Synchrony: a neuronal mechanism for attentional selection?

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Attentional selection involves brain processes that select and control the flow of information into the mechanisms that underlie perception and consciousness. One theory proposes that the neural activity that represents the stimuli or events to be attended to is selected through modification of its synchrony. Recent experimental evidence supports this theory, by showing that changes in attentional focus increase the synchrony of neural firing in some neuron pairs and decrease it in others.

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Abbreviation
S2 secondary somatosensory cortex

Introduction

Although many studies have investigated the effects of selective attention, few have addressed directly the underlying neural mechanisms. Psychophysical studies have shown that selective attention brings into focus specific sensory events or stimuli that are relevant for behavior while suppressing events that are irrelevant.

In this review, we focus on the neural mechanisms of descending attentional selection. What are the neural mechanisms that allow some neural representations to be selectively activated while other representations are suppressed? We discuss hypothetical mechanisms that might account for the selection process and we concentrate on the potential role of synchronous firing among populations of neurons.

Mechanisms for selection

Attention can be regarded as a mechanism for controlling perception — that is, what enters consciousness and what does not. Perception is more than sensation; it is the result of an interaction between sensation and memory. In principle, attention could function by affecting in a selective way what is accessed in memory, by selecting the sensory information that enters into perception, or by a combination of the two. Many studies have shown that neural activity at early stages of cortical sensory processing is affected by changes in the focus of attention [1–4]. We assume that these changes in neural activity are a manifestation of the mechanisms that select the sensory information that enters perception.

The simplest selection process is a rate-based mechanism, in which the responses of neurons in early processing stages that convey information to be selected are made more prominent by raising their firing rates, whereas the responses of neurons that convey information to be ignored are made less prominent by suppressing or decreasing their firing rates. In the extreme, such a mechanism might block some sources of information completely by inhibition, making us oblivious to them. Indeed, many studies have shown that the firing rates of neurons in the sensory pathways are strongly dependent on the focus of attention; although the effect is variable, some neurons become completely unresponsive when attention is directed away from their sensory input [1,5].

Selection of sensory information by modifying firing rates is a powerful way of affecting the relative importance of different sources of information [6], but it raises the objection that it may interfere with the representation of sensory information by rate coding. If the pattern of firing rates within and between neurons in a population bears the responsibility for stimulus representation, then modification of those rates for the purpose of selection would seem to interfere with the information conveyed by the firing rates.

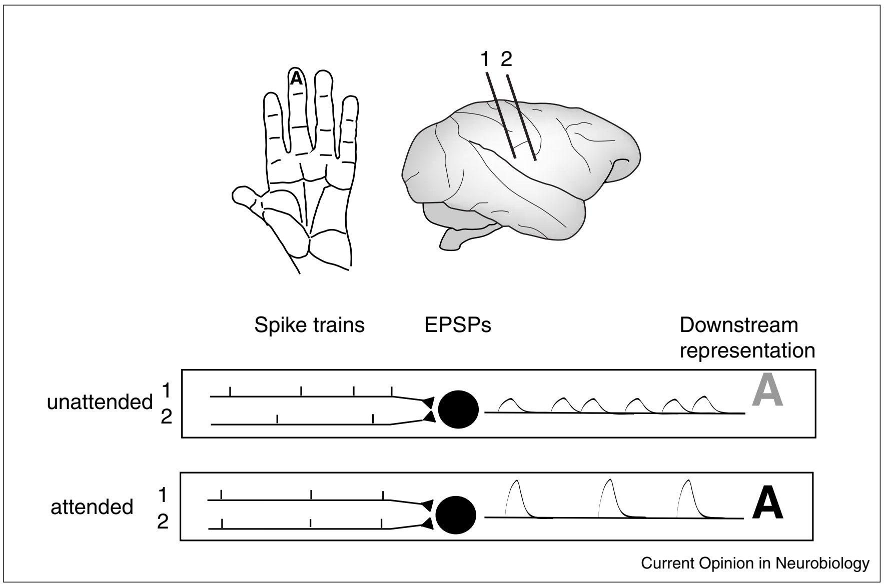
A second possible mechanism of selection involves 'shifter circuits' [7] — specialized circuits that function as switches that route information from neurons carrying the desired information to a focal processing stream. Olshausen *et al.* [8] have shown that a sufficient number of neurons are available in primate striate and extrastriate cortex to support this mechanism. Although Connor *et al.* [9] have provided evidence that neuronal receptive fields in V4 visual cortex shift toward the focus of attention, as predicted by this model, other neural correlates of the shifter control mechanism have not been found.

