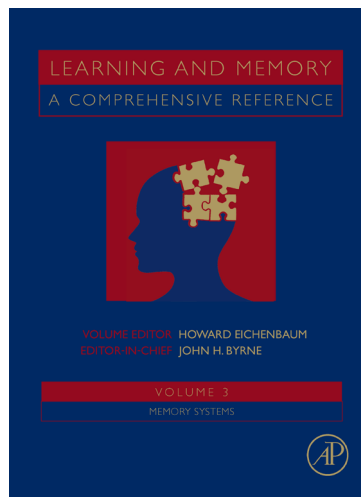


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## 3.12 Visual Priming

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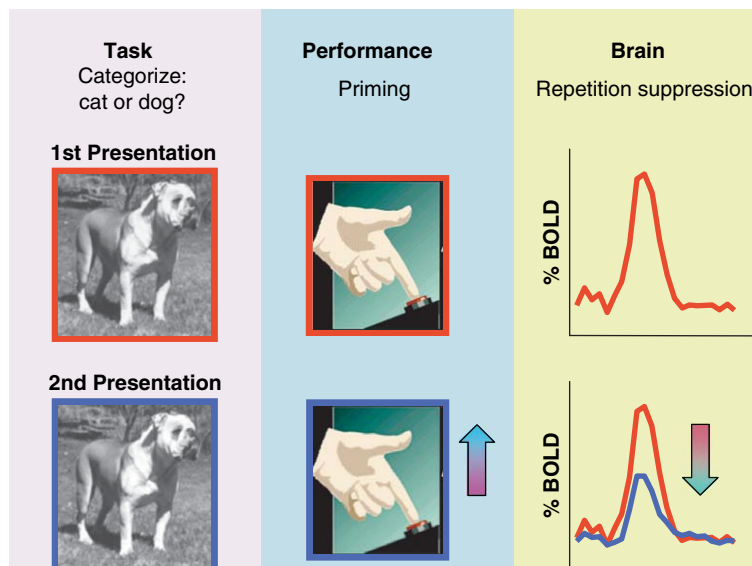
### 3.12.1 Introduction

A fundamental property of the brain that distinguishes it from artificially constructed computational devices is its ability to continuously update its functional properties based on prior experience. This property, plasticity, is apparent in many forms of learning and memory in humans. One important manifestation of plasticity in the brain is priming: the behavioral phenomenon of improved processing of a stimulus following prior experience. Priming typically manifests as increased accuracy and/or faster speed in making judgments on a stimulus that has been previously encountered (Figure 1). It is thought to reflect an implicit form of memory and learning, as it does not involve explicit memory of the prior experience.

This chapter is concerned with visual priming (priming related to presentation of visual stimuli) and the neural correlates underlying this phenomena. Visual priming is one of the most ubiquitous

manifestations of priming and has been extensively studied in many levels from the behavioral level to the neural level in both humans and animals. Thus, visual priming is an excellent model to study plasticity in the visual system and its relation to object perception. Studying the neural mechanisms of visual priming is important because it enables understanding the neural bases of cortical representations as well as the mechanisms involved in rapid implicit learning. In particular, recent interest for understanding priming and its neural correlates has been heightened as an increasing number of scientists use priming methods to characterize representations in the human brain.

This chapter is organized into three main sections: it begins with a review of the behavioral aspects of visual priming, then examines neuroimaging experiments of the neural correlates of priming, and concludes with a theoretical overview of three models that have been recently suggested for explaining the neural bases of priming.



**Figure 1** Schematic illustration of priming and repetition suppression/adaptation. *Left:* subjects are asked to perform a task, for example, classify an object. *Middle:* performance is measured on the first presentation and subsequent presentations of the same stimulus. During repeated presentations (e.g., the second presentation), performance improves (i.e., priming), as indicated by the arrow. Typically, accuracy increases and response time decreases. *Right:* Brain activity in object-selective cortex measured during the same experimental conditions shows lower BOLD responses for repeated presentations (blue) of the object compared to the initial presentation (red).

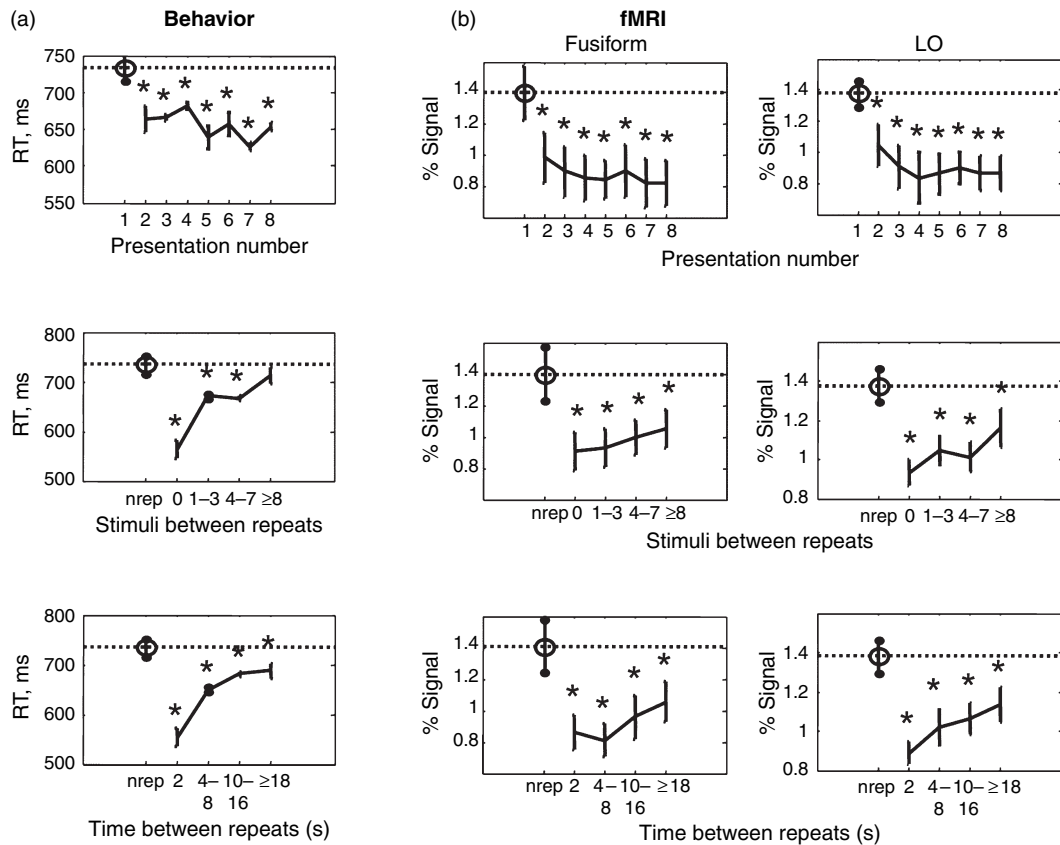
### 3.12.2 Behavioral Aspects of Visual Priming

In a typical priming experiment, subjects are shown an initial stimulus (prime) and are required to make a decision (e.g., categorize the stimulus; **Figure 1**) or produce a response (generate a word) on a subsequent stimulus (test) that is identical or related to the initial stimulus (e.g., the same object in different views, or a new object that is related perceptually, conceptually, or semantically to the prime). The priming effect (i.e., improvement in performance) is largest when the repeated stimulus is identical to the initial stimulus (prime). In some behavioral paradigms of priming, many intervening stimuli occur between the test and the prime. However, in other paradigms, the test immediately follows the prime. One particular striking aspect of priming is that it can be manifested after a single exposure to an object and is preserved in timescales ranging from seconds to even an year (Cave, 1997).

