

Visual priming: The ups and downs of familiarity

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A dynamic picture of the neural processes underlying the 'priming' effects on the visual system of repeated object presentation has been obtained by combining functional magnetic resonance imaging with a gradual 'unmasking' procedure that slows down the process of visual recognition.

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Visual objects are perceived more quickly and easily if you have previously been exposed to them, regardless of whether you actually remember having seen them before. This ubiquitous phenomenon, called 'priming', implies that prior exposure to an object changes its representation in the brain, but what do we know about these changes? In most neuroimaging [1] and neurophysiological studies [2] task-irrelevant object repetition has been found to lead to reduced brain activity in both the inferotemporal and frontal cortex. This suppression is thought to indicate that visual priming results from a 'sharpening' process in neural networks representing objects [3]. According to this view, new objects are initially represented by many broadly tuned neurons and, over repetitions, the responsiveness of most neurons, carrying little information, is decreased. At the same time, the selectivity of the most informative cells is increased and the population response becomes more efficient.

One problem for this theory, however, is that in many experiments — in particular those investigating the repetition effects of originally unfamiliar objects — object repetition has been found to enhance, rather than suppress, responses [4,5]. In a paper published recently in *Current Biology*, James *et al.* [6] report a study using functional magnetic resonance imaging (fMRI) that adds to the debate in an interesting manner. These authors observed both suppression and enhancement in the same brain area, with the same object and within the same trial! Several aspects of the experiments may have been of key importance in obtaining these effects: I shall discuss three of them here, namely the role of stimulus degradation, access to a name for the objects and a contribution of explicit memory.

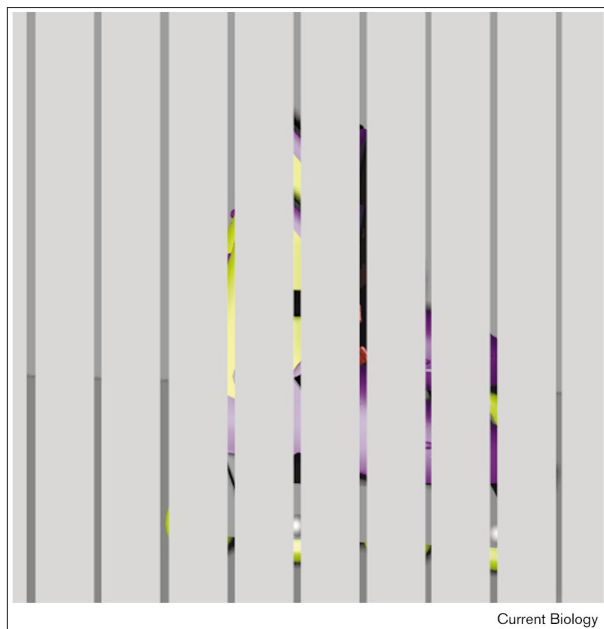
James *et al.* [6] compared the effects of priming before and after object identification. Subjects first passively viewed a sequence of 12 objects, each appearing for

one second and repeated ten times. The fusiform gyrus, posterior parietal cortex and frontal lobe all showed typical repetition suppression responses, with decreasing activity as pictures were repeated. Next, six of these objects and six new ones were used in a gradual 'unmasking' paradigm. Over periods of 46 seconds, objects were revealed gradually from behind vertical blinds or through random noise, and subjects pressed a button when they could confidently name them. Importantly, fMRI images were taken before and after subjects felt they could name the object. In two brain areas, the fusiform gyrus and posterior parietal cortex, the fMRI results revealed a surprising interaction between stimulus repetition and the period of processing. Primed objects evoked more activity than unfamiliar objects prior to identification, whereas after identification, more activity was evoked by unfamiliar objects.

An interesting aspect of this study is how the researchers slowed down the time-course of priming in order to study it by fMRI, a technique notorious for its temporal sluggishness. In the 1960s, Bruner and Potter [7] carried out experiments that indicated how visual object recognition can be slowed down. They found that prior exposure to a blurred image of an object slows down and impedes its recognition. The longer the exposure to a degraded image, the more interference on subsequent recognition: evidently the more opportunity one has to generate incorrect hypotheses about the image, the longer it takes to recognize the object correctly. Thus, in the gradual unmasking paradigm, recognition of a semi-camouflaged object will be hindered by the guesses generated earlier in the sequence when viewing even more degraded versions of the object (see Figures 1 and 2).