A third mechanism, which is the focus of this review, involves the use of synchrony to select sensory information. In this mechanism, the selection of specific sensory information is implemented by increasing the synchrony between neurons that represent the information. Synchrony is a powerful selection mechanism because action potentials that arrive synchronously at a neuron summate to evoke larger postsynaptic potentials than do action potentials that arrive asynchronously; thus, synchronous action potentials have a greater effect at the next processing stage than do asynchronous action potentials (Figure 1).

Synchrony as a mechanism of selection

An advantage of synchrony as a mechanism for selection is that it need not interfere with rate coding. A substantial change in synchrony across a population of neurons can be effected by shifting the temporal positions of action potentials slightly, so that they are aligned between neurons without any change in the mean firing rates.

Figure 1



How synchrony may function to modify the representation of selected stimuli. The stimulus is an embossed letter (A) pressed into the distal finger pad of a monkey (top left). In the attended state, the animal is required to discriminate the shape of the letter. In the unattended state, the letter is ignored while the animal performs a task unrelated to the tactile stimulus. Neurophysiological recordings are made simultaneously from pairs of neurons in somatosensory cortex (top right) that are involved in the neural representation of the letter. Below are shown examples recorded from the two electrodes of two spike trains (labeled 1 and 2) arriving at a neuron that receives inputs from the two recorded neurons. In the unattended state (top), the action potentials arrive asynchronously at the neuron; the excitatory postsynaptic potentials (EPSPs) evoked in this neuron are small and consequently produce few or no postsynaptic spikes. In this behavioral state, the downstream neural representation of the stimulus letter is weak or suppressed. In the attended state (bottom), the action potentials arrive synchronously at the neuron; the effect of synchronous inputs is to produce larger EPSPs that result in higher postsynaptic firing rates, which leads to an enhanced representation of the stimulus letter. Increasing the degree of synchrony at earlier stages also results in increasing the degree of synchrony in downstream neurons, which further strengthens the representation of the attended stimuli.

The theoretical basis for synchrony as a mechanism for attentional selection comes from conceptual work by Crick and Koch [10,11]. These authors suggested that the neural basis of visual selective attention is a change in the temporal structure of neural spike trains within the ‘focus of attention’, the part of the visual field that is attended at a given time. Crick and Koch proposed that this ‘temporal tag’, which distinguishes attended from unattended parts of the visual field, consists of oscillations in the γ range (around 40 Hz). In more detailed models, Niebur and Koch [12] and Niebur *et al.* [13] have shown that attentional selection can be produced by inserting synchronous impulses into the spike trains of pairs of neurons. The synchronous pulses can be either periodic [13], as suggested by Crick and Koch [11], or aperiodic [12]. These researchers showed that models based on this mechanism explain quantitatively rate changes in neurophysiological studies of attention in animals performing a stimulus selection task in the visual system [14]. Although the models use synchrony to predict rate changes, they also predict that the degree of synchronous firing of a neural population representing a stimulus will vary with the attentional focus. These models also account for decreased firing rates in neurons by postulating that there is synchrony based lateral inhibition (for details of these mechanisms, see [12,13]).

