Reductions in cortical activity during priming
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Priming is a nonconscious form of memory in which an encounter with a stimulus influences the subsequent identification, production or classification of the same or a related stimulus. Neuroimaging studies have revealed that behavioral priming is typically accompanied by reduced activity in several cortical regions. We review recent studies that have concerned two key issues. First, specificity effects produced by changes between study and test in either the physical features of stimuli or the behavioral response reveal cortical sensitivity to the perceptual, conceptual and stimulus-to-decision mapping properties of primed items. Second, correlations between behavioral priming and activity reductions are robust across a range of tasks and procedures in prefrontal regions but not in posterior regions. On the basis of these recent studies, we suggest that the reduction in cortical activity during priming involves at least two different mechanisms.

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Introduction
Priming refers to an improvement or change in the identification, production or classification of a stimulus as a result of a prior encounter with the same or a related stimulus. Cognitive and neuropsychological evidence indicates that priming reflects the operation of implicit or nonconscious processes that can be dissociated from those that support explicit or conscious recollection of past experiences [1]. More recently, neuroimaging studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have revealed that priming is often accompanied by decreased activity in a variety of brain regions [2–4], although conditions exist in which priming-related increases are also observed [5–7]. At the same time, fMRI studies have likewise revealed decreased brain activity during

stimulus adaptation procedures, in which items are repeated (producing a corresponding decrease in the fMRI signal for the repeated items) and are then transformed along dimensions of theoretical interest, such as the orientation or color of a visual stimulus; the aim of these procedures is to make inferences about the properties of stored representations based on the extent of neural reductions across a particular transformation [8•,9]. Stimulus-related decreases in activation during priming and adaptation have been related to the phenomenon of repetition suppression in single-cell recordings, where decreased neural responding is observed as a function of stimulus repetition [4,10].

Do the activity reductions observed across the numerous cortical regions reflect the operation of a single process or multiple independent processes? What mechanisms produce these reductions? Is the repetition suppression effect observed in single-cell recordings and neuroimaging studies the neural basis of behavioral priming? There are at least two general approaches to addressing such fundamental questions: to begin with behavioral priming, and ask questions concerning its relationship to activation decreases; and to begin with repetition suppression, and approach behavioral priming as one subset of relevant phenomena. Here, we adopt the former approach (a recent review by Grill-Spector *et al.* takes the latter approach [8•]). We focus on recent studies that investigate the nature of the reductions in activation (which we will also refer to as 'neural priming') that are observed during studies of behavioral priming. We argue that the emerging evidence is inconsistent with a single-mechanism account of all neural priming, and instead supports the idea that multiple mechanisms are involved in different types of behavioral priming and corresponding neural priming. We focus on two broad domains that have been studied intensively during the past few years in neuroimaging studies: specificity of priming; and correlations between behavioral priming and neural priming.

Specificity of priming
The effects of priming vary in their extent of specificity — that is, the degree to which priming is disrupted by changes between the study and test phases of an experiment. Several types of priming specificity have been distinguished [11] but most research has focused on stimulus specificity, which occurs when priming is reduced by changing physical features of a stimulus between study and test. The extent of stimulus specificity has been a central issue for cognitive models of behavioral priming [11] and is also crucial for understanding neural priming: high degrees of stimulus specificity implicate perceptual

brain mechanisms as the source of priming. For example, neural priming in early visual areas, such as the posterior lateral occipital complex, exhibit a high degree of stimulus specificity for changes in viewpoint, illumination, size and position, whereas later, more anterior aspects of the lateral occipital complex exhibit greater invariance across changes in size and position relative to illumination and viewpoint [9]. Recent evidence reported by Vuilleumier et al. [12] likewise indicates a high degree of stimulus specificity in early visual areas. Overlapping shapes were presented, and subjects were cued to attend to one of them. Behavioral priming was subsequently documented on an object decision task (classification of objects as real versus non-sense) for shapes presented in the same or mirror-image orientation compared with the original study shape. Orientation-specific neural priming was observed in early visual areas: in the left medial occipital and right lingual gyri regardless of attention, and in the bilateral lateral occipital complex and lingual gyri only for attended objects.

