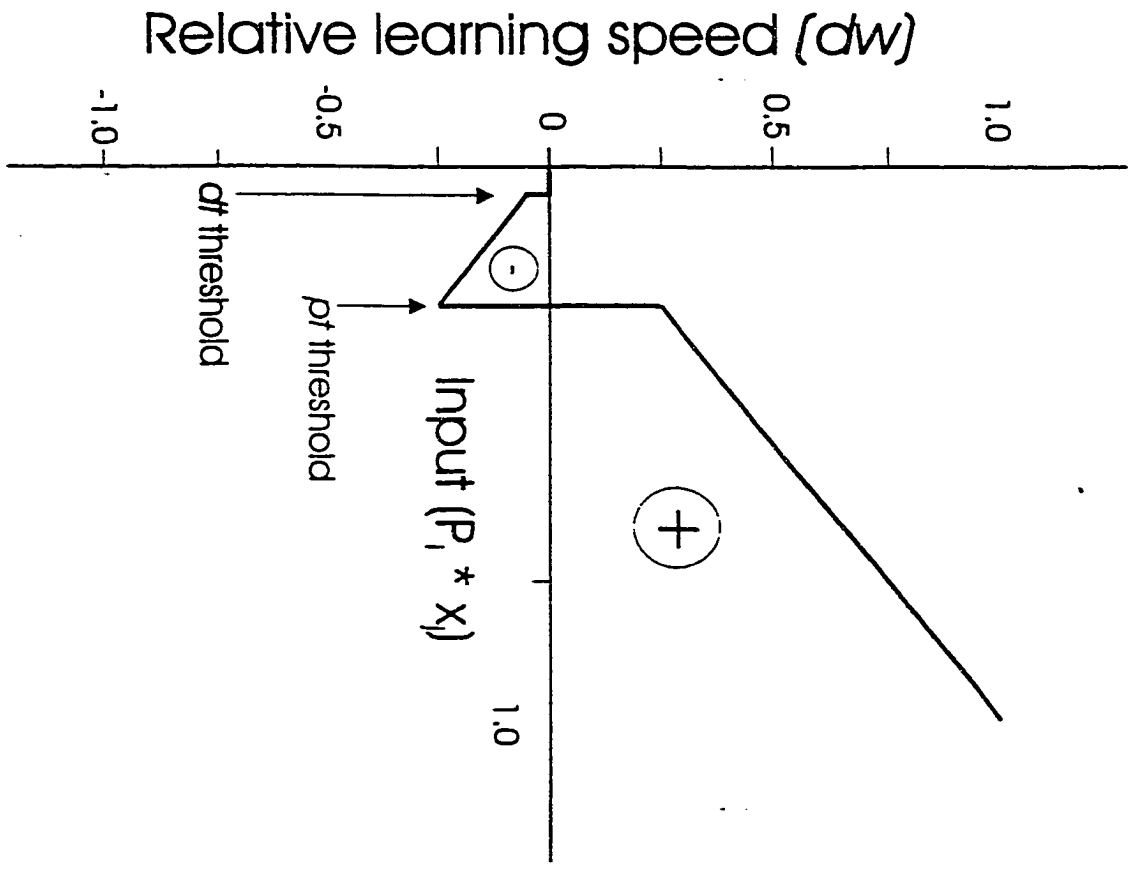
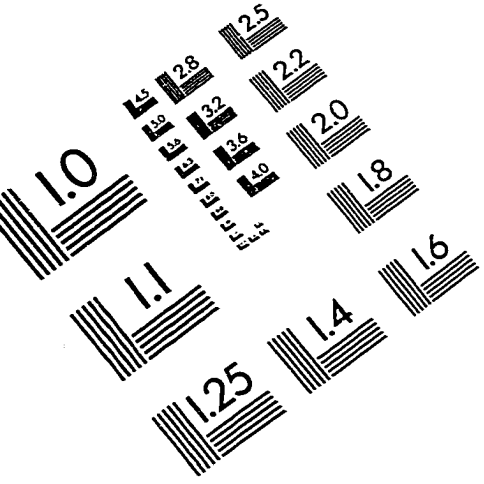
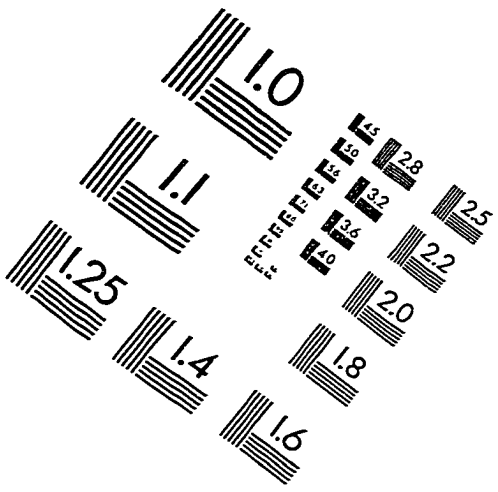
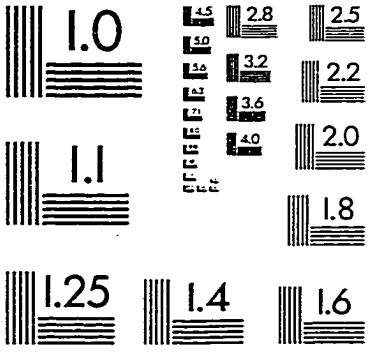
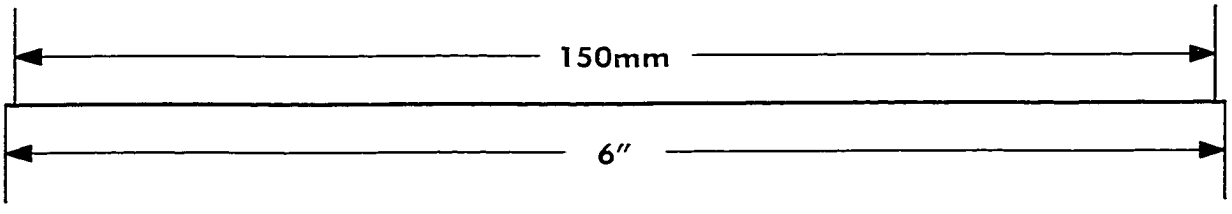