The level of priming is modulated by several factors such as the number of stimulus repetitions, the number of intervening stimuli, and the time between repeats (**Figure 2(a)**). The magnitude of response time (RT) priming increases with the number of stimulus repetitions both in short timescales

(seconds/minutes) and in longer timescales (days and weeks), and this advantage remains over week-long delays compared to single exposures of stimuli (Brown et al., 1996). Similarly, RT priming is largest when there are no intervening stimuli between the prime and the test stimulus and when the temporal interval between them is shortest (**Figure 2(a)**). Thus, immediate repetitions produce a larger priming effect compared to when repetitions occur after several minutes or days (van Turennout et al., 2000; Sayres and Grill-Spector, 2006). Interestingly, the graded nature of priming is reliable even in patients who are unable to remember the stimuli or judge the frequency of these stimuli in explicit tests (Wiggs et al., 1997).

Another important aspect of visual priming is its specificity, because visual priming has been used as an experimental tool to infer the characteristics of object representations. Visual priming is preserved even when the appearance of objects changes across repetitions. Visual priming is invariant to changes in object size (Cooper et al., 1992; Fiser and Biederman, 1995), position (Cooper et al., 1992), color (Cave et al., 1996), symmetry (Fiser and Biederman, 2001), and to some degree the viewing angle of the object (Biederman and Bar, 1999; Biederman, 2000). However, a recent experiment suggests that there



**Figure 2** Effect of repetition parameters on priming and repetition suppression in object-selective cortex as measured with functional magnetic resonance imaging (fMRI). (a) Mean response time. (b) BOLD response amplitude for object-selective regions in the fusiform gyrus (middle) and lateral occipital (LO) (right). Error bars indicate SEM across eight subjects. BOLD responses are averaged across hemispheres. Asterisks indicate significantly lower than first presentation ( $p < .05$ ). Dashed line: response to the first presentation. *Top*: sorting by presentation number. *Middle*: sorting by intervening stimuli between repeats. *Bottom*: sorting by time between repeats. Adapted from Sayres R and Grill-Spector K (2006) Object-selective cortex exhibits performance-independent repetition suppression. *J. Neurophysiol.* 95: 995–1007.

may be an interaction between the effects of shape and location on visual priming (Newell et al., 2005). Further, visual priming is diminished but still preserved for new exemplars from the same category (e.g., upright piano vs. grand piano). Experiments in which subjects viewed stimuli that were presented either in the right or left visual field suggest differential priming effects across the left and right hemispheres; priming effects show higher specificity when stimuli are presented to the left visual field, as they do not generalize across object rotation and exemplars of a category, whereas priming effects generalize across exemplars and rotation when stimuli are presented to the right visual field (Marsolek, 1995; Burgund and Marsolek, 2000; Koutstaal et al., 2001; Vuilleumier et al., 2002; Simons et al., 2003). These experiments have led to suggestions that

object representations in the right hemisphere are more specific than left-hemisphere representations, which may be more abstract in nature (Marsolek, 1995; Burgund and Marsolek, 2000; Koutstaal et al., 2001; Vuilleumier et al., 2002; Simons et al., 2003).

Several lines of research suggest that visual priming is an implicit form of learning and memory. A particularly important finding is that priming occurs in amnesic patients even though they are unaware of prior exposure to the primed stimulus (Tulving et al., 1991; Hamann and Squire, 1997) and they are significantly impaired on explicit tests (such as recognition memory, recall, and recollection of contextual information) on the same stimuli (Hamann and Squire, 1997).

Another striking aspect of priming is subliminal priming (Dehaene et al., 1998; Bar and Biederman,

1999; Naccache and Dehaene, 2001), that is, priming without awareness of the content of the priming stimulus. For example, Bar and colleagues (Bar and Biederman, 1999) showed subjects briefly presented stimuli (average 47 ms) that were masked. Subjects' naming performance on these stimuli was low (~14%). However, when the same stimuli were presented for the second time, naming performance on primed stimuli significantly increased (to about 35%). Subliminal priming may show higher specificity than suprathreshold priming, as it generalizes only to objects presented in the same hemifield. Therefore, Bar and colleagues have suggested that subliminal priming may be mediated by neural mechanisms distinct from suprathreshold priming. Other priming experiments of briefly presented masked stimuli show that the magnitude of priming is larger for the specific items that were primed compared with other exemplars of the category (Furmanski and Engel, 2000; Grill-Spector et al., 2000), and that priming effects increase across days and repeated exposures (Grill-Spector et al., 2000) and generalize across object size (Furmanski and Engel, 2000). Further, experiments of subliminal priming of words show generalization of priming effects across fonts and letter size (Naccache and Dehaene, 2001).

Overall, evidence from amnesic patients and subliminal priming experiments suggests that awareness may not be necessary for priming. These experiments lead to the prevailing theory that posits that priming reflects an implicit form of memory that is distinct from explicit memory and that relies on distinct neural and cognitive mechanisms.

### 3.12.3 Neural Correlates of Priming

Many studies have investigated the neural correlates of priming in humans using functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and magnetoencephalography (MEG). Under experimental situations similar to behavioral paradigms of visual priming, the most robust and consistent finding with fMRI is reduced brain activations to repeated presentations of a stimulus relative to the initial presentation of that stimulus (Figure 3). This reduction has been referred to as repetition suppression (RS), fMRI-adaptation (Sobotka and Ringo, 1994; Ringo, 1996; Grill-Spector and Malach, 2001), mnemonic filtering (Miller et al., 1993), repetition suppression (Desimone, 1996), decremental

