

Properties and mechanisms of perceptual priming

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Recent evidence suggests that the behavioral phenomenon of perceptual priming and the physiological finding of decreased neural responses with item repetition have similar properties. Both the behavioral and neurophysiological effects show graded changes with multiple repetitions, are resistant to manipulations of particular stimulus attributes (e.g. size and location), and occur independently of awareness. These and other recent findings (e.g. from functional brain imaging in humans) suggest that perceptual priming may be mediated by decreased neural responses associated with perceptual learning.

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Abbreviations

ERP event-related potential
PET positron emission tomography

Introduction

Perceiving and identifying an object or word is improved by experience with that object or word. For instance, people typically have lower perceptual identification thresholds for repeated stimuli, and are faster and more accurate at naming or reading repeated stimuli compared with new stimuli [1]. This nonconscious form of memory, referred to as perceptual priming, has motivated a large body of research aimed at revealing the phenomenon's underpinnings. By and large, unique properties have been attributed to perceptual priming, suggesting that it may reflect a distinct memory system. A particularly important finding is that perceptual priming is preserved in amnesia, despite patients' devastating impairments on explicit tests of episodic memory (i.e. tests, such as recognition or recall, that require conscious recollection of information tied to a specific context; see [2•] for a recent report). This dissociation provides key evidence for the existence of multiple memory systems [3,4], although this view is not without its opponents [5,6•].

In this review, we summarize current data indicating that perceptual priming operates according to rules distinct from episodic memory. We begin by reviewing recent advances in documenting the general behavioral properties of perceptual priming, including how these properties are affected over the life span. We then turn to neurophysiological research in animals, as well as neuroimaging

and neurological research in humans, that has examined neural mechanisms for priming. The scope of this review is limited to visual perceptual priming; we will not address issues related to semantic priming, procedural tasks (e.g. pursuit rotor task), priming in other modalities (e.g. auditory, haptic), or conceptual priming tasks that do not involve visual processes (e.g. category exemplar production task). We do, however, include reports of tasks that are primarily perceptual but may include a conceptual component (e.g. stem completion [7••]).

General properties of perceptual priming

Although previous reviews have described general properties of priming (e.g. [8]), recent findings have expanded the boundaries of these properties. For instance, it has long been noted that, whereas retention on standard explicit memory tests typically declines with the passage of time [9], perceptual priming effects are long-lasting in normal adults [10,11] and amnesic patients [12,13]. Recently, Cave [14••] documented that perceptual priming can be detected on an object-naming task after as much as a 48 week delay between the first and second exposure of an item. Although priming diminished as delays increased, it remained significant, even in subjects who performed at chance on recognition. Thus, even with chance-level performance on explicit tests, priming can still be detected in normal subjects. These results imply that performance on priming and explicit tasks is independent.

Recent findings have not only expanded the boundaries of perceptual priming, but, in some cases, have also altered the previous conception of what these properties are. Although perceptual priming has been characterized as 'all or none' [10], recent evidence suggests it is incremental and can be modulated by the number of repetitions. The amount of priming increases with multiple repetitions, and this advantage remains over week-long delays [15]. The percent decline over one week (relative to delays of several minutes) is less after multiple repetitions than for single exposures of stimuli. Moreover, priming is sensitive to the actual number of repetitions [16,17•]. That is, the magnitude of priming increases significantly with each additional exposure to a stimulus. This finding is in line with performance on explicit tests of memory, as subjects are generally accurate in judging how often an event occurred [18]. However, the graded nature of priming is reliable, even in patients who are unable to remember the stimuli or judge frequency on explicit tests [17•]. These findings suggest that a mechanism exists that automatically monitors how often an item repeats and that this mechanism operates outside of conscious awareness.

Perceptual priming is sensitive to changes in physical appearance in some instances, but not others. In general,

alterations made in stimulus attributes (e.g. color, pattern, luminance, contrast, location, left–right reflection, and size) impair performance on explicit tests [19–22], but priming tends to be similar whether the stimuli are changed or unchanged from one presentation to another ([19–24]; but see [25]). At the same time, perceptual priming can be attenuated when stimuli are changed so as to affect the ability to identify stimulus form. Specifically, priming is not affected by relatively small changes in orientation (i.e. rotations in depth up to 67°) but is eliminated by large changes in orientation (i.e. rotations in depth $\geq 80^\circ$) [26]. Furthermore, priming is diminished (but still present) with changes in an object's exemplar (i.e. a different picture of the same-named object) [23,24], and with changes in a word's typography [27–29] from study to test. These results suggest that physical attributes that are not essential to the formation of a shape representation (e.g. color) do not influence perceptual priming. In contrast, physical attributes that are essential to the representation of object form (e.g. line elements of drawings) or written word form (e.g. print typography of letters) do influence perceptual priming.