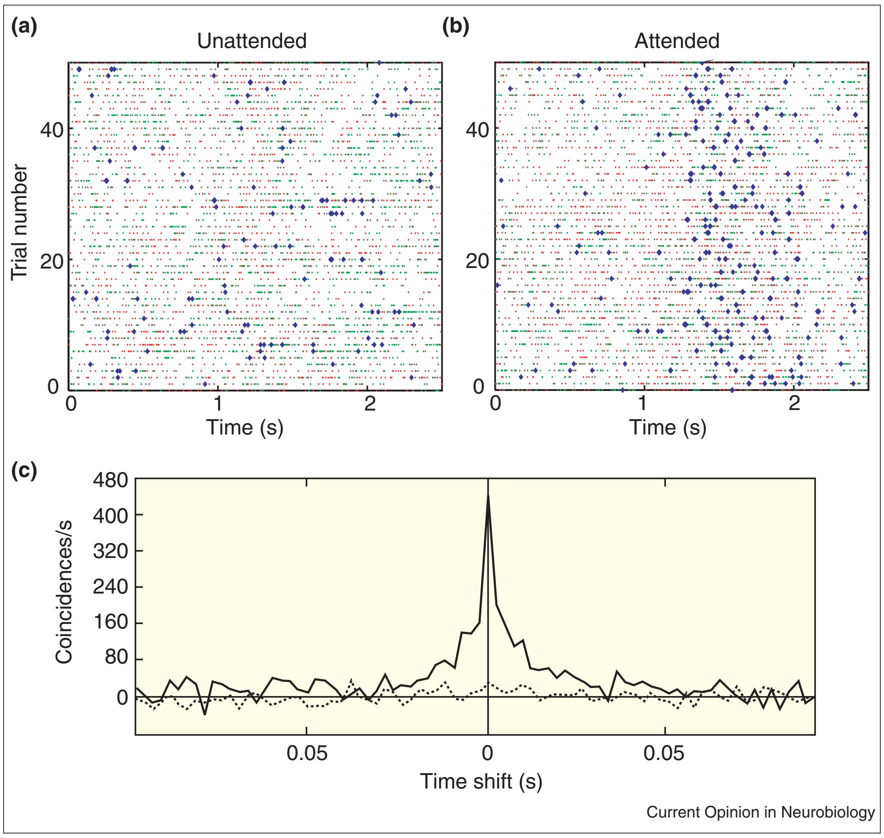
Evidence relating synchrony to selective attention

Although many studies have shown that firing synchrony in the brain is related to cognitive states including arousal, expectation, vigilance and attention [15–20], only two studies involving single-unit and multi-unit recordings (see below) have linked neural synchrony to attention in experiments in which attentional focus is controlled. De Oliveira *et al.* [21] also found that firing synchrony changed during a discrimination task and suggested that this effect was due to changes in attentive expectation, but they did not control the focus of attention.

The first direct evidence that linked changes in synchrony with changes of the attentional focus came from neurophysiological studies of neurons in the somatosensory system. Steinmetz *et al.* [22••] investigated the synchronous firing of neuron pairs in secondary somatosensory cortex (S2) of macaque cortex — an area whose spike rates are known to be influenced by selective attention [1]. Three animals were trained to switch their attentional focus between visual and tactile stimuli in discrimination tasks. In the tactile tasks, the animals were required either to discriminate the orientation of a bar or to identify embossed letters of the alphabet. In the visual tasks, the animal received the same tactile stimulation while detecting the dimming of a square on a screen.

In the monkey performing the most difficult task (letter identification with constantly changing targets), 78% of the neuron pairs fired synchronously and 35% of these pairs changed their degree of synchrony when the monkey switched attention between the tactile and visual tasks. Synchrony increased in 85% and decreased in 15% of these neuron pairs when the monkey attended to the tactile task. Note that the fraction of cells in which synchrony changed is larger than the corresponding fraction of pairs; more

Figure 2



Synchronous neural activity enhanced by selective attention. **(a, b)** Responses of a typical neuron pair in S2 while a macaque monkey attends to a visual stimulus (a) and a tactile stimulus (b). Each row in the raster represents one stimulus period of 2.5 s, which corresponds to the presentation of one letter. The letter enters the receptive field at a time of about 1.25 s. Red and green dots represent the action potentials of the neuron pair. Synchronous events, defined as spikes from each neuron that are within 2.5 ms of each other, are represented as blue diamonds. The number of synchronous events is much higher when attention is directed towards the visual stimulus (a) than when it is directed towards the tactile stimulus (b). **(c)** The difference between synchrony states can be quantified by the difference between the cross-correlation function (after subtraction of rate effects) with attention on the tactile stimulus (solid line) and that with attention on the visual stimulus (broken line). Data are taken from [22••].

specifically, the fraction of cells is the square root of the fraction of pairs. The observed 35% of cell pairs for which synchrony changed with attention therefore suggests that the fraction of cells showing changes in their pattern of temporal firing is about 60%. This is similar to the total fraction of cells in S2 whose firing rate is affected by selected attention (80%, see [1]).