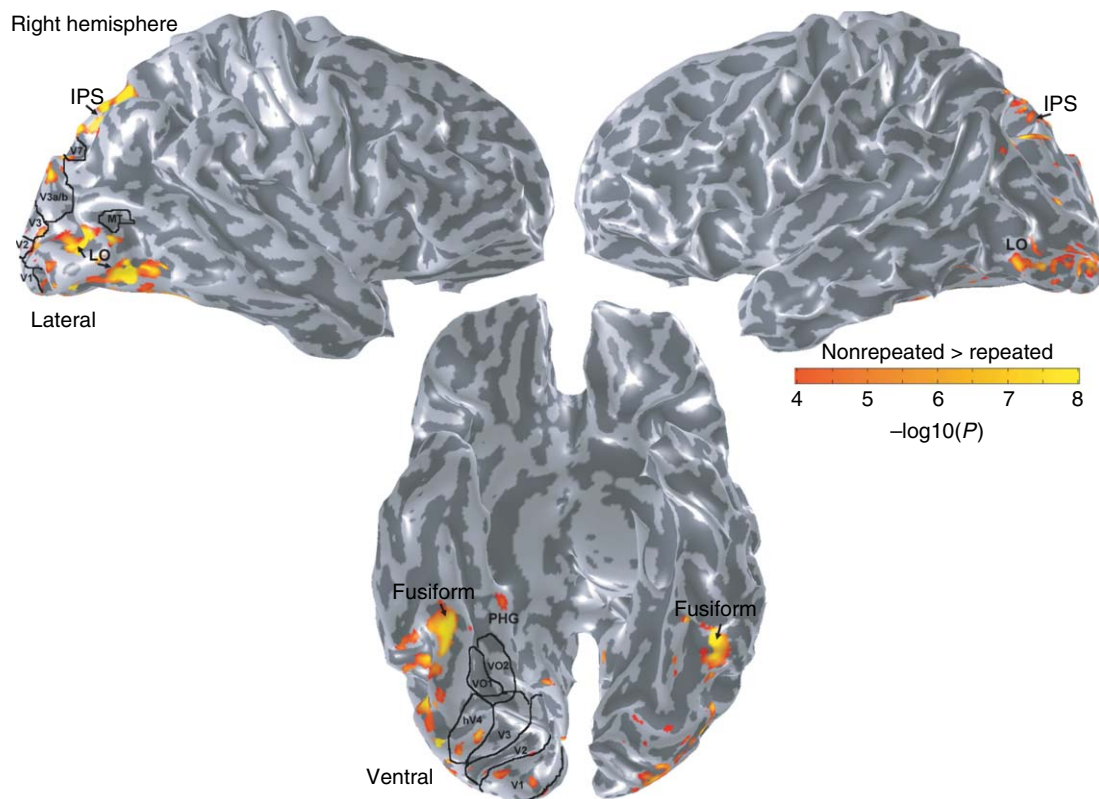
responses (Brown and Xiang, 1998), and neural priming (Maccotta and Buckner, 2004). We use RS to refer to decreased neural responses following stimulus repetition. However, it remains mysterious how reduced cortical responses provide for improved performance. Further, although the most ubiquitous cortical phenomenon related to stimulus repetition is reduced responses, in some cases there is evidence for increased responses with stimulus repetition or repetition enhancement (RE) (Dolan et al., 1997; George et al., 1999; Grill-Spector et al., 2000; Henson et al., 2000; James et al., 2000; Kourtzi et al., 2005; James and Gauthier, 2006; Turk-Browne et al., 2006). We consider both phenomena and their relation to priming in turn.

#### 3.12.3.1 Repetition Suppression

When stimuli are repeated, as in typical priming paradigms, neural activity is usually reduced. This neural repetition effect has been reported at multiple spatial scales, from the level of individual cortical neurons in monkeys (Li et al., 1993; Miller and Desimone, 1994; Sobotka and Ringo, 1996) to the level of hemodynamic changes (measuring the pooled activation of millions of neurons) in humans, using functional imaging such as fMRI (Buckner et al., 1995; Demb et al., 1995; Stern et al., 1996; Grill-Spector et al., 1999; Henson et al., 2000; Jiang et al., 2000; Naccache and Dehaene, 2001). Repetition-related reductions also occur at multiple temporal scales, both in their longevity – from milliseconds (Sobotka and Ringo, 1996) to minutes (Henson et al., 2000) and days (van Turennout et al., 2000) – and in the latency of their expression (Dale et al., 2000; Henson et al., 2004). Therefore, RS is a robust phenomenon that occurs across many timescales, in multiple brain regions, and across an impressively large number of experimental conditions.

In experiments when subjects view repeated presentations of objects and scenes, there is robust and reproducible RS as measured with fMRI also referred to as fMRI-adaptation (for reviews, see Grill-Spector and Malach, 2001; Kourtzi and Grill-Spector, 2005; Grill-Spector et al., 2006a). RS/fMRI-adaptation typically occurs in object-selective cortex (Figure 3) including the lateral occipital complex (LOC – consisting of regions overlapping the lateral occipital sulcus, inferior occipital gyrus, and occipitotemporal sulcus), as well as more ventral regions including the fusiform gyrus (Fusiform) and the parahippocampal





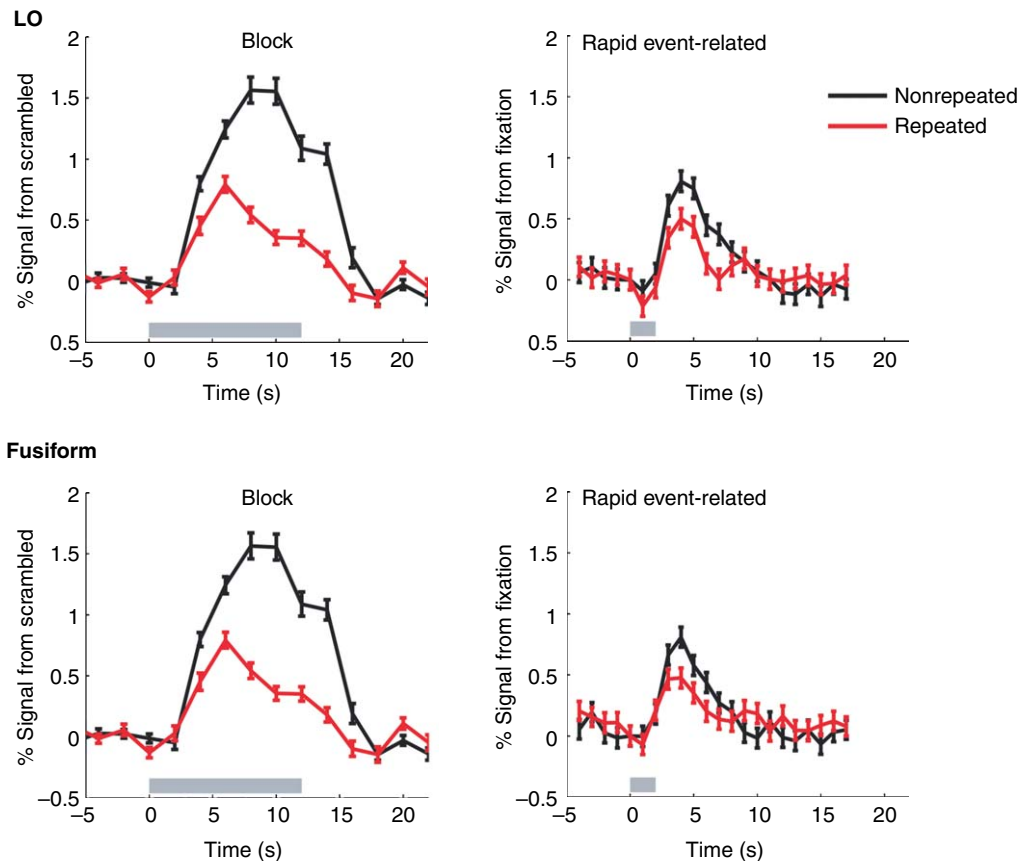
**Figure 3** Occipitotemporal regions that show reduced responses to repeated versus nonrepeated stimuli ( $p < 10^{-4}$ , voxel level uncorrected). Color bar indicates statistical significance. Data are shown for a representative subject on her partially inflated brain. Dark gray regions indicate sulci, and lighter gray regions indicate gyri. Retinotopic visual areas (delineated by black lines) were defined from independent retinotopic scans of polar angle and eccentricity and are shown for simplicity only on the right hemisphere. Abbreviations: PHG, parahippocampal gyrus; IPS, intraparietal sulcus.

