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12 Conclusion

Our tentative theory, most of the elements of which have already been proposed by others, is a program for research rather than a detailed model.

What are the essential features of visual awareness? The first requirement is for a form of running short-term memory, an idea that is certainly more than 100 years old (see ref 29.) We postulate two distinct forms of this running memory, a very transient iconic one that records built-in visual features and a working memory that lasts for a somewhat longer time and can also store combinations of features. We presume that parts of iconic memory form the basis of working memory.

The information about a single object is distributed about the brain. There has, therefore, to be a way of imposing a temporary unity on the activities of all the neurons that are relevant at that moment. (Incidentally we see no reason at all why this global unity should require fancy quantum effects.) The achievement of this unity may be assisted by a fast attentional mechanism, the exact nature of which is not yet understood. This mechanism is postulated to concentrate on one object at a time, choosing by a winner-take-all process the next object that appears to it to be the most salient. The required unity takes the form of the relevant neurons firing together in semi-synchrony, probably at a frequency in the 40-70 Hz range. We tentatively suggest that this activates the appropriate parts of the working- memory system. The neural basis of this memory system is at the moment obscure, although the transient alteration of synaptic strengths is one likely mechanism.

There is also much neural activity in the visual system that does not reach full awareness. Much of this corresponds to the computations needed to arrive at the best interpretation of all the incoming information that is compatible with the stored, categorical information acquired in the past. It is this 'best interpretation' of which we become aware.

Why, then, is consciousness so mysterious? A striking feature of our visual awareness (and of consciousness in general) is that it is very rich in information, even if much of it is retained for only a rather brief time. Not only can the system switch rapidly from one object to another, but in addition it can handle a very large amount of information in a coherent way at a *single moment*. We believe it is mainly these two abilities, combined with the very transient memory systems involved, that has made it appear so strange. We have no experience (apart from the very limited view provided by our own introspection) of machines having complex, rapidly changing and highly parallel activity of this type. When we can both construct such machines and understand their detailed behavior, much of the mystery of consciousness may disappear.

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11 Some experimental approaches

There are at least three possible methods of directly approaching working awareness. One is to exploit the process known as rivalry, an example of which is the two alternative ways of viewing the well-known Necker cube drawing. Here the visual input is constant but the percept varies from one interpretation to the other. A form of rivalry that is easier to study neurophysiologically is binocular rivalry, where one eye is given one constant visual input and the other a constant but rivalrous one. An example studied by John Allman and his colleagues (personal communication) involved projecting a small horizontal grating into one eye of a macaque monkey and a small vertical one into the other eye so that their visual fields overlap. In the same circumstances people see first one grating and then the other, the two percepts alternating every second or so. Detailed psychophysical studies on both monkeys and humans, where the monkeys signalled the change by pressing one of two keys, give fairly similar results, so it is reasonable to assume that the monkey has an awareness of the changing percepts. Most neurons in the first visual area fire in response to the constant visual input and do not change but the firing of others tends to change with the monkey's apparent percept. A similar experiment involving horizontal gratings moving either upwards (in one eye) or downwards (in the other) produces a similar variety of responses in area MT of the monkey[52,53].

The second approach,[54] using cats, is to let the animal view the same set of visual signals first while it is awake and then again when it is in slow-wave sleep. The neurons studied were mainly in the first visual area. The general result is that the response of any given neuron is broadly the same in the two conditions but neurons in the lower layers are often markedly less active in slow-wave sleep. This was confirmed by experiments in which activity was monitored histochemically using deoxyglucose. (Note that all this was done before the 40 Hz oscillations were discovered.) Both these types of experiments are obviously in their infancy but they certainly suggest that visual awareness can be directly approached by suitably designed experiments.

A third approach to working awareness would be to study the effect of anaesthetics on awareness and recall in humans and on neuronal responses in monkey under similar conditions. Surprisingly, no reliable means exists today to test whether a patient is unconscious during modern anaesthetic procedures,[12] which usually includes muscle relaxants to block voluntary and involuntary movements. Even the EEG is no reliable indicator of depth of anaesthesia, as it is often not distinguishable from that of a sleeping person. It has been claimed, however, that the disappearance of a 40 Hz wave in the auditory evoked potential correlates with loss of consciousness under anesthesia[55]. Four to six cycles of such an oscillation, with a period of about 25 ms, can be seen following stimulation by a single or a series of sharp clicks[56]. More work on this is obviously very desirable.

Much useful information can also be obtained by careful studies on humans with brain damage who have selective impairment of different aspects of visual perception[7,57] and especially of attention and binding.