Figure 2 illustrates the responses of one pair of neurons recorded while the animal switched its attention back and forth between the tactile and visual tasks. Figure 2a,b shows an example of two neural spike trains recorded simultaneously (red and green dots), and instances of correlated firing (blue diamonds) when the animal was attending and not attending to the tactile stimulus. Figure 2c shows the existence of strong cross-correlation when the animal attended to the tactile stimulus and the absence of cross-correlation when the animal attended to the visual stimulus.

In a study of visual attention, Fries *et al.* [23••] recorded multi-unit activity and local field potentials in extrastriate area V4 while the monkeys switched attention between behaviorally relevant visual stimuli and distractors. A sensitive measure of the correlation between population activity and neuronal firing is the spike-triggered average of the local field potential. Spectral analysis of the spike-triggered average showed increased high frequency (>35 Hz) synchronization, and decreased low frequency (<17 Hz) synchronization, when the animal attended to the stimulus within the receptive field of the neuron.

How is synchrony induced?

If a (periodic or aperiodic) change in synchrony is fundamental to the implementation of selective attention, then how is it generated? In other words, what types of neural mechanisms can rearrange the timing of impulses between neurons so that they are more or less synchronous?

There are at least two plausible neural mechanisms that might induce synchrony in a population that conveys sensory information. The first mechanism is based on lateral coupling between neurons. Circuitry of this type has been studied mainly in the context of periodic synchrony — that is, synchronous oscillations [24–26]. In these studies, emphasis was mainly on the binding problem [27] rather than on selective attention. It is not clear how a descending attentional mechanism could selectively synchronize one neuronal subpopulation in preference to another. It is also unclear whether such a mechanism would have the speed required of mechanisms that are responsible for selective attention.

The second mechanism is based on common input. Once an unspecified mechanism has identified the neuronal population whose activity is to be selected, synchrony can be induced by sending simultaneous action potentials to all neurons in that population. Each neuron that receives the simultaneous input is nudged towards a threshold, which increases the probability of firing of all neurons whose generator potentials are already close to threshold, thereby enhancing synchronous firing in this selected population [28]. Between these two mechanisms, the latter seems more likely. The large, descending feedback projections within each of the sensory systems provides an anatomical basis for the second mechanism. It also accounts well for the stochastic nature of the synchrony.

Conclusions and future directions

An important component of perception is the active selection of information from the wealth of input provided by all of the senses. The effects of selective attention have been studied extensively, but the essential nature of the underlying neuronal mechanisms is not understood.

The hypothesis discussed here — that selection occurs through changing the synchrony of firing in the neural populations that convey the relevant sensory information to perception — leads to quantitative predictions that have been confirmed at least partially in the somatosensory [22••] and visual systems [23••]. Future studies will determine the precise role (if any) that synchrony plays in attentional selection. Further studies of at least two types are required. First, the relationship between synchrony and attentional selection needs to be characterized in greater detail. Second, and perhaps more important, the mechanism of the changing synchrony needs to be understood. If synchrony is, in fact, induced by volleys of synchronous action potentials in descending fiber systems, the case for synchrony as a mechanism for selection is enhanced. If, on the other hand, it is a byproduct of a rate mechanism, the case is weakened. Steinmetz *et al.* [22••] showed that the change in synchrony was greater than could be accounted for in the changes in rates of the neuron pairs being recorded from, but that does not rule out changes in synchrony due to changes in excitability at earlier stages of sensory processing.

Acknowledgements

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