gyrus (PHG). RS also occurs in dorsal regions (Figure 3), including regions lateral to and partially overlapping V3a and regions in the posterior bank of the intraparietal sulcus (IPS). Other regions that show RS to repeated presentation of object and scene images include medial temporal cortex (Stern et al., 1996) and frontal cortex (Wagner et al., 1997; Buckner and Gauthier, 1998; van Turennout et al., 2003).

RS is not an all-or-nothing phenomenon: The magnitude of RS in object-selective cortex increases with repetition number and with fewer intervening stimuli between repetitions (Figure 2(b)). Therefore, the magnitude RS in block-design fMRI experiments is typically larger than during event-related fMRI experiments in which many intervening stimuli occur between repetitions of the same image (Figure 4). A recent study (Ganel et al., 2006) suggests that RS to immediate repetitions of identical stimuli is more prominent in object-selective regions of the LOC

and fusiform cortex, whereas RS effects for stimuli that had been presented several minutes previously and occur after many intervening stimuli are more prominent in more anterior and medial regions of the temporal lobe. Further, they suggest that effects of immediate repetition and long-lagged repetition with intervening stimuli are largely additive (except for the left fusiform gyrus).

Repetition suppression in high-level visual areas has been associated with visual priming (Schacter and Buckner, 1998; Wiggs and Martin, 1998) because both phenomena occur under the same experimental conditions (Figure 1). However, it is mysterious why reduced cortical responses provide for improved behavioral performance. Notably, RS measured by fMRI may be related to other factors (unrelated to priming), such as repetition effects independent of behavioral improvements (Sayres and Grill-Spector, 2006), attentional differences between conditions (Yi and Chun,



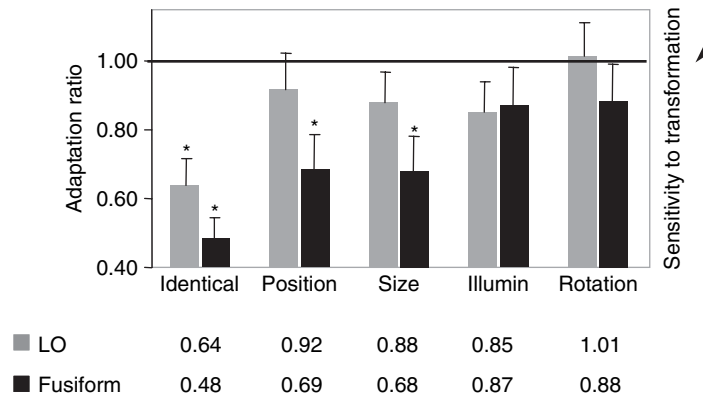
**Figure 4** Repetition suppression in object-selective cortex: time course data. Data are shown for one representative subject. Object-selective cortex regions were defined as regions that showed higher activation for animals than scrambled animals with  $p < 10^{-3}$  at the voxel level. *Black*: first presentation of the stimulus; *Red*: Repeated presentations of the same stimulus. In the block design fMRI experiment, stimuli were repeated up to 12 times within a block. In the rapid event-related fMRI experiment, stimuli were repeated up to eight times across a 4-min and 38-s experiment. Horizontal gray bar: duration in which stimulus was presented. Error bars indicate SEM across trials for this subject. Adapted from Grill-Spector K, Henson R, and Martin A (2006) Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* 10: 14–23.

2005; Yi et al., 2006), and/or learning of a response mapping between a stimulus and a cognitive decision (Dobbins et al., 2004; Schacter et al., 2004). Conversely, behavioral effects, such as visual priming, may be a consequence of activity in multiple cortical regions. Thus, RS in specific cortical regions may not relate directly to the behavioral changes associated with priming.

While keeping these caveats in mind, the section titled ‘Investigations of the relation between RS and priming’ describes several experiments that investigated the relation between priming and RS, and the section titled ‘Neural models of repetition suppression and priming’ lays out three models of the neural bases of priming, providing hypotheses for the relation between reduced cortical responses to repeated stimuli and improved performance – namely, visual priming.

### 3.12.3.1.1 Characterizing neural representations using repetition suppression

In addition to examining the relation between RS and priming, many neuroimaging experiments use RS to probe the functional properties of neural populations. This tool has been termed fMRI-adaptation (Grill-Spector and Malach, 2001) and also the priming method (Naccache and Dehaene, 2001; Vuilleumier et al., 2002). In the basic paradigm used in fMRI experiments, one first measures the basic RS (or fMRI-adaptation) effect induced by repetitions of identical stimuli. This is done by measuring the level of RS or adaptation to repeated presentations of identical stimuli relative to the response of nonrepeated stimuli (Figure 5 – identical). Subjects are also presented with repeated stimuli that vary along



**Figure 5** Using fMRI-adaptation to measure sensitivity to face transformations. To examine the level of adaptation to face transformations, we measured the adaptation ratio: repeated/nonrepeated. Repeated reflects blocks in which the same face was repeated, and nonrepeated reflects blocks that included nonrepeated presentations of different male faces in the same view, illumination, size, and position. An adaptation ratio of 1 indicates no adaptation (solid line); ratios that are significantly less than 1 are indicated by asterisks. Identical: repetitions of identical images of the same face; Position: repetitions of the same face in different retinal positions ( $\sim 6^\circ$  around fixation); Size: repetitions of the same face in different sizes ( $\sim$ threefold size change); Illumin: repetition of the same face illuminated from different directions; Rotation: Same face at different rotations around the vertical. Gray bars: lateral occipitus; Black bars: Fusiform; Error bars indicate SEM across 14 subjects. Numbers indicate adaptation ratios for each of the conditions. Data from Grill-Spector K and Malach R (2001) fMRI-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychol. (Amst.)* 107: 293–321.

some dimension (e.g., the same object, but different sizes). The hypothesis tested is whether the underlying neural representation is sensitive or not to change along this dimension. If the underlying neural representation is insensitive to the change in the stimulus, then neurons will show a reduced response to repeated transformed versions of the object, and the fMRI signal will be reduced (i.e., fMRI-adaptation will be observed) similar to the reduction produced by repetitions of identical stimuli. Alternatively, if the neurons are sensitive to the change, the level of the fMRI signal will be similar to the initial level, and no RS/adaptation will be measured.