9.1 Fleeting awareness

Can a spotlight of attention, moving over the visual field from one 'salient' location to the next, explain the perceptual richness of our environment? Would such a mechanism not lead to a sort of 'tunnel vision', in which the currently attended location appears in vivid detail with its associated perceptual attributes while everything else is invisible? We suggest, very tentatively, that this richness may be mediated by another form of awareness that is very transient, being associated with iconic memory and having a very large capacity at any one time. This form, that we propose to call 'fleeting awareness', we expect not to solve the *ad hoc* binding problem (as working awareness does) but to embody 'features' that are bound only epigenetically or by overlearning. Attention can then focus on a subset of relevant items within iconic memory for further processing. Because fleeting awareness is very transient it may be especially difficult to study. Whether it really exists remains to be seen.

10 Experimental problems

To understand working awareness it seems clear that experimental studies of three somewhat different phenomena are needed. The first is the 40 Hz oscillations, and indeed all other oscillations and any other kinds of coherent firing. In what cortical areas are oscillations found, especially in alert animals? What is their natural history: when do they occur? How long do they take to set up? How long does any one of them last? Are there, simultaneously, several different frequencies and/or phases? Are they indeed mainly correlated with objects? Do they solve the well-known figure-ground problem? Do they ever occur in the thalamus or the basal ganglia? Is the claustrum[21] involved—it is ideally placed to help synchronize neurons in different places?

The second is attention. Are any of the oscillations associated with it? How does the mechanism work in neural terms? It is already known that neurons in area V4[50] and in the parietal region[51] in the macaque monkey are influenced by attention. Evidence on humans with brain damage implicate parts of the thalmus in certain aspects of attention,[22] as do certain experiments on monkeys,[23] but we need to know much more about how attention works neurobiologically.

The third is the neural basis of both iconic and working memory. These are neglected subjects that urgently demand an experimental attack. If there are reverberating circuits, where are they? Under what circumstances do they oscillate? Are there special mechanisms within certain neurons that make it easy for them to continue firing? How widely is the short-term synaptic modification mechanism distributed? What are its characteristics in different places? Is there any sign of a Hebbian form of modification? What exactly are the biochemical and biophysical mechanisms[34,35] underlying it? In addition we need to relate the neural activity to psychological observations.

We plan to discuss these experimental questions more fully in a later paper and to offer some tentative answers based on more detailed theoretical arguments.

feature maps. The various parts of the visual thalmus are well suited to influence the behavior of neurons in those parts of the neocortex from which they receive information and to which they project back. Some such feedback pathways then activate or synchronize the oscillations at the corresponding locations in areas such as V1, V4, and MT, so that a coherent set of features is bound. Of course, the system has to decide, using the categorical knowledge stored in the connections, exactly which neurons must oscillate together to produce a veridical representation of the object being attended to. This is probably not an easy task. These are the problems that concern much theoretical work in cognitive science and computational neuroscience. It is well known that making sense of our perceptual inputs is an 'ill-posed' problem and much 'computation' must be done to produce veridical solutions.

It seems likely that, for one reason or another, certain neurons in the cortical areas involved tend to oscillate at around 40 Hz. This could make it easier to activate such oscillations quickly. The effects of the 40 Hz oscillations is probably greater than the same amount of random firing for two reasons: first, because spikes arriving at a neuron simultaneously will produce a larger effect at the soma; and second, because the 40 Hz oscillations may promote 40 Hz 'resonances' elsewhere.

To be effective the phases of the relevant neurons must be synchronized. A recent mathematical analysis[48] shows that a set of oscillating neurons can very quickly be frequency- as well as phase-locked if there is a centralized feedback unit. On the other hand phase-locking is much slower and more difficult to achieve if the interactions have to pass over long chains of interneuronal connections.

As there has probably been strong evolutionary pressure to produce appropriate phase-locking as quickly as possible, it may be a general principle that all phase-locking interactions use only pathways with as few links as possible; these may be within a cortical area, between cortical areas (in adjacent levels in the hierarchy) or to and from one or more global coordinating regions, such as the thalamus or the claustrum.

We suggest that one of the functions of consciousness is to present the result of various underlying computations and that this involves an attentional mechanism that temporarily binds the relevant neurons together by synchronizing their spikes in 40 Hz oscillations. These oscillations do not themselves encode additional information, except in so far as they join together some of the existing information into a coherent percept. We shall call this form of awareness 'working awareness'. We further postulate that *objects for which the binding problem has been solved are placed into working memory.* In other words, some or all of the properties associated with the attended location would automatically be remembered for a short time. One very attractive possibility, with no experimental support, is that the 40 Hz oscillations themselves preferentially activate the mechanisms underlying working memory and possibly other longer term forms of memory as well.

The likelihood that only a few simultaneous, distinct oscillations can exist happily together might explain,[49] in a very natural way, the well-known limited capacity of the attentional system. The 40 Hz oscillations may also be an important element in laying down and improving stored, categorical information, because at any moment they represent the brain's concensus as to what it is seeing.

