Temporal tagging of attended objects

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Complex organisms in a complex world need sensors that provide the information necessary to cope with any situation they are likely to encounter. Because circumstances vary widely, at any given time the sensory periphery therefore provides much more data than is needed and can be processed in detail by the central nervous system. Selective attention is the triage process of extracting the most relevant sensory information and suppressing the remainder. In a recent issue of PNAS, through an ingenious psychophysical experiment, Bauer et al. (1) provide insight into the mechanisms underlying this cognitive function.

How Is Attention Implemented in the Brain?

The study addresses the question of how the attentional state is represented in the nervous system. The physical properties of sensory stimuli are usually encoded by the mean firing rates of neurons or neural populations: "orientation tuned" neurons fire at maximum rate when a stimulus of a specific (their "preferred") orientation is presented (2), higher contrast usually leads to higher firing rates, etc. Most neurons represent more than a single stimulus feature: their firing rate may vary with orientation, contrast, color, depth, etc. Conversely, the mean rate of a distributed neural population is used to represent the set of all physical features of a stimulus.

At first sight, it seems that a similar rate code could be used to represent attention: the firing rate of a neuron should be higher when it responds to an attended stimulus compared with when the same stimulus is present but unattended. The latter then will have little or no effect on downstream neurons and little influence on perception or behavior. A large number of physiological studies show, indeed, that attention goes along with higher mean firing rates (3, 4).

Simply increasing the firing rates of attended stimuli over those of unattended stimuli, thus treating the attentional state of a stimulus like one of its physical properties, is problematic, however. If some neural population fires at, say, an intermediate mean rate, is this in response to a preferred but unattended stimulus or to an attended but less preferred input? An additional degree of freedom is needed to avoid confounding the attentional state with stimulus features. This degree of freedom could be provided by the structure of the neuronal population; for instance, if in addition to a subpopulation whose firing rate depends on both stimulus properties and attention there is another subpopulation whose firing rate is independent of attention. Then, a suitably-constructed downstream system could deduce both attentional state and stimulus properties from the combined activity of these 2 populations (5). A concern is, however, that this process required (5) a quite sophisticated statistical procedure (support vector machines), and it is not clear how actual neural circuitry would extract information about physical stimulus properties and attentional state from the population activities. More importantly, representing the attentional state is not a goal by itself. What is needed is a computational mechanism that enhances the impact of attended over unattended stimuli, that does so without introducing confounds, and that can be plausibly implemented in neural circuitry.

> **Attended stimuli might be distinguished from unattended stimuli by a form of 'temporal tagging.'**

For at least a generation, there have been reports (e.g., refs. 6 and 7) of intriguing correlations between oscillatory activity in the gamma range (≈30–80 Hz) and mental processing, particularly attention, awareness, and decision making. Crick and Koch (8) proposed that attended stimuli might be distinguished from unattended stimuli by a form of "temporal tagging," such that the activity of neurons responding to attended stimuli consists of synchronized oscillations whereas unattended stimuli result in less-organized neuronal firing. A detailed computational model (9) based on this concept showed that such a temporal tag can be "read out" (i.e., used to increase the firing rate of neurons representing attended stimuli over those responding to unattended stimuli) by simple neural circuitry, and that the tag is preserved in this read-out process. This process of biasing the competition between attended and unattended stimuli (10) can therefore be repeated over several stages, resulting in a hybrid representation of selective attention: while preserving the temporal tagging of attended stimuli, the difference in firing rates between attended and unattended stimuli becomes more and more pronounced as the stimuli are processed by higher and higher stages in the cortical hierarchy, and eventually unattended stimuli are strongly suppressed.

This model does not require sophisticated statistical methods to "decode" the attentional state of a stimulus: the weak frequency selectivity found in generic neuron models is sufficient to bias the competition (9). Aperiodic synchronous modulation can also serve as a tag for attended stimuli because it likewise results in enhanced postsynaptic firing rates (11).