Later visual regions can also show stimulus-specific neural priming [13] but several studies indicate that this specificity often exhibits a laterality effect. This pattern was first observed in an object-priming paradigm, where stimulus-specific neural priming (i.e. greater reduction in activation for repeating the same object versus different exemplars of objects that share the same name) was observed to a greater extent in the right than in the left fusiform cortex [14]. Vuilleumier et al. [12] also reported such a pattern for orientation-specific object priming in their overlapping shape paradigm (see also another study by Vuilleumier et al. [15] for a similar pattern in size-specific priming). Eger et al. [16] reported a similar stimulus-specific laterality effect using faces: neural priming was more viewpoint dependent in the right fusiform gyrus than in the left fusiform gyrus. In addition, both Vuilleumier et al. [12] and Eger et al. [16] report evidence for greater stimulus-specific neural priming in the posterior compared with the anterior fusiform gyrus. Other studies indicate that later perceptual regions exhibit largely nonspecific priming, for both visual stimuli (e.g. scenes [17]) and auditory words [18•,19]. However, evidence provided by Bunzeck et al. [20•] suggests that such effects are nonetheless category specific: neural priming was selective for faces in fusiform and related face-responsive regions but was selective for places in place-responsive regions of the parahippocampal cortex.

By contrast, regions of the inferior frontal gyrus and left inferior temporal cortex seem to respond invariantly to the perceptual features of an item, and are instead sensitive to its abstract or conceptual properties — even when the degree of perceptual overlap between initial and subsequent presentations of a stimulus is minimal to nonexistent. Neural priming has been observed in these regions during reading of mirror-reversed words that were initially presented in a normal orientation [13] and also when silently reading semantically related, but not unrelated, word pairs [21] (see also studies by Koutstaal et al. [14] and Simons et al. [22] for related examples of neural priming across exemplars of objects). Moreover, neural priming in these regions is independent of stimulus modality [23], even when the modality differs between the first and second presentations of a stimulus (e.g. change from a visual to an auditory stimulus) [19,24].

Although priming research has focused on stimulus specificity, recent work shows that both behavioral and neural priming can also exhibit response or decision specificity. In a study by Dobbins et al. [25], common objects were shown once or repeated three times, and subjects indicated whether each stimulus was 'bigger than a shoebox'; next, the cue was inverted and subjects indicated whether each item was 'smaller than a shoebox'. Finally, the cue was restored to 'bigger than a shoebox'. Neural priming was observed in left prefrontal, fusiform and extrastriate regions of interest. However, when the cue was reversed, neural priming was eliminated in the left fusiform cortex and disrupted in the prefrontal cortex; there was a parallel effect on behavioral response times. When the cue was restored to the original format, neural priming returned (again, there was a parallel effect on behavioral response times). Such priming seems to reflect the formation and retrieval of a link between a particular stimulus and the response or decision made about that stimulus; this is consistent with the observation that the response specificity effect occurs only when the identical object (versus a different object with the same name) is presented at study and test [26], and the finding that the effect is disrupted in amnesic patients with medial temporal lobe damage who exhibit intact response-independent priming [27].

Correlations between behavioral priming and neural priming

Although neuroimaging studies have documented neural priming since the early 1990s, until recently little was known about its direct relationship to behavioral priming. In the aforementioned study by Dobbins et al. [25], multiple regression analysis revealed that activity in the left prefrontal cortex predicted the disruptive effects of response switching on behavioral priming for individual subjects: greater initial reductions in prefrontal activity were associated with greater subsequent disruptions of behavioral response times. To the extent that activation reductions in the prefrontal cortex indicate less reliance on controlled processing, and greater reliance on automatic processing, these data suggest that performance disruptions attributable to response switching reflect a need to re-engage slower-controlled processes to make object decisions. This idea is consistent with the finding that reductions in fusiform activity did not predict the behavioral costs of switching cues [25], suggesting that these reductions might be incidental to behavioral priming.