Perceptual priming is typically unaffected by the same interference manipulations that impair episodic memory on explicit tests. It is well established that attention is beneficial, if not essential, for successfully retrieving information on explicit tests of memory (see e.g. [30]). Yet, the degree of attention devoted to encoding typically does not affect the magnitude of priming. Thus, when attention is divided during encoding, priming is no different than when attention is focused [31]. Priming is as strong following the presentation of irrelevant information (i.e. information eliciting little attention) than following the presentation of information to which subjects attend [32].

Perhaps even more striking are reports of perceptual priming in the absence of conscious perception. Intact priming has been reported for information presented auditorily during anesthesia [33]. Bar and Biederman [34•] extended such findings to the visual domain. Subjects were shown line drawings of objects that were masked to produce very low levels of identification accuracy. When the same objects were shown a second time, identification accuracy increased significantly, even though recognition memory for those objects was at chance. This phenomenon, however, occurred only for stimuli that were physically identical to the stimuli presented previously. Counter to the evidence reviewed earlier, changing the location of the object reduced (but did not eliminate) priming. Moreover, priming was extinguished when the object presented at test had the same name as, but a different physical form than, the object presented at study.

These data suggest that perceptual priming does not require the same degree of encoding as do explicit tests

of memory. Nevertheless, attentional manipulations can impair perceptual priming under certain conditions. In particular, some minimal level of attention at encoding must be attained for priming to occur [35]. Furthermore, where attention is directed when an item recurs can affect the degree of priming. For instance, MacLeod [36] asked subjects to study words and later measured priming on two tasks: one required subjects to read words (ignoring the print color of the words), whereas the other required subjects to name the print color of the words (ignoring the words). Priming occurred for the word reading task but not the color naming task. Thus, in this case, reading a word at study facilitated reading that word again at test, but did not affect performance on a test in which reading the word was irrelevant (i.e. color naming). Thus, perceptual priming reflects an interplay between the processes required when first encoding an item and when it repeats. If a previously encoded item is not in the focus of attention when it reappears, and is unnecessary to accomplish the task at hand, the fact that it was recently processed is not influential.

Developmental course of priming

Given that the properties of perceptual priming are distinct from those of episodic memory in young adults, do priming and episodic memory also have different developmental courses? Infants once were believed to have only a single primitive memory system (priming), with episodic memory unfolding later in development [37]. However, current evidence suggests that many of the nonverbal tests used with infants in fact measure rudimentary forms of episodic memory. This new interpretation is attributable to two general findings. First, developmental changes (e.g. longer retention spans, increased memory capacity) have been found in infant memory paradigms, such as conditioning [38••], object search paradigms [39], and deferred imitation [40]. Second, amnesic patients are impaired on some of these same tasks [37,41].

What, then, in infants, reflects the perceptual priming phenomena found in adults? Researchers have attempted to measure an analog of priming in pre-verbal infants [38••,42]; however, the paradigms are quite different from those used with adults. Hence, interpretation of these data is problematic. Although limitations in the experimental methods available for infants have made it difficult to study perceptual priming in infants, data for older children come from paradigms that mirror those used with adults, and thus are more comparable to the adult literature. Typically, as children grow older, one sees improvement on explicit tests of memory, but no changes in priming [43]. Moreover, the properties of priming appear to remain stable across the developmental time line. For instance, similar to reports with adults, children show smaller but significant priming effects after changes in an object's exemplar compared with same-item primes, and this effect does not vary with the children's age [44•].

The effect of advancing age on performance in priming and explicit tasks is that older adults are inferior to younger adults on most explicit tasks of episodic memory, but, in general, they do not differ from younger adults on perceptual priming tasks (for reviews, see [45,46•]; but see also [47]). Moreover, many of the properties of perceptual priming remain intact. For example, priming in young and elderly subjects shows similar incremental changes with repetition [16] and similar attenuation with changes in typography [29,48]. However, it remains to be determined whether all properties are unaffected. For example, is priming as long-lasting in the elderly as in the young?

