Visual Priming: **the ups and downs of familiarity**

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A gradual unmasking procedure slows down the process of visual recognition so that fMRI can reveal a more dynamic picture of the effects of object repetition.

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Visual objects are perceived more quickly and easily if you've previously been exposed to them, regardless of whether you actually remember having seen them before. Called "priming", this ubiquitous phenomenon implies that prior exposure to an object changes its representation in the brain, but what do we know about these changes? In the majority of neuroimaging[1] and neurophysiological studies [2] task-irrelevant repetitions lead to reduced brain activity, both in inferotemporal and frontal cortex. This suppression is thought to indicate that visual priming results from a sharpening process in neural networks representing objects[3]. 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. However, one problem for this theory is that in many experiments (and in particular for repetition effects of originally unfamiliar objects) repetition enhancement rather than suppression is observed[4, 5]. A recent functional Magnetic Resonance Imaging (fMRI) study by James and colleagues[6] adds to the debate in an interesting manner, by obtaining both suppression and enhancement in the same brain area, the same object and within the same trial! Several aspects of the experiments may have been key in obtaining these effects: I 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. compared the effects of priming before and after object identification. Subjects first passively viewed a sequence of 12 objects each appearing for 1 second and repeated ten times. The fusiform gyrus (FG), the posterior parietal (PP) and the frontal lobe (FL) showed a typical repetition suppression response, 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 sec, 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 FG and PP) 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 researchers slowed down the timecourse of priming in order to study it with fMRI, a technique notorious for its temporal sluggishness. How could this be done? Experiments by Bruner & Potter in the sixties[7] suggest that the perception of images is especially suited to this experimental device. Prior exposure to a blurred image of an object slows down and impedes the process of recognizing it (even compared to no prior experience). 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 objects will be hindered by the guesses generated earlier in the sequence when viewing even more degraded versions of the object (see Figure 1).

Degradation of a stimulus influences its processing: How crucial is this factor for the priming effects observed during gradual unmasking? It turns out that even without slowing down the recognition process and with very short presentation times, a recent fMRI study reveals that repetition of briefly (40 ms) presented objects (a temporal degradation) followed by a mask leads to an enhanced response in FG and the lateral occipital cortex [8]. Use of spatial image degradation also led to surprising results in recordings of prefrontal (PF) neurons of monkeys matching images to degraded targets[9]. The monkeys practiced a matching task with both 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 expected, familiar objects elicited less activity from PF neurons than unfamiliar ones, and fewer neurons responded selectively to the familiar than unfamiliar stimuli. However, 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 PF neurons with practice was accompanied with a better efficiency of the representation.

These neurophysiological[9] and fMRI[8] results are difficult to compare because the fMRI study alternated long blocks of multiple trials and has poor temporal resolution. In the gradual unmasking study, whether repetition produced enhancement vs. suppression is correlated with the degree of stimulus degradation. Somewhat consistently with both studies, during the period when objects are most degraded James et al. obtains repetition enhancement in the FG but not in the frontal cortex. A more consistent pattern would be suppression in the frontal lobe, but this could have occurred in regions that were not examined in the fMRI analyses (because they were not object sensitive in the first phase).

Difficulty in integrating results from different techniques appears a general problem in the study of visual repetition. According to James et al., the results of the gradual unmasking study can reconcile the typical finding of repetition suppression in fMRI studies with evidence for repetition enhancement in ERP studies[10]. As the argument goes, several fMRI studies obtained repetition suppression because stimuli were presented for a short duration, were easily and quickly recognized and activity mainly reflected the post-recognition period. The ERP repetition effect on the other hand, because of finer temporal resolution, can reflect the pre-recognition period too. One difficulty with this hypothesis is that the typical ERP repetition effect (enhancement) occurs in the period from 250 to 550 ms post stimulus onset. This is very late relative to other perceptual potentials that differentiate between object categories (e.g, the N170) and relative to the repetition suppression obtained in monkey physiology, starting around 80 ms post-stimulus onset.