Several other studies have likewise indicated that the extent of behavioral priming can be specifically associated with neural priming in prefrontal regions. Maccotta and Buckner [28] showed that behavioral priming for repeated words in a living or nonliving classification task was significantly correlated with the extent of neural priming in regions of the left inferior frontal gyrus and pre-supplementary motor area (pre-SMA) previously implicated in controlled processing. No such correlation was found in late visual regions that showed neural priming. Using the same task, Lustig and Buckner [29] documented significant correlations between behavioral and neural priming in the left inferior frontal gyrus for young adults, healthy older adults and patients with Alzheimer's disease. A similar pattern has been documented in the auditory domain: Orfanidou et al. [18•] found that the degree of auditory word priming on a lexical decision task was predicted by the extent of neural priming in the left inferior frontal gyrus and SMA, regardless of whether the speaker's voice was the same or different on initial and repeated presentations.

Bunzeck et al. [20•] found that the correlation between behavioral priming and prefrontal neural priming can be category specific. As noted earlier, face-responsive regions in the fusiform cortex showed selective reductions in activation for repeated faces; place-responsive regions in the parahippocampal cortex showed decreases for repeated places. However, neural priming effects in both regions were uncorrelated with behavioral priming. By contrast, correlations between neural and behavioral priming were specific for scenes in the left inferior prefrontal cortex but specific for faces in the left middle frontal gyrus.

Other evidence indicates that behavioral priming can correlate with neural priming in regions outside the prefrontal cortex. Bergerbest et al. [30] found that behavioral priming for environmental sound stimuli correlated with neural priming in the right inferior prefrontal cortex and also in two secondary auditory regions: the bilateral superior temporal sulci and the right superior temporal gyrus. Using a stem-completion task, Carlesimo et al. [24] found that the magnitude of behavioral cross-modality priming (auditory to visual) was correlated with the extent to which activation was reduced at the junction of the left fusiform and inferior temporal gyrus.

Turk-Browne et al. [31•] took a different approach. They examined the relationship between priming and subsequent memory effects, in which neural activity during encoding is sorted according to whether items are subsequently remembered or forgotten [32]. Behavioral and neural priming was produced for repeated scenes, but only for those that were subsequently remembered. For these scenes only, there was also a correlation between the magnitude of behavioral and neural priming in the

fusiform gyrus; this relationship approached significance in the right inferior prefrontal cortex, and was not significant in the parahippocampal cortex. The finding that the degree of behavioral and neural priming depended on subsequent memory points towards a link between implicit and explicit memory, perhaps involving shared encoding processes that similarly support both subsequent priming and explicit memory (but see studies by Schott et al. [33,34••] for fMRI evidence of dissociations between implicit and explicit memory).

Sayres and Grill-Spector [35] examined the relationship between behavioral and neural priming in early visual regions using an object-classification task and an fMRI adaptation procedure. Repetition of objects was accompanied by neural priming in regions of the lateral occipital complex and posterior fusiform gyrus. However, in contrast to the correlation between neural and behavioral priming in frontal and temporal regions in the aforementioned studies, neural priming in earlier visual regions was unrelated to the facilitation in response time that accompanied repeated classification.