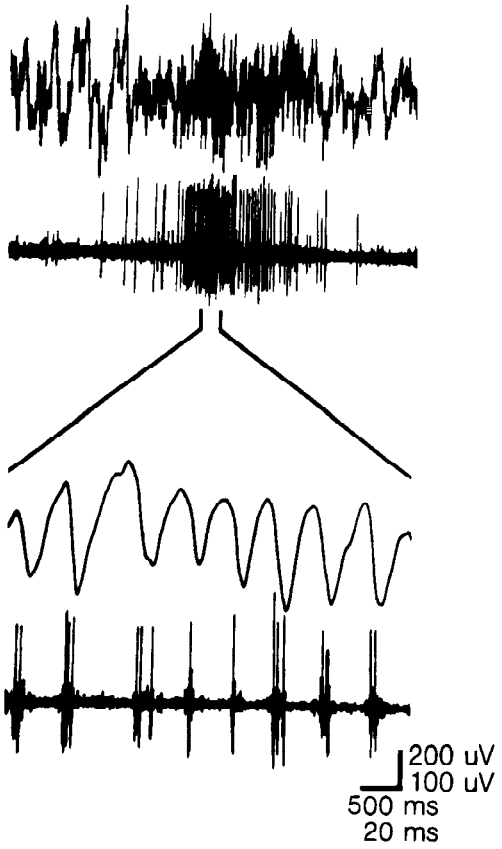

Figure 2:
The local field potential (upper trace) and multiunit activity (second trace) recorded from an electrode in the first visual area of an adult cat in response to an optimally oriented light bar moving across the receptive field. The third and fourth traces show a corresponding part of the first and second ones (respectively) on an expanded time scale. Note the presence of rhythmic oscillations (35–45 Hz). The multiunit activity occurs near the peak negativity of the local field potential. Reproduced, by permission, from ref 42.

8 Neuronal oscillations

It has often been hypothesized, in particular by von der Malsburg,[37] that in neural terms binding means the temporarily correlated firing of the neurons involved. In other words, neurons in different parts of cortex responding to the currently perceived object fire action potentials at about the same time. The main theoretical requirement is for correlated firing. It now seems theoretically plausible that this is most easily implemented using oscillations. There are many oscillations known in the cortex, among them the α-rhythm and the θ-rhythm of the hippocampus. Experimental work on 'γ-oscillations' in mammalian olfactory cortex[38,39] and in the visual cortex[40–46] indicates that an important mechanism may involve neurons firing in semisynchrony at a frequency in the 40-70 Hz range (at least in the cat) (see Figure 2). In the visual cortex, only a proportion of the active neurons fire in this way. Most of the neurons that do oscillate appear to be complex cells rather than simple cells, so that very few are found in cortical layer IV[45].

It has been shown[41] in cat primary visual cortex that in many cases two neurons some distance apart, but both responding to a particular moving bar, can show frequency-locked oscillations with no measurable phase shift in their cross-correlations. More tellingly, the activity of two relevant neurons, some 7 mm apart, showed[41] more highly correlated oscillations (at about 50 Hz) to a single moving bar than did the same two neurons stimulated by two shorter, separate, moving bars. That is, the correlation was much greater in response to an obviously single object than to a pair of somewhat distinct objects. The activity of the relevant neurons in both the first and second visual areas has also been shown to be correlated[44]. We shall refer to these neuronal oscillations as the 40 Hz oscillations, though the frequency on any one occasion is not very precise and can vary between 35 and 75 Hz.

Most of these experiments have been done on lightly-anaesthetized cats whose exact state of awareness is unknown but as similar oscillations have also been seen in neurons in alert cats,[46] they are unlikely to be merely an artifact of the anaesthetic.

9 A sketch of a theory

The role of the oscillations in binding may be as follows. Objects in the visual field give rise to appropriate responses in the appropriate cortical areas. Visual attention now has to select one of these objects at a particular location. Exactly how this works is not yet known. One possible solution[25,28,47] is that the brain has some sort of topographic saliency map that codes for the conspicuousness of locations in the visual field in terms of generalized center-surround operations. This map would derive its input from the individual feature maps and give a very 'biased' view of the visual environment, emphasizing locations where objects differed in some perceptual dimension, i.e. color, motion, depth, from objects at neighboring locations. Where this map might be located is unclear but parts of the thalamus,[22,23] such as the pulvinar, might be involved. (Note that the pulvinar receives a projection from the superior colliculus, an area that could be thought of as having a saliency map for eye movements.)