The degradation of a stimulus influences its visual processing — but how crucial is this factor for the priming effects observed during gradual unmasking? It turns out, as revealed by a recent fMRI study [8], that even without slowing down the recognition process and with very short presentation times (40 milliseconds), the repetition of briefly presented objects, each followed by a mask, leads to an enhanced response in the fusiform gyrus and lateral occipital cortex [8]. The use of spatial (as opposed to temporal) image degradation also led to surprising results obtained when recording from neurons in the prefrontal cortex of monkeys matching images to degraded targets [9]. The monkeys practiced a matching task with unfamiliar sets of objects as well as with one familiar set used repeatedly over sessions. The images were degraded with variable amounts of noise. As

Figure 1



An example of the interference effect described by Bruner and Potter [7] with the type of mask used in the gradual unmasking study. Look at this image for about 10 seconds, trying to identify the object, then look at Figure 2.

expected, familiar objects elicited less activity from prefrontal cortex neurons than unfamiliar ones, and fewer neurons responded selectively to the familiar than to the unfamiliar stimuli. But the neurons' selectivity to images was more robust in the face of stimulus degradation for the familiar than the unfamiliar objects. In other words, the reduced response of prefrontal cortex neurons with practice was accompanied by the formation of a more efficient representation.

These neurophysiological [9] and fMRI [8] results are difficult to compare, because the fMRI study [8] involved alternating long blocks of multiple trials and, as mentioned above, fMRI has poor temporal resolution. In the gradual unmasking study [6], whether stimulus repetition produced an enhancement or a suppression of the neural response was found to correlate with the degree of stimulus degradation. Such results are at least partly consistent with the earlier human fMRI [8] and monkey neurophysiology [9] studies: during the period when the objects were most degraded, repetition led to enhancement in the fusiform gyrus but not in the frontal cortex. A more consistent pattern would also involve suppression in the frontal lobe, but such suppression might have been missed in the fMRI analyses, if it occurred in regions not object sensitive in the first phase.

The difficulty of integrating results obtained using different techniques appears to be a general problem in the study of visual repetition. According to James *et al.* [6], the results of their gradual unmasking study can reconcile the typical finding of repetition suppression in fMRI studies with evidence for repetition enhancement in studies that recorded event-related potentials (ERPs) [10]. As the argument goes, several fMRI studies observed repetition suppression because stimuli were presented for a short duration, were easily and quickly recognized and activity mainly reflected the post-recognition period. But because of their finer temporal resolution, ERPs can reflect the pre-recognition period too and this explains the repetition enhancement observed using this technique. One difficulty with this hypothesis is that the repetition enhancement typically observed in ERP studies occurs in the period from 250–550 milliseconds post stimulus onset. This is very late relative to other perceptual ERPs that differentiate between object categories and also to the repetition suppression observed in monkey neurophysiology studies, which starts around 80 milliseconds post-stimulus onset.

Even if it cannot offer an all-encompassing explanation of priming effects across species and techniques, the recent study of James *et al.* [6] is particularly timely. In particular, it sheds new light on another recent fMRI study [4], which offers an explanation for why visual priming sometimes leads to suppression [1] and at other times to enhancement [5] of activity. This work [4] built on earlier ERP studies [11] which found that priming effects depend on the familiarity of the stimuli: enhancement of activity is obtained only for familiar objects associated with a name and semantic information, whereas when novel objects are used, a decreased amplitude is observed with repetition. When fMRI was used to compare priming of familiar and unfamiliar faces and signs — with famous faces and signs such as punctuation marks as familiar stimuli — a region of the fusiform gyrus showed suppression for repeated familiar stimuli, but enhancement for repeated unfamiliar stimuli [4]. Interestingly, this interaction remained even after multiple exposures to the images, so merely seeing an object in recent trials is not enough to make an object 'familiar'.

Perhaps objects for which priming leads to suppression are those for which subjects have names, such as a famous face or a sign such as an exclamation mark. But why, then, should the easily nameable objects used in the gradual unmasking paradigm [6], such as 'dog' or 'key', have caused repetition enhancement in the pre-recognition period? A revised hypothesis is that it is the access to a name that is crucial here — not whether objects have one or not. That is, enhanced activity in the early part of the unmasking procedure might reflect processing occurring before a name is generated. In other fMRI paradigms in which the stimulus is revealed in its entirety right away,

the name might be available too quickly to allow a significant contribution of the pre-naming period. Because both enhanced and suppressed priming responses can be obtained with the same stimuli, we can question the idea that a stimulus property (such as familiarity) is sufficient to predict which of the two responses should be obtained in other situations.