The encoding of the attentional state happens just as naturally as the decoding, i.e., the generation of the modulation that distinguishes attended from unattended stimuli. If all neurons that represent an attended stimulus receive input from some control structure (perhaps in parietal cortex) in the form of the brain's universal currency, trains of action potentials, then it is nearly unavoidable that these neurons will become more synchronized than other populations that do not receive such common input. Note that this modulation does not necessarily increase the mean firing rate of its target population; whether the rate increases, decreases, or remains unchanged depends on the relative weights of the synapses between the modulating neurons and the excitatory and inhibitory neurons in the target population (9, 11). Thus, temporal tagging by synchronized, potentially oscillatory activity naturally distinguishes attended from unattended stimuli.

A clear prediction of this model is the presence of synchronized firing in early cortex, which should be substantially stronger for attended than for unattended stimuli. This prediction was confirmed in extrastriate visual and so-

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matosensory cortex (12–14), and there is evidence that synchrony may play more of a functional role than oscillations (15).

Could temporal modulation influence attentional selection not only when generated internally but also when imposed from the outside? Attentional modulation by external oscillations is not a mandatory prediction of temporal tagging (one could imagine that peripheral filters were set up to prevent any "bleed through" of external oscillations), but it is certainly consistent with the hypothesis, and any observation of such influences would be difficult to explain in a pure rate model. This is where the Bauer et al. study (1) comes in. In their first experiment, the amplitude of a visual stimulus is modulated in the gamma range, and they show that this modulation enhances its detectability and discriminability, as if it received more attentional resources. The effect is limited in frequency: it is absent at 35 Hz, present at 50 Hz, and absent again at 100 Hz. The 50-Hz flicker is not consciously perceived but it nevertheless seems to attract the participants' attention. This finding is supported by a second experiment in which Bauer et al. pit flicker against cue validity. Now, observers know that they should attend to the nonflickering stimulus for optimal performance. At low frequency (25 Hz) where the flicker is consciously perceived, subjects indeed orient toward the nonflickering stimulus, as they are instructed. At 50 Hz, the modulation is usually not perceived but subjects (with a small, but significant, margin) orient toward the flickering stimulus more often than toward the unmodulated stimulus, even though instructions request the opposite. Attention seems drawn to the oscillating stimulus even though subjects are not aware of the oscillation.

Oscillations Attract Attention Even When They Are Not Perceived

Like many good experiments, this one raises as many questions as it answers. Attention is frequently seen as a perceptual filter that limits access to awareness and memory (16). However, in Bauer et al.'s results (1), attention is directed to the oscillating stimuli without awareness. This dissociation between selective attention and awareness is very much in line with newer thinking that sees these 2 phenomena as closely related but distinct and experimentally dissociable (17). They can therefore, as in the Bauer et al. experiment, have opposing effect, and the paradigm in ref. 1 may open new methods for studying this dissociation. Another question is whether (and, if yes, how) the proposed temporal code for attention is related to the binding-by-synchrony hypothesis of perceptual grouping (18). And is the temporal tag implemented by mere synchrony, or is it necessary that synchronous events occur periodically (in oscillations)? Bauer et al. show that it is not the presence of amplitude changes per se that attracts attention: aperiodic intensity changes had no significant effect (figure 1*D* in ref. 1), although it is noted that the frequency of zero crossings in their aperiodic stimulation paradigm was an order of magnitude lower than in their periodic stimulus. If periodicity is confirmed to be essential, can the range of effective frequencies be more closely determined in the broad range between 35 and 100 Hz?

Do the results have consequences in daily life? A considerable fraction of neurons in monkey primary visual cortex can phase-lock to visual input in the gamma range, and there is good evidence that the same is true for humans (19). As Williams et al. (19) note, television screens flicker at 50–60 Hz, resulting in a natural experiment of 1 billion people regularly exposing themselves to gamma-range modulation of their visual cortex while watching television. The Bauer et al. results imply that attention to objects outside of the television screen should then be subtly impaired. Even if the effect were small, with a population of this size it might be detectable.

The question of how attended and unattended stimuli are distinguished from each other in the central nervous system is far from being solved. Although being of high interest in itself, it is part of the more general question of how internal states of higher organisms are represented, and how these mental entities interact with sensory input to generate behavior. Bauer et al. (1) provide support for a simple, parsimonious model, and their approach opens the door to new experimental and theoretical approaches. It will be fascinating to see how these central questions of cognitive neuroscience will be answered.

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