An example of using fMRI-adaptation to characterize neural representations is shown in **Figure 5**. In these experiments, subjects were shown either repeated presentations of the same image of a face (identical) or images of the same individual that varied in size (up to threefold changes in size), position ( $\sim 6^\circ$  around fovea), illumination (five different illuminations), viewpoint (rotation around the vertical,  $-90^\circ$  to  $90^\circ$ ). Activations to repeated versions of the same face were compared to nonrepeated presentations of faces of different individuals that were taken under the same viewing conditions (e.g., same size, position, illumination, and view). We found differential effects of fMRI-adaptation across object-selective cortex: LO regions show fMRI-adaptation for repetitions of

identical images of objects but no fMRI-adaptation when the object varied in position, size, illumination, or viewing angle. In contrast, more ventral regions along the fusiform and occipitotemporal sulcus showed fMRI-adaptation for changes in object position and size but no fMRI-adaptation for different illuminations or rotations of the same object. These experiments provide evidence for differential sensitivity to object transformations across the human ventral stream.

fMRI-adaptation has been widely used by researchers to examine sensitivity in object-selective cortex to object size and position (Grill-Spector et al., 1999; Vuilleumier et al., 2002), viewpoint (Grill-Spector et al., 1999; James et al., 2002; Vuilleumier et al., 2002; Epstein et al., 2003), object format (Kourtzi and Kanwisher, 2000), perceived shape (Kourtzi and Kanwisher, 2001), contrast (Avidan et al., 2002; Murray and He, 2006), contour completion (Kourtzi et al., 2003), and face representation (Grill-Spector et al., 1999; Andrews and Ewbank, 2004; Winston et al., 2004; Eger et al., 2005; Loffler et al., 2005; Rotshtein et al., 2005; Jiang et al., 2006). fMRI-adaptation has also been used to probe higher-level conceptual representations using object pictures (Koutstaal et al., 2001) and words (Wheatley et al., 2005). Overall, these studies have documented that RS in occipitotemporal cortex is not limited to the identical image but also occurs, albeit to a lesser



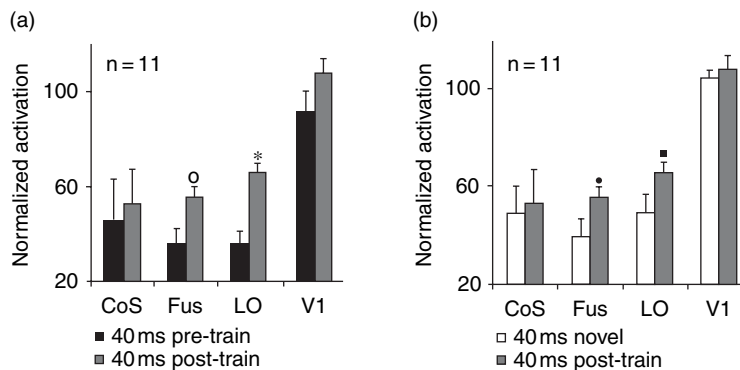
extent, to transformed versions of the same object, to different exemplars that share the same name (e.g., two different umbrellas), and even to different words that are conceptually related (Wheatley et al., 2005).

### 3.12.3.2 Repetition Enhancement

Although the most ubiquitous cortical phenomenon is repetition suppression, there is evidence also that some aspects of visual priming are related to repetition enhancement (RE) (Dolan et al., 1997; George et al., 1999; Grill-Spector et al., 2000; Henson et al., 2000; James et al., 2000; James and Gauthier, 2006; Kourtzi et al., 2005; Turk-Browne et al., 2006). RE effects have been reported for improved recognition of repeated degraded stimuli (compared to performance on their initial presentation). RE was observed when repeated exposure to subthreshold, briefly presented objects led to better recognition (Grill-Spector et al., 2000) (Figure 6), when repeated exposure to unfamiliar shapes made them familiar (Henson et al., 2000), when inverted contrast faces (that were initially unrecognizable) were primed with positive contrast faces and became recognizable (George et al., 1999), and when observers learned to detect low-salience shapes

in noisy backgrounds (Kourtzi et al., 2005; Turk-Browne et al., 2006).

One possibility is that RE and repetition suppression reflect dissociable forms of visual priming (Henson et al., 2000; Gruber and Muller, 2005); thus, repetition suppression may reflect supra-threshold priming, and RE may reflect subliminal priming (see also Kourtzi et al., 2005). These findings suggest that learning of unfamiliar or degraded stimuli is mediated by increased neural activity across high-level visual areas as new representations are formed for these previously unseen or unfamiliar stimuli. In contrast, learning of prominent suprathreshold (and/or familiar) stimuli is mediated by the sharpening of existing representations, leading to sparser coding of objects. An alternative account suggests that there is only one underlying mechanism, but it produces differential signals below and above recognition threshold (James et al., 2000; James and Gauthier, 2006). James and colleagues (James and Gauthier, 2006) proposed an accumulation model for recognition, in which recognition occurs when sufficient evidence for identifying an object has accumulated (See Chapter 2.23). Accumulation predicts a faster rise of activity



**Figure 6** Repetition enhancement in object-selective cortex. Subjects were first scanned in the pretraining session when they viewed briefly presented images for 40 ms followed by a 460-ms mask. Subjects then viewed these masked images during five training sessions, and then they were scanned again in a second posttraining scan in which they viewed the same briefly presented stimuli (posttrain) and another set of novel masked images shown for the same duration (40 ms – novel). Initial recognition performance (40 ms pretrain) was about 25% and posttraining about 60%. (a) Normalized BOLD signal elicited by identical images viewed for 40 ms during pretraining and posttraining scans. Activations are plotted as percentage of activation to object stimuli shown for 120 ms followed by a mask for 380 ms. Recognition of 120 ms stimuli was close to ceiling. X-axis, brain area; Y-axis, normalized signal compared to activation elicited by stimuli presented for 120 ms. Dark bars: pretraining; Gray bars: identical stimuli posttraining. Error bars: SEM. Asterisks ( $p < .001$ ) and circles ( $p < .03$ ): significantly larger signal posttraining versus pretraining. (b) Normalized BOLD signal in the posttraining scan for two sets of images (trained and novel) shown for 40 ms. White bar: novel images; Gray bars: trained images; Error bars: SEM. Square ( $p < .01$ ) and circle ( $p < .05$ ): significantly stronger signal for trained images compared to novel images. Abbreviations: CoS: collateral sulcus; Fus: Fusiform gyrus; LO: lateral occipital. Adapted from Grill-Spector K, Kushnir T, Hendler T, and Malach R (2000) The dynamics of object-selective activation correlate with recognition performance in humans. *Nat. Neurosci.* 3: 837–843.

for primed compared to unprimed stimuli, as the evidence accumulates faster for primed stimuli. Another consideration for interpreting RE effects is that, close to perpetual threshold, recognition performance on trials in which subjects recognize objects (hits) is correlated with a higher signal than trials in which subjects fail to recognize objects (misses) (Bar et al., 2001; Grill-Spector, 2003; Grill-Spector et al., 2004). Thus, RE associated with improved recognition of previously unrecognized stimuli could reflect a higher hit rate for repeated stimuli that is not related to priming per se.