Once a particular salient location has been selected, probably by a winner-take-all mechanism, the information associated with it must be activated by referring back to the individual

Intracellular recordings show that the cell bodies of retinal ganglion cells remain depolarized for 200 ms or longer following a very brief flash of light within their receptive field[31]. How neurons further in the system express a transient memory remains to be seen. In a memory task in which a trained monkey had to discriminate and retain individual features of compound stimuli, about 15% of the neurons in inferotemporal cortex continued to fire for 10–20 s after the stimulus[32]. The mechanism producing (and terminating) this sustained firing is unknown. It is not yet known whether this firing is oscillatory or not. It may not have to be oscillatory, since a task can be remembered well enough without one being vividly conscious of it all the time.

A phenomenon that may correspond to the first mechanism was discovered many years ago at the neuromuscular junction and called post-tetanic potentiation. This is not to be confused with the much studied long-term potentiation (LTP)[33] that has a longer time course. The terminology for these short-lasting changes has now become more complicated,[34,35] with effects variously labelled facilitation (with two time constants of decay, of 50 ms and 300 ms), augmentation (7 s) and potentiation (30 s to minutes). There is also depression (5 s). We shall refer to all these collectively as 'short-term synaptic modification'. Note that the decay times are in general in the same range as the times required for the decay of working memory. Short-term modification has also been observed in the hippocampus and, in one case, in the neocortex. These temporary changes in synaptic strength can be surprisingly large (see figures 11 and 13 in ref 33).

7.2 Hebbian or non-Hebbian?

The causes of the various aspects of short-term modification are not fully understood but many of them seem to result from calcium accumulation in the presynaptic terminal[34,35] and are not influenced by activity in the postsynaptic cell. For this reason they are probably all non-Hebbian[36] in character. ('Hebbian' means that the alteration in synaptic strength depends on activity, at about the same time, in both the presynaptic and the postsynaptic cell.) Non-Hebbian implies that the change is not (to a first approximation) just at an individual synapse but at all the synapses associated with that particular presynaptic cell, so that the 'unit of change' is the presynaptic cell, not a single synapse. Such changes may form part of the neuronal basis of (short-term) priming[17].

Von der Malsburg[37] in 1981 postulated on theoretical grounds a fast (fraction of a second) mechanism for increased synaptic efficiency, having a broadly Hebbian[36] character. So far this transient Hebbian alteration to synaptic strength has not been observed, although if it existed it would provide very considerable theoretical advantages.

We know almost nothing concerning the anatomical localization of iconic and working memory, except that (as discussed above[13]) the hippocampal system need not be present in order to remember for short times. Both iconic and working memory are likely to be distributed throughout the appropriate cortical areas, with auditory events transiently stored in auditory cortices, visual events in the visual cortices, and so on. No case of a person who is conscious but has lost all forms of short-term memory has been reported.

features may be quite novel to us. The neurons actively involved are unlikely all to be strongly connected together, at least in most cases. This binding must arise rapidly. By its very nature it is largely transitory and must have an almost unlimited potential capacity although its capacity at any one time may be limited. If a particular stimulus is repeated frequently, this third type of transient binding may eventually build up the second, overlearned type of binding.

6.3 The role of attention[25–28]

This form of transient binding probably depends on a serial attentional mechanism, sometimes called the spotlight of attention[25,28]. It is thought by some to concentrate on one place in the visual field after another, possibly moving every 60 ms or so. It is faster than eye-movements (another, slower, form of attention), and can work across different spatial scales. We suggest (the idea goes back to the last century[29]) that what reaches visual awareness is usually the result of this attentional step. In other words, *that awareness and attention are intimately bound together*. Note that although the results of attention are postulated to reach consciousness the attentional mechanisms themselves are probably largely unconscious.

7 Short-term memory

It has long been argued that awareness is not only associated with attention but also with some form of short-term memory. We have to distinguish two forms, iconic and working memory.

Iconic memory is similar to a sensory input buffer, storing information mainly at a pre-categorical level, i.e., in terms of simple visual primitives such as orientation or movement, although it may also involve more complex features, such as familiar words. It has a very large capacity but decays very quickly, perhaps in half a second or less[8]. Working memory, in contrast, may last for seconds[9,10]; it seems to have a rather limited capacity (a figure often quoted is seven items[30]), is different for different modalities and seems to use a much more abstract representation (post-categorical memory). It can be prolonged by rehearsal, as when one rehearses a telephone number. We suspect that it is this form of memory that is strongly activated in the binding process.

7.1 Neural basis of short-term memory

The neural basis of these two forms of memory is much understudied. Three broad types of mechanisms might underlie either iconic or working memory, either singly or in combination:

(i) the strength of certain synapses is temporarily increased or decreased;

(ii) a neuron keeps on firing for some time due mainly to its intrinsic biophysical properties;

(iii) a neuron keeps on firing mainly due to extrinsic circuit properties ('reverberatory circuits').