Even if it cannot offer an all-encompassing explanation of priming effects across species and techniques, the James et al. study is particularly timely. In particular, it sheds new light on another recent fMRI study that also gave a shot at the problem of priming sometimes resulting in suppression[10] and other times in enhancement[5] of activity. The study built on findings from ERPs showing that priming effects depend on the familiarity of the stimuli: enhancement of activity (increased amplitude) 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[11]. When fMRI was used to compare priming of familiar and unfamiliar faces and signs (with famous faces and signs like punctuation marks as familiar stimuli), a region of the FG showed suppression for repeated familiar stimuli but enhancement for repeated unfamiliar stimuli. 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 famous faces and signs like "exclamation point"). But why then should the easily nameable objects used in the gradual unmasking paradigm (such as "dog" or "key") lead to 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 could 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 is 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 (recollection of having seen the objects in the study phase). In a landmark neurophysiology 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 (e.g., ABBA) and monkeys had to learn to ignore such repetitions. Most IT cells revealed the typical suppression for the matching samples (A), but they also showed the same suppression to repeated non-matching items (B). This supports the existence of a mechanism sensitive to stimulus repetition regardless of task, i.e. a possible animal model for priming. However, a new finding in this “ABBA” task 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, an hypothesis that comes to mind is likely to promote the retrieval of the prior exposures to this object (possibly 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 phenonemon: better performance on repeated images regardless of the task. It is a humbling observation to realize that despite a large number of clever and careful 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 factors. Those 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. reveal 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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Figure legends.

Figure 1. Example of the interference effect described by Bruner & 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.

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.

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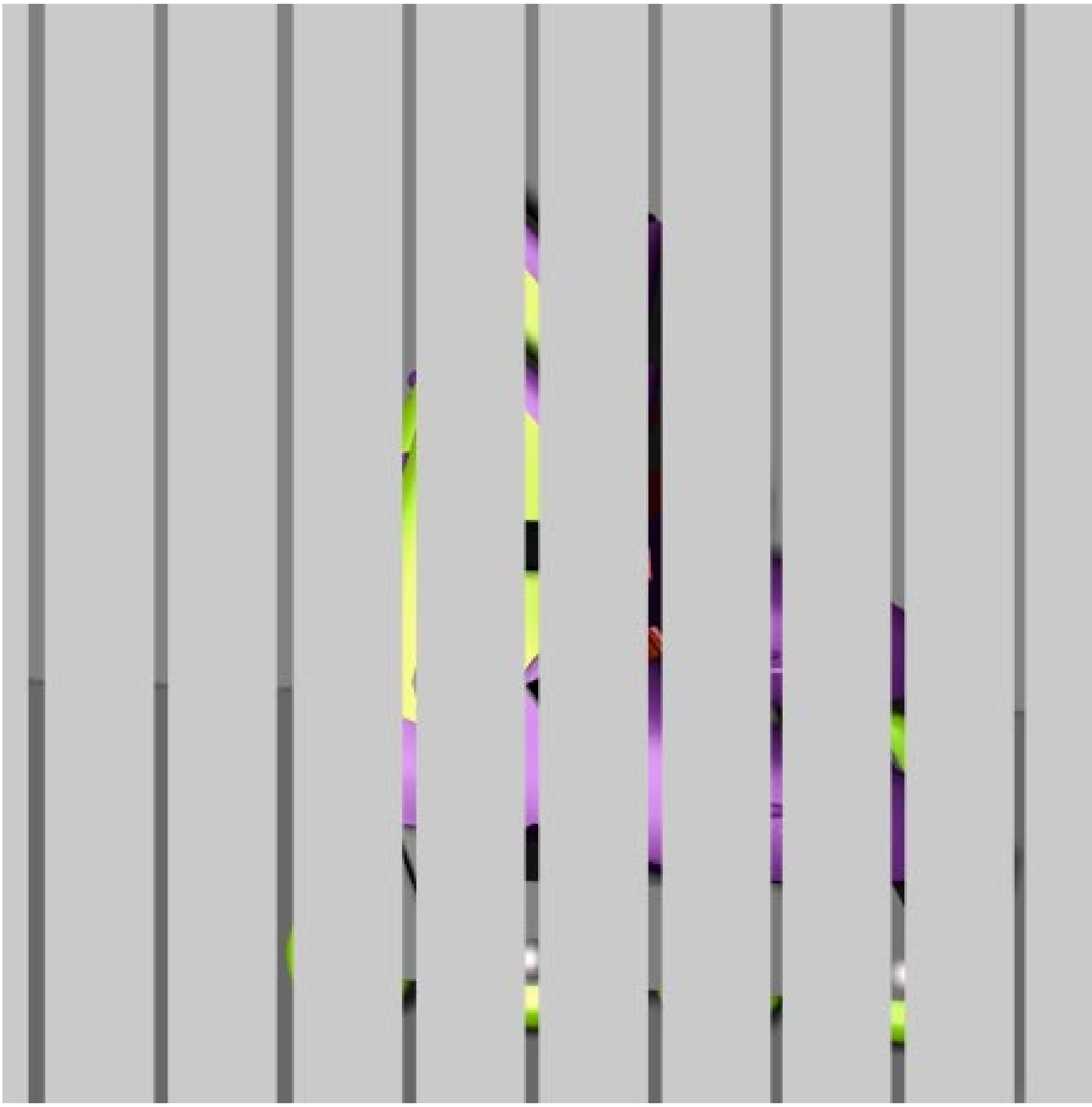