Although RE has been suggested to reflect a distinct form of priming than RS, to date there is no parametric study that systematically varied factors that affect RE and visual priming to test whether RE and visual priming are quantitatively linked.

### 3.12.3.3 Repetition Effects Measured with EEG and MEG

Repetition effects have also been studied by measuring changes in the electrical (EEG) or magnetic (MEG) field, usually recorded above the scalp. These effects reflect changes in the amplitude and/or synchrony of local field potentials (LFPs) caused by transmembrane currents in large numbers of neurons.

Most EEG studies examine event-related potentials (ERPs), which reflect changes in electrical potential during the few hundred milliseconds following stimulus onset, averaged across trials. The earliest object repetition effects are typically observed approximately 200 ms after stimulus onset (Eimer, 2000; Doniger et al., 2001; Schendan and Kutas, 2003; Henson et al., 2004; Schweinberger et al., 2004; Gruber and Muller, 2005), but some experiments show earlier repetition effects 150–170 ms after stimulus onset. Campanella, Henson, and colleagues (Campanella et al., 2000; Henson et al., 2004) found repetition effects when the same view of an object was repeated, as early as 160–190 ms when there were no intervening objects; with one or more intervening objects, repetition effects only emerged from approximately 200 ms onward.

Other EEG studies concentrate on changes in the power of electrical or magnetic oscillations that are induced by stimulus repetition (high-frequency oscillations are not observed in ERPs if they are not phase-locked across trials). Some studies report decreased high-frequency (>40 Hz) power around 220–350 ms for repetition of familiar objects across lags of one or two intervening objects (Gruber and Muller, 2005).

Such changes in power in certain frequency bands have been shown to correlate with the blood-oxygen-level-dependent (BOLD) changes measured by fMRI (Brookes et al., 2005; Sayres and Grill-Spector, 2006).

### 3.12.3.4 Investigations of the Relation between RS and Priming

One useful approach used to examine the relation between priming and RS is to parametrically manipulate factors that influence the level of priming and/or RS and to examine whether the modulation of priming and RS effects covary or follow distinct profiles. Researchers have shown that many factors modulate the level of priming and also the level of RS. These include the number of stimulus repetitions (Henson et al., 2003; Sayres and Grill-Spector, 2006), frequency of repetition (Sayres and Grill-Spector, 2006), duration of stimulus presentation (Zago et al., 2005; Sayres and Grill-Spector, 2006), stimulus contrast (Avidan et al., 2002), and amount of noise added to the stimulus (Turk-Browne et al., 2006), as well as high-level cognitive factors such as attention (Eger et al., 2004; Murray and Wojciulik, 2004; Yi and Chun, 2005; Yi et al., 2006), relevance to the task (Henson et al., 2002b; but see Jiang et al., 2000), familiarity (Henson et al., 2000), and emotion (Ishai et al., 2004, 2006).

Recently, researchers have used this approach to examine the correlation between RS and priming (Dobbins et al., 2004; Maccotta and Buckner, 2004; Zago et al., 2005; Sayres and Grill-Spector, 2006). Results of these experiments are mixed. Some experiments suggest that some factors modulate the level of priming and RS in a similar way, suggesting a quantitative relation between priming and RS (Maccotta and Buckner, 2004; Zago et al., 2005). However, other factors may affect priming, but not RS (or RS but not priming), suggesting that RS in specific occipito-temporal regions may not be a direct neural correlate of visual priming (Henson et al., 2003; Dobbins et al., 2004; Sayres and Grill-Spector, 2006).

#### 3.12.3.4.1 Evidence for a correlation between priming and repetition suppression

Several recent studies have reported a correlation between the level of response time priming and RS in prefrontal cortex (PFC) (Dobbins et al., 2004; Lustig and Buckner, 2004; Maccotta and Buckner, 2004). Lustig and Buckner (2004) report across-subject correlation between the level of

priming during a meaning-based word classification task and PFC activity across young adults, older adults, and adults with initial signs of Alzheimer's disease (Lustig and Buckner, 2004). Similarly, Maccota and Buckner (2004) showed that the level of priming as a function of number repetitions of a word and the level of RS in PFC was correlated across subjects. Dobbins and colleagues (Dobbins et al., 2004) also reported a positive within-subject correlation between response time priming induced by repeated presentations of visually presented objects and RS in PFC. In the same study they reported a negative within-subject correlation between priming and RS in the left fusiform cortex.

Zago and colleagues (Zago et al., 2005) showed that both visual priming and RS vary as a function of the initial exposure of the stimulus, which varied between 40 and 1900 ms. The largest priming and RS effects were observed for 250-ms exposure durations. Further, the average level of priming across subjects is correlated with the average level of RS in occipito-temporal object-selective regions. However, Zago and colleagues do not report within-subject correlations between visual priming and RS.

Together, these studies suggest that under some circumstances there is a correlation between priming and RS. The most consistently reported cortical region in which activation is associated with priming is PFC. Further research is necessary to examine the generality of these results to additional stimulus manipulations to understand whether these effects are modality specific and to investigate more comprehensively whether the correlation between priming and RS can be found within individual subjects, as responses and brain activations are likely to vary across individuals.

#### **3.12.3.4.2 Evidence for dissociable effects of performance and repetition on the level of repetition suppression**

Priming effects can be reduced when the responses to a stimulus are changed across repetitions. A recent study examined whether changes in priming effects and RS effects were dependent on the particular response/judgment made about the stimulus. Dobbins and colleagues (Dobbins et al., 2004) measured priming and RS effects as a function of repetition number under two experimental conditions – when the same judgment was made on the stimulus (indicate whether an object is larger than a shoebox, for both initial and repeated presentations) and when different judgments

were made (initially subjects judged whether the item was larger than a shoebox, and when the item was repeated they were asked if it was smaller than a shoebox). Priming effects were larger when the question was identical in the initial and repeated conditions. However, priming was observed even when the judgment differed. RS in PFC was correlated with priming effects in both experimental conditions. In contrast, RS in fusiform cortex was observed when items were repeated and the judgment was identical but was abolished when the judgment changed. These data suggest that RS in fusiform cortex was related to the ability of the subject to use prior responses during repeated trials, rather than reflecting a priming effect.