The foregoing correlations (and also a study by Zago et al. [36]) suggest that neural priming effects in prefrontal and other regions might support behavioral priming but they do not enable conclusions to be drawn regarding a causal role. Wig et al. [37••] provided such evidence by combining fMRI with transcranial magnetic stimulation (TMS), using a semantic classification task (living versus non-living) for primed and novel objects. The results revealed that the classification of objects that had previously been accompanied by left frontal TMS failed to demonstrate subsequent behavioral priming and neural priming in the left inferior frontal gyrus and lateral temporal cortex; TMS had no effect on neural priming in early visual regions (left middle occipital gyrus). Crucially, control-site stimulation had no disruptive effects on either behavioral or neural markers of priming in any of the three regions (left inferior frontal gyrus, left lateral temporal cortex or left middle occipital gyrus). Consistent with this finding, Thiel et al. [38] provided evidence for a disruptive effect of left-frontal TMS on behavioral priming during a lexical decision task. Together, these results provide evidence for a causal link between behavioral and neural priming in frontal and temporal regions.

Conclusions: mechanisms of priming

Our review of recent neuroimaging studies of reduced activation during behavioral priming reveals several emerging trends in the literature (Figure 1). First, stimulus-specificity effects (for visual stimuli) seem to be most pronounced in early visual regions, with specificity effects for individual objects in later visual regions tending to be right-lateralized. Fewer studies have been carried out in the auditory domain but, at least with auditory words, stimulus-invariant priming has been

Figure 1
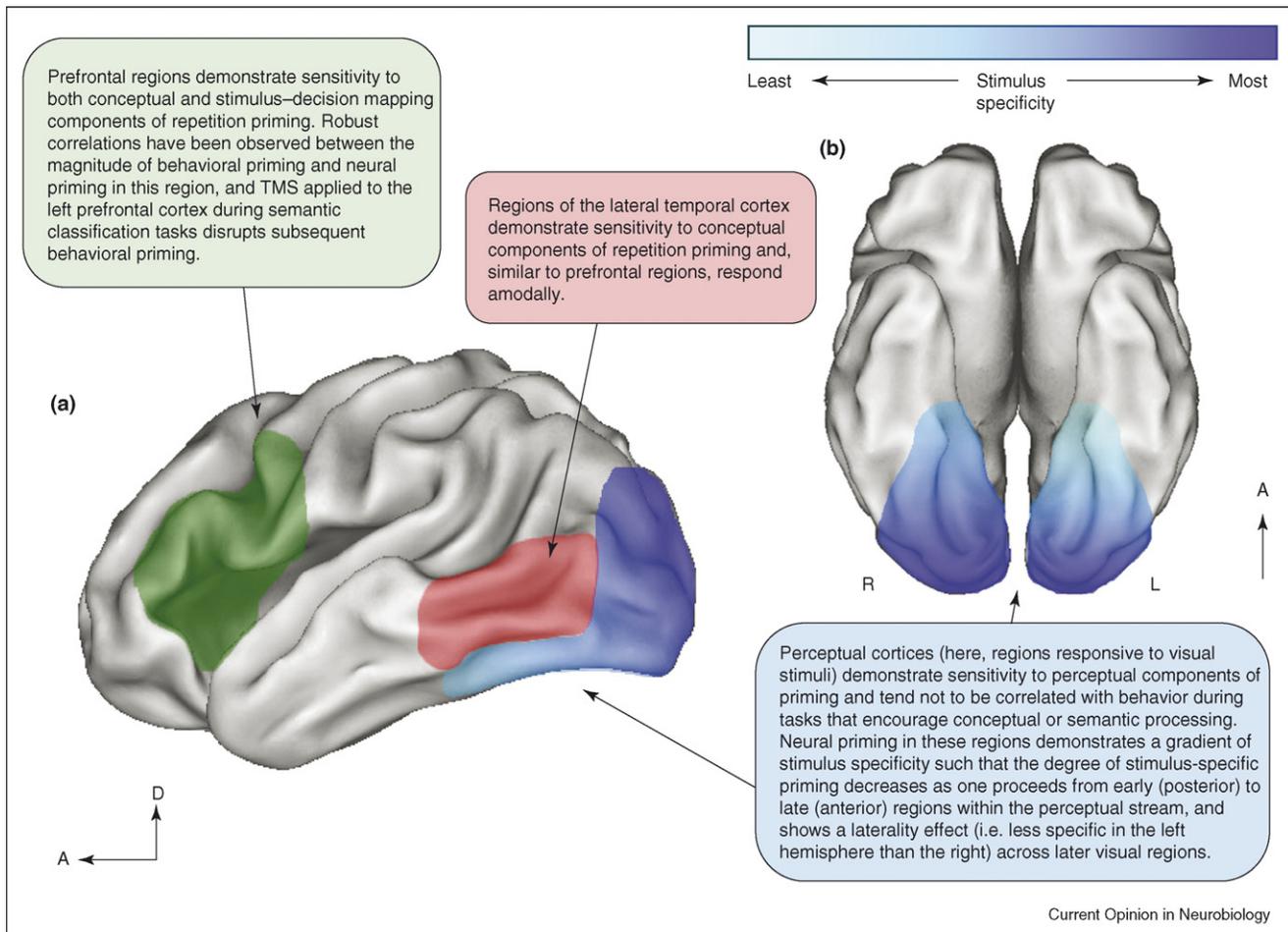
Proposed components of priming. **(a)** A lateral view of the left hemisphere, tilted in the dorsal–ventral plane to expose the ventral surface. **(b)** A ventral view of the left and right hemispheres. Abbreviations: A, anterior; D, dorsal; L, left; R, right. The color coding of anatomical regions is intended to serve as a heuristic for the proposed components. The color gradient within the ventral visual stream (blue) is intended to represent approximately the gradient of stimulus specificity that has been observed within these regions.