Taken together, these studies suggest a pattern of memory performance over the life span that depicts an inverted U-shaped function for explicit tasks of episodic memory and a relatively flat function for perceptual priming [49]. In other words, performance on explicit tasks initially improves with age (in children), and then declines with advancing age (in the elderly), but priming remains relatively stable from age 3 to 80. These findings suggest that the systems subserving perceptual priming and episodic memory have distinct developmental trends over the life span. Nevertheless, more work is needed to establish whether all properties are conserved over the life span.

A neural mechanism for perceptual priming

The behavioral data reviewed above suggest that perceptual priming and episodic memory depend on different memory systems in the brain. What has been lacking, however, is evidence that each type of memory system is associated with different types of neural mechanisms. Recent data from single-cell recordings from monkey cortex, functional brain imaging and event-related potential (ERP) studies of normal human subjects, and behavioral studies of brain-damaged humans, provide converging evidence about the neural mechanism that mediates perceptual priming. These data provide a biological basis for distinguishing priming from other forms of memory.

Repetition suppression

In 1987, Brown *et al.* [50] and Baylis and Rolls [51] reported that some neurons in the monkey's ventral temporal lobe had a reduced response to the re-presentation of a stimulus, but not to the presentation of novel items. Since then, several studies have appeared that have begun to define the properties of this 'repetition suppression' effect (for recent reviews, see [52••,53•]):

1. Approximately a quarter [53•] to one-third [54] of inferior temporal lobe neurons show repetition suppression.
2. Although repetition suppression has been recorded most often from the inferior temporal cortex (including area TE, perirhinal, and entorhinal cortex) [55,56•], the phenomenon has also been observed in other regions (e.g. prefrontal cortex) [57•].
3. Repetition suppression is stimulus specific, occurring even when a large number of items (>150) intervene between repeated presentations of an item [58].
4. Repetition suppression appears to be long-lasting. Neurons show a reduced response to the re-presentation of a specific item with delays of up to 24 hours (the longest delay tested) [59].
5. Repetition suppression is graded. Neurons show a continual reduction in firing rate with each presentation, up to six to eight repetitions, after which the response plateaus to approximately 40% of its initial firing rate [58]. Thus, the response continues to reduce as the stimulus becomes more familiar.
6. Repetition suppression survives object transformations of size and location, suggesting that it operates on a relatively abstract structural representation [60].
7. Repetition suppression can be recorded during passive fixation [61], under anesthesia [62], and after cholinergic blockade [63], suggesting that it is an automatic, intrinsic response of cortical neurons.
8. The onset of repetition suppression can be very short, occurring approximately 100 ms after the onset of the initial neural response for a repeated item, and in as little as 10 ms after the third repetition of an item [58].
9. Repetition suppression occurs when an item is repeated, regardless of its behavioral significance. Miller and Desimone [64] studied working memory using a delayed matching-to-sample task in which some of the distractor items, presented during the interval between the first and second presentation of the target item, also repeated. Under these conditions, repetition suppression was associated with item repetition, regardless of whether the repeated item was a distractor or the target. Therefore, repetition suppression did not convey information about a specific item that was behaviorally significant (i.e. the item that the monkey had to respond to in order to obtain a reward). In contrast, another population of cells showed the opposite response: an enhanced response to item repetition. Critically, this enhanced response occurred only when the target items, not the distractor items, were repeated, suggesting that these neurons conveyed information about the behaviorally relevant item.

These properties of repetition suppression mirror many of the salient behavioral characteristics of perceptual priming (e.g. it is long-lasting, shows a graded response, and is resistant to manipulations of particular stimulus attributes and awareness). These parallels suggest that repetition suppression is a good candidate for the mechanism mediating perceptual priming. Indeed, supporting evidence for this idea has come from human neuroimaging studies, which have documented an association between