Another consideration when relating BOLD responses to performance is that several factors may contribute to BOLD responses measured in a specific brain region, and performance is likely to be an outcome of activation across several brain regions. Therefore, while RS and priming occur in the same experimental situations, the two phenomena may not coincide under all experimental conditions. For example, RS may be driven by shorter RT (e.g., shorter RT may produce lower BOLD responses) but not repetition. This alternative predicts lower BOLD responses for trials with shorter RT regardless of whether these trials contain stimuli shown for the first time or contain stimuli that have been seen previously. Alternatively, repetition may produce lower responses independent of performance changes. This alternative suggests that repeated trials will correspond to trials with lower BOLD response, even if there is no change in performance – that is, a memory component to RS that is independent of performance.

Another question is whether RS and visual priming reflect changes in neural activity during the recognition process, or whether they reflect changes after recognition has occurred. Under many experimental conditions the stimulus is presented for longer periods than the minimal time necessary for recognition (Grill-Spector and Kanwisher, 2005) (~67–120 ms), yet both performance and BOLD signals are measured after recognition has occurred.

In a recent study (Sayres and Grill-Spector, 2006), we examined both factors: Is RS in object-selective cortex correlated with response time priming or repetition independent of performance changes? Second, do RS and priming occur during or after recognition? To quantitatively examine the relation between priming and RS, we first measured the

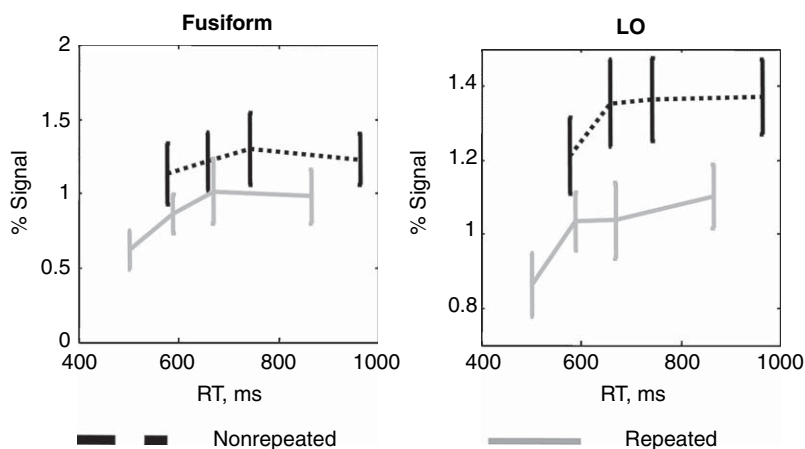
relation between priming and RS in object-selective cortex as we parametrically varied repetition parameters (number of repetitions, number of intervening stimuli, time between repeats). We then measured whether there are independent contributions of RT and repetition to RS effects. Second, to assess whether RS and priming occurred during or after recognition, we compared RS and priming effects for long exposure durations (1750 ms) and for short exposures (67–101 ms). Exposure durations were set for each subject to be the minimal duration for 85% accuracy performance on a classification task (67–101 ms for our subjects). Stimuli were presented briefly and then masked for the remainder of a 2-s trial. These brief presentations allowed us to tap into repetition effects during recognition.

We found that both RT priming and RS occurred for both long and short exposures, and these effects were modulated by repetition parameters (Figure 2). The level of RS also varied with stimulus duration, as the magnitude of RS was lower for short compared to long exposure durations. In contrast, the magnitude of RT priming was not significantly different across these exposure durations. We did find an improvement in accuracy for short exposures, but not long exposures (perhaps due to a ceiling effect), but this did not depend on repetition parameters.

Importantly, we found that when exposure durations were long (1750 ms), there was significant correlation between RS in object-selective cortex and RT priming for some repetition parameters (stimuli between repeats, time between repeats) but

not others (number of repeats). When exposures were short (67–101 ms), we observed significant priming and significant RS, but they were not correlated. Thus, both priming and RS can occur under the same experimental conditions, but they do not always covary. These data suggest that RS in object-selective cortex may not reflect improved RT performance observed during priming.

Finally, we examined whether there are separable contributions of response time and repetition to RS by sorting our data into repeated and nonrepeated conditions. For each condition, we ranked each subject's trials according to response time and grouped the trials into four equally sized bins according to RT. Responses to repeated trials were lower than nonrepeated trials even when response times were equated between conditions (Figure 7). Importantly, for both long and short image durations and all object-selective regions of interest (ROIs), we found a significant effect of repetition independent of response time. In contrast, we did not find significant effects of response time independent of repetition. There was a weak, statistically significant effect present in LO and only for stimuli that were presented for 1750 ms. Finally, we found no significant interaction between repetition and response times. Taken together, these data reveal that RS in object-selective cortex reflects stimulus-specific repetition, even when performance is matched between repeated and nonrepeated objects and when stimuli are presented close to the minimum time required for recognition. This suggests that there is a



**Figure 7** Separable contributions of repetition and response-time. Data were sorted first into repeated (solid gray) and nonrepeated (dashed black) correct trials and then grouped into four response time bins for each subject. The first response time bin represents fastest quartile of correct trials for each subject. Error bars indicate SEM across seven subjects. Adapted from Sayres R and Grill-Spector K (2006) Object-selective cortex exhibits performance-independent repetition suppression. *J. Neurophysiol.* 95: 995–1007.

performance-independent component to RS in object-selective cortex that may be an implicit form of memory.

Overall, our experiments show that both priming and RS effects depend on repetition parameters. However, different factors have dissociable effects on priming and RS. These experiments underscore the importance of conducting future experiments using parametric designs, systematically varying factors that modulate priming and RS to quantitatively measure the relation between these phenomena.

### 3.12.4 Neural Models of Repetition Suppression and Priming

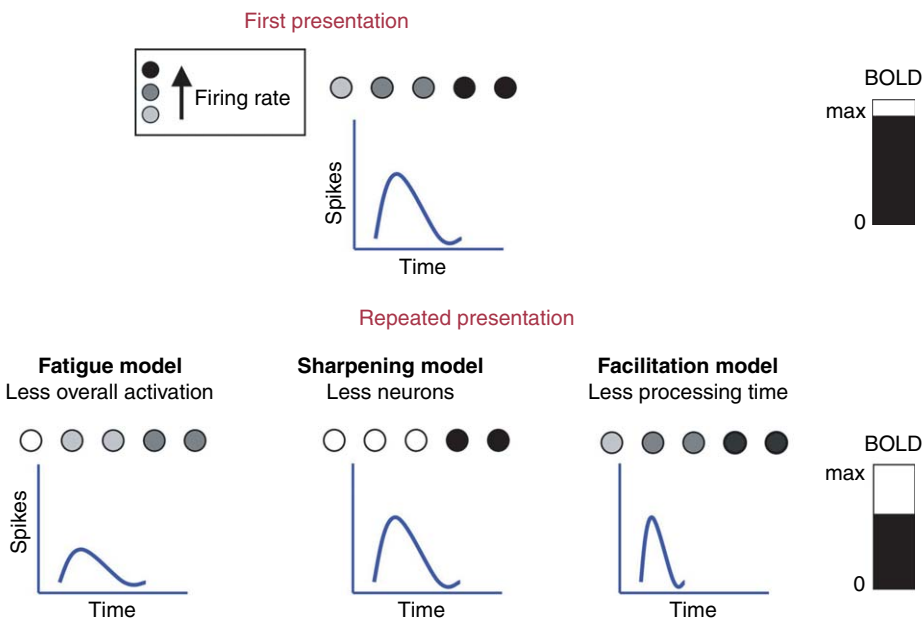
Experiments have provided important insights about the characteristics of priming, RS, RE, and their relation. However, the neural mechanisms underlying visual priming and RS are yet unknown.