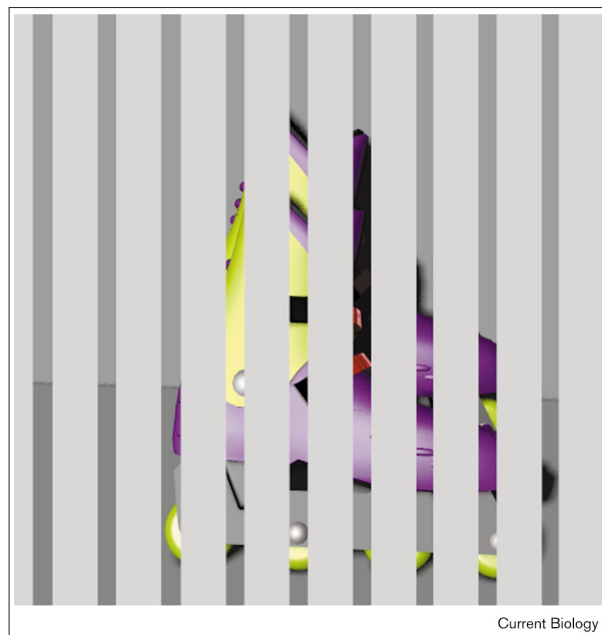
Finally, an additional factor that may influence the neural response to a repeated stimulus is a contribution from explicit memory — that is, recollection of having seen the objects in the study phase. In a landmark neurophysiological study [2], researchers used a modified version of the traditional match-to-sample task. Typically, a series of stimuli, such as ABCA, is used — the first A is the sample, and a matching response is required on the second A. In the modified version, repetitions of non-matching items were introduced — as in the sequence ABBA — and monkeys had to learn to ignore such repetitions. Most cells in the inferotemporal cortex showed the typical suppression for the matching sample (A), but they also showed the same suppression to repeated non-matching item (B).

This finding supports the existence of a mechanism sensitive to stimulus repetition regardless of task — a possible animal model for priming. A new finding in the ‘ABBA’ task, however, was that 35% of the cells gave enhanced responses to the matching samples (A) but showed no repetition effect to the non-targets (B). Thus, a subpopulation showed an enhanced response to primed targets only when the monkeys needed to keep a target ‘in mind’ to perform the task. Similarly, in the gradual unmasking procedure, subjects may use the explicit memory of previously presented objects in order to generate better hypotheses about the degraded images.

Even without voluntarily using this strategy, a hypothesis that comes to mind is likely to promote the retrieval of the prior exposures to this object (perhaps the degraded image can then be completed from memory using mental imagery). That the enhancement occurs before subjects could identify the object does not preclude the possible recruitment of explicit memory (that is, when I ask myself what I did this week end, I am searching explicit memory even before I am conscious of the answer). In order to resolve whether the pre-recognition enhancement reflects implicit memory, the gradual unmasking paradigm could be used in combination with techniques that allow the dissociation of the two types of memory (such as using very shallow encoding procedures that reduce explicit but not implicit memory).

On the face of it, visual priming is a fairly simple phenomenon: performance is better on repeated images regardless of the task. It is a humbling observation to realize that, despite a large number of clever and careful

Figure 2



This image should be more difficult to identify if you generated an incorrect hypothesis on Figure 1. You can try asking friends to identify the object in this image, either after having seen Figure 1 or not.

studies using many of the tools of cognitive neuroscience, the puzzle of priming will not be entirely resolved before first understanding the contribution of, and interactions between, numerous complicating factors. These factors include the availability of names for the primed objects, the contamination by explicit memory and the processing of degraded stimuli. Just as it seemed that familiarity was the key to whether one should expect suppression or enhancement for repeated images [4], James *et al.* [6] have revealed a much more dynamic picture in which both enhancement and suppression can take place for the same stimulus, within the same trial. This is likely to encourage researchers to integrate different existing hypotheses about the respective roles of stimulus characteristics and subject’s retrieval strategies.

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