Relative learning speed (dw)
-1.0
-0.5
0
0.5
1.0
df threshold
pf threshold
Input (P_i * x_i)
1.0
-
+

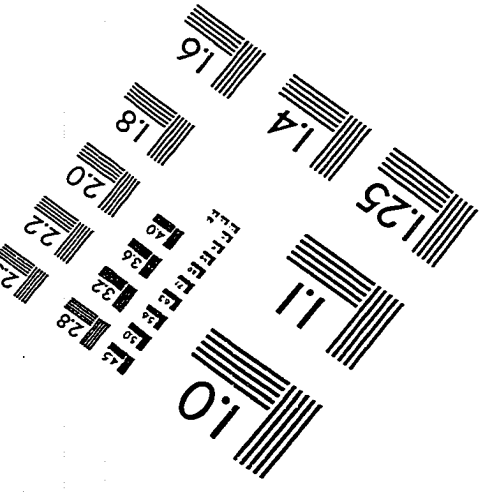
IMAGE EVALUATION
TEST TARGET (QA-3)

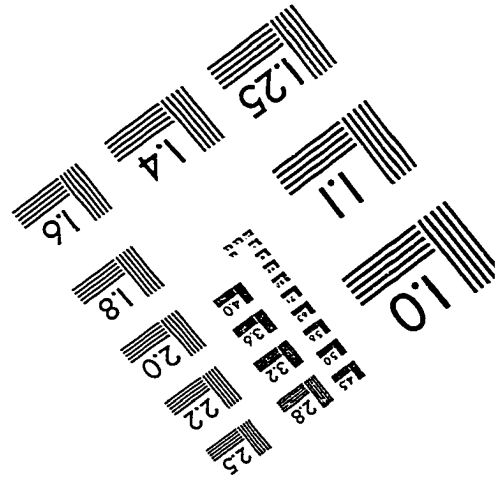












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