Three models have been suggested for the neural mechanisms underlying repetition suppression that

may explain priming effects (Grill-Spector et al., 2006a) (Figure 8): (1) the Fatigue model, whereby the amplitude of firing of stimulus-responsive neurons decreases (Miller and Desimone, 1994; Grill-Spector and Malach, 2001), (2) the Sharpening model, whereby fewer neurons respond (Li et al., 1993; Desimone, 1996; Wiggs and Martin, 1998), and (3) the Facilitation model, whereby the latency (James and Gauthier, 2006) and/or duration of neural activity is shortened (Sobotka and Ringo, 1996; Henson and Rugg, 2003). An important consideration to keep in mind is how each of these models may account for visual priming.

#### 3.12.4.1 Fatigue Model

According to this model, all neurons initially responsive to a stimulus show a proportionally equivalent reduction in their response to repeated presentations of the same stimulus. As a consequence the mean population firing rate declines, but there are no changes in the pattern of relative responses across



**Figure 8** Models for repetition suppression. The top panel indicates neural responses in a putative brain region to the initial presentation of a stimulus. The bottom panels indicate responses in this region to repeated stimuli as posited by each of the three models. *Left:* Neural responses. Circles indicate the peak spiking rate of neurons in this region (darker circles indicate higher spiking rates). Blue time courses illustrate the spiking rate as a function of time for the most responsive neurons (indicated by black circles). *Right:* BOLD response in this region of cortex. Since the BOLD signal integrates neuronal activity over time, all of these models predict reduced BOLD responses for repeated stimuli, but due to different reasons: Fatigue: lower firing rates across the entire time window; Sharpening: fewer neurons respond, but those which remain active show similar spiking as for the first presentation; Facilitation: shorter duration of neural processing, but the peak firing is similar to the initial presentation. Adapted from Grill-Spector K, Henson R, and Martin A (2006) Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* 10: 14–23.



neurons or in the temporal window in which neurons are responding. One mechanism for fatigue may be firing-rate adaptation, in which the reduction in a neuron's firing rate is proportional to its initial response (Li et al., 1993; Avidan et al., 2002) (similar to a gain mechanism; Carandini and Ferster, 1997). However, this mechanism does not explain the specificity of RS, that is, why the neuron's response is reduced to some stimuli, yet resumes high firing rates to other stimuli. An alternative mechanism is reduced synaptic efficacy of specific synapses from connected neurons (synaptic depression). In this manner, only specific patterns of presynaptic input to the neuron (which are stimulus dependent) reduce its firing rate. This type of mechanism has been implicated in early visual cortex and usually occurs with prolonged repetitive stimulation.

One prediction from this model is that the amount of RS will be greater in neurons that respond optimally to a stimulus than in other neurons. As a result, the sensitivity of the system to stimuli that are different from the repeating stimulus is increased, thereby providing a mechanism for 'novelty detection.' Reducing the firing rate may also help prevent saturation of the neural response function by increasing its dynamic range. Another advantage hypothesized for such a mechanism is that it reduces redundancies in the neural code, which increases the efficiency of information encoding (Muller et al., 1999).

However, it is not immediately clear how reduced firing rates can account for increased speed and accuracy of processing repeated stimuli (in addition to increased sensitivity to novel stimuli), as arises in priming. One explanation is provided in a computational model by Gotts (2002), in which a reduction in the mean and variance of firing rates allows for greater synchrony of neural responses. Since greater synchrony of presynaptic input is believed to be more effective in triggering a postsynaptic response (Fries et al., 2001), this would imply more rapid transmission of information throughout the network, resulting in faster responses (priming). A key prediction of this model is that synchrony can increase while stimulus-specific firing rates decrease. While there is evidence in support of this possibility (Stopfer and Laurent, 1999), others have argued for the opposite effect (Chawla et al., 1999). An increase in synchrony may also be difficult to reconcile with observations of reduced oscillatory power following stimulus repetition (Gruber and Muller, 2005), though it is possible that decreased amplitude of

local field potentials outweighs the increased synchrony of those potentials.

#### 3.12.4.2 Sharpening Model

Desimone (1996) and Wiggs and Martin (1998) have suggested that repetition results in a sparser representation of stimuli across cortex. According to this model, some, but not all, neurons that initially responded to a stimulus will show RS to subsequent presentation of that stimulus. Thus, repetition-related changes are viewed primarily as a learning process, in which representations (e.g., tuning curves) are 'sharpened,' and as a consequence, the distributed representation becomes sparser, resulting in fewer responsive neurons in total (Figure 8). An important difference between the Sharpening and Fatigue models is that for Sharpening, many of the neurons that are optimally tuned to the repeating stimulus show little or no response reduction, rather than exhibit the greatest response reduction, as in the Fatigue model.

Sparser representations clearly have adaptive value in terms of a reduced metabolic cost. Also, because the representation becomes sharper (tuning curves become narrower), the neurons become more sensitive to change. Sparser representations may also allow for more efficient or faster processing, though this depends on the manner in which their information is read out by downstream neurons. Because the Sharpening model suggests a changed and improved representation for repeated stimuli, this model has been widely used to explain priming (Wiggs and Martin, 1998; Henson and Rugg, 2003; Zago et al., 2005). However, a recent study suggests that RS in object-selective cortex may reflect response learning and implies that object representations do not necessarily reorganize as a consequence of repetition (Dobbins et al., 2004).

The mechanism underlying the formation of sparser representations is unknown but could reflect inhibition from lateral connections between neurons within a population. For example, Norman and O'Reilly (2003) used a competitive Hebbian learning rule to simulate the sharpening of representations with repetition (within medial temporal cortex). Initially, many neurons respond weakly to a distributed input pattern representing the stimulus. Through competitive interactions, the neurons with the strongest initial response get 'stronger' and inhibit the 'weaker' neurons. Thus, some neurons show increased firing rates following repetition, whereas

others show decreased firing rates. By assuming that the number of 'strong' units is less than the number of 'weak' units, the population response decreases with repetition because there are more neurons showing reduced activity than showing increased activity. If information only from those neurons with high firing rates is 'read out' by downstream neurons, their increased firing rate following repetition (