Figure 1

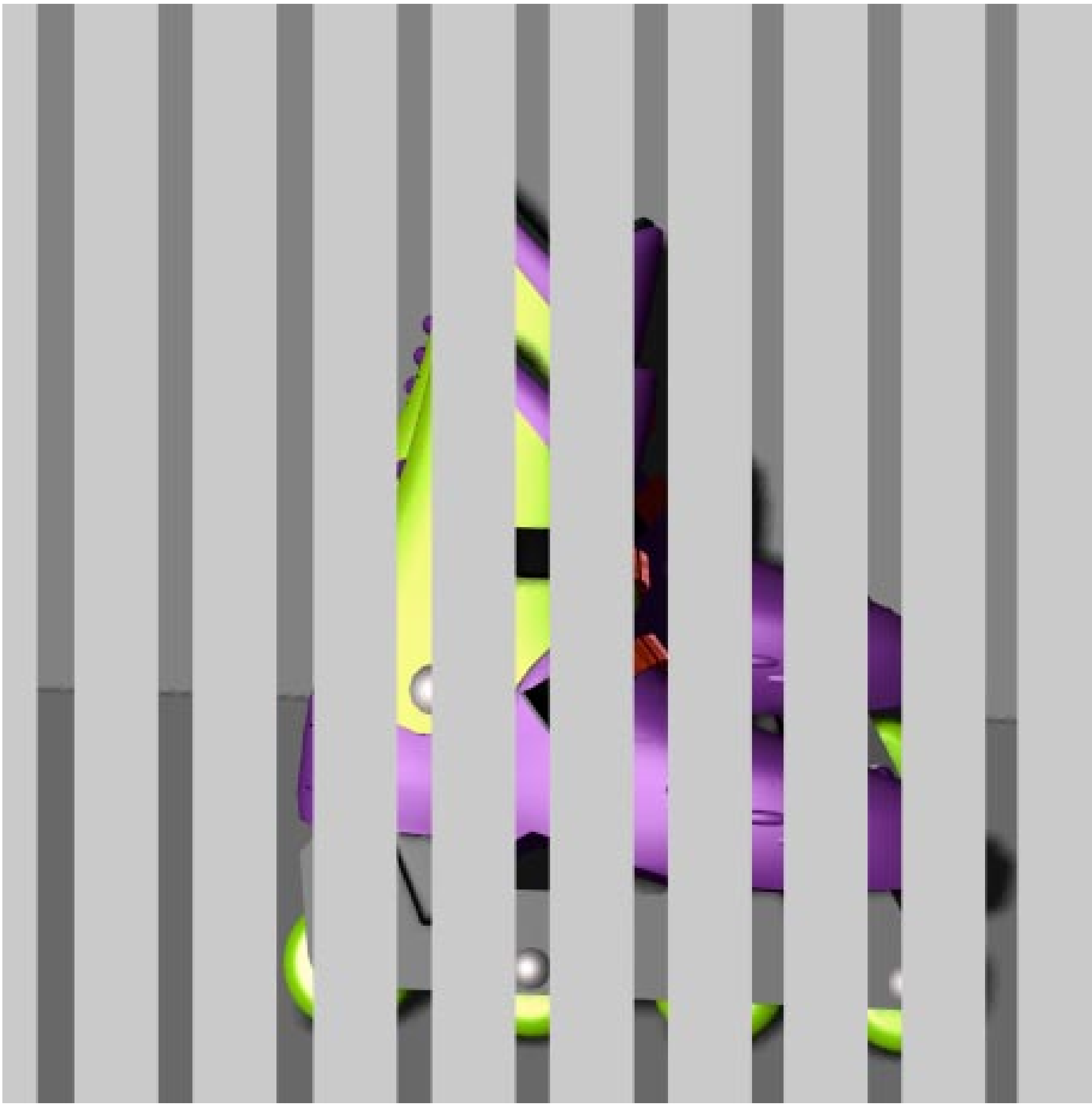

Figure 2