Figure 1

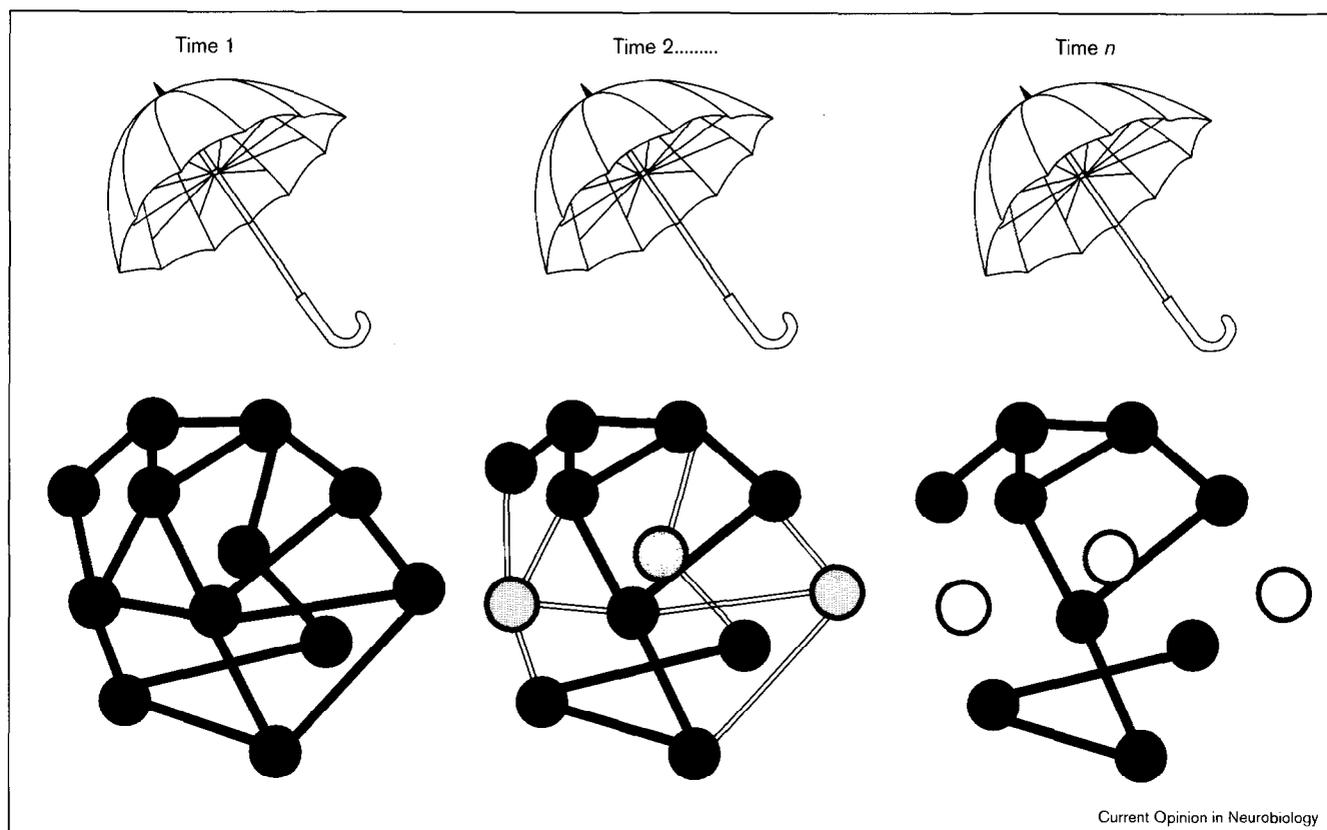


Illustration of the changes in a neuronal network representing visual object features as a function of repeated experience. As an object is presented repeatedly, neurons coding features that are not essential for recognizing the object decrease their responses (from black to gray to white), thereby weakening connections with other neurons in the ensemble (from black, to open lines, to no lines). As a result, the network becomes both sparser and more selective, yielding enhanced object identification.

perceptual priming and decreased neural activity (see [7••] for a recent review). Several studies using positron emission tomography (PET) have reported reduced cerebral blood flow (and thus a reduced neural response) associated with stem-completion priming [65–67]. In each study, the reduction was observed in posterior ventral occipitotemporal cortex (stronger on the right than on the left). Reduced activity, however, was not limited to this region, but was also reported (in one or more of the studies) in insular, parietal, and prefrontal cortices, as well as the thalamus and basal ganglia.

Similarly, using functional magnetic resonance imaging (fMRI), Demb *et al.* [68] found decreased activation in left inferior prefrontal cortex (the only area they recorded from) associated with the second presentation of words relative to the first presentation. In a different study, which used an object-naming task, our group (A Martin *et al.*, *Soc Neurosci Abstr* 1995, 21:1497) found that the second presentation of objects was associated with reduced activation relative to the first presentation of these same objects. The level of activation returned to its initial level when a novel set of objects was presented. The

reduced activity was not localized to one specific brain region, but rather was present throughout all areas that initially responded during the naming task, including the ventral occipitotemporal region, and parietal, insular, and prefrontal cortices.