observed in late (secondary) auditory regions [18●,19]. In general, stimulus-invariant priming occurs more commonly as one proceeds from posterior to anterior regions, with category-specific priming occurring in fusiform and parahippocampal areas [20●], and sensitivity to abstract or conceptual features more prominent in inferior temporal and frontal regions. In addition, studies that have examined correlations between neural and behavioral priming indicate that such correlations are consistently robust in prefrontal regions across a range of tasks and procedures. There is scant evidence that neural priming in posterior regions is correlated with behavioral priming effects under the task conditions outlined here.

On the basis of this pattern of results, we suggest that there are at least two distinct mechanisms involved in the reductions in activity observed during priming experiments. One corresponds approximately to the descrip-

tion by Wiggs and Martin [4] of 'sharpening' or 'tuning', which occurs when exposure to a stimulus results in a sharper, more precise neural representation of that stimulus (see also the review by Grill-Spector *et al.* [8●] for more detailed consideration of sharpening and related ideas). Such tuning effects are likely to predominate in posterior regions that code for the perceptual representations of items, and perhaps in anterior regions that underlie conceptual properties of these items [39–41]. However, tuning effects are unable to account for response-specific priming effects [25] and seem to be less correlated with behavioral priming observed during tasks that are semantic or conceptual in nature. Based on these observations, we propose a second mechanism that primarily reflects changes in the prefrontal cortex that drive behavioral priming effects in a top-down manner, as initially controlled processes become more automatic [25,42]. As a result of repeated experience with an item,

prefrontal regions might become more synchronized [5,43,44] with other regions, enabling efficient processing that reflects a tighter coupling between the stimulus and decision. Consistent with this general claim, Fiebach *et al.* [5] and Ganel *et al.* [45] have provided preliminary evidence that distinct mechanisms underlie different types of neural priming, although their distinctions differ from ours (see also James and Gauthier [46] for useful discussion).

The foregoing discussion highlights several tasks for future studies of behavioral and neural priming. It will be crucial to test, within a single experiment, the specific multiple-process view suggested here, and to determine how particular types of neural priming are related to the behavioral facilitation afforded to the repeated processing of items. Identifying the underlying mechanisms that drive the neural priming effects will provide insight into how brain plasticity subserves observable changes in learning and memory.

Acknowledgements

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