Priming effects have also been studied using ERPs. Consistent with the PET findings, two recent studies reported a repetition-related reduction in the amplitude of the ERP waveform that appeared within the first 200 ms after stimulus onset, and was maximal over posterior recording sites [69,70]. This reduction may reflect reduced neural activity when items recur [70]. However, this finding stands in marked contrast to several previous reports of a repetition-related increase in the amplitude of the ERP waveform (see [69] for a discussion of this point). Additional studies are clearly needed to forge a more direct link between repetition-related ERP effects, repetition-related decreased activation in functional brain imaging studies, and the behavioral characteristics of perceptual priming. For example, are these brain-related events impervious to manipulations of attention? Do they survive delays of weeks and months?

While single-cell recordings from monkey cortex and human functional brain imaging studies have shown that reduced activity is most common in, though not limited to, temporal and occipital cortices, recent studies of brain-damaged patients suggest that the occipitotemporal region may be the critical site for mediating perceptual priming. For example, a patient with a right occipital lobectomy studied by Gabrieli and colleagues [71,72] had impaired perceptual priming as measured by word identification and stem-completion tasks. This finding is consistent with the reduced activity in right occipitotemporal regions reported in PET studies of stem-completion [65–67] and with behavioral evidence [73] in normal subjects. Importantly, the patient's recognition memory for the same words used in the priming studies was intact. However, the patient was not impaired on all perceptual priming tasks. For example, he showed normal facilitation on an object-naming priming task (JDE Gabrieli *et al.*, *Soc Neurosci Abstr* 1994, 20:413). This suggests that the critical brain region(s) mediating perceptual priming may vary as a function of the specific priming task employed (for additional evidence of impaired priming following damage to the occipitotemporal region, see [74,75]).

Linking repetition suppression and behavioral performance

Behaviorally, visual perceptual priming is defined by improved processing of previously seen material, relative to novel material (e.g. decreased naming times for an object). How might this behavioral effect be linked to reduced neuronal activity? A likely possibility, suggested by Desimone [52••], is that repeated experience with a novel item leads to a sharpening of the stimulus representation in the cortex (i.e. a representation of the essential features needed to identify the object). In this view, it is the neurons that continue to give a robust response when items recur that carry the critical information about the object. The neurons showing a decreased response, on the other hand, are dropping out of the responsive pool, perhaps because they encode features not needed to identify that specific object (although, presumably they would be critical for the identification of other objects). Thus, repetition suppression is a by-product of this sharpening process occurring in the cortex. Experience leads to both a smaller representation (with respect to the number of neurons maintaining their response rate) and a more selective representation (limited to critical stimulus-specific features that these neurons encode) (Figure 1). This more selective, or sharpened, representation would then result in a faster, more efficient, behavioral response. Moreover, this process happens automatically in the cortex. Repetition suppression is an intrinsic property of cortical neurons, providing a form of perceptual learning that allows us to identify previously encountered objects quickly and efficiently.

Conclusions

Principles continue to emerge, supporting claims that distinct memory systems underlie perceptual priming and episodic memory. Perceptual priming is impervious to long retention intervals, stimulus attribute alterations (e.g. size), attentional manipulations (e.g. dividing attention), and developmental changes, all of which affect episodic memory.

Recent work has illuminated the neural mechanisms that might underlie this phenomenon. One suggestion is that perceptual priming is mediated by repetition suppression, which appears to operate according to rules similar to those that operate for priming. Moreover, decreased neural activity has been reported in imaging studies using priming paradigms. These links, however, remain somewhat speculative. Several lines of research will be useful to test the degree to which characteristics between behavioral and neurophysiological responses are the same. For instance, how long does repetition suppression last (i.e. as long as behavioral data imply)? Is repetition suppression sensitive to changes in stimuli that affect the ability to identify stimulus form (e.g. extreme changes in stimulus rotation or different exemplars of the same-named object)? Is repetition suppression sensitive to attentional manipulations (as selective attention generally enhances neural activity, see [76])? Is repetition suppression linked to other forms of priming (e.g. semantic priming)? Are there developmental changes seen in repetition suppression? Moreover, it will be important to determine how different priming paradigms are affected by lesions in different cortical regions. Clarifying what properties collectively define perceptual priming, and linking this phenomenon with neural mechanisms, can be expected to have a pivotal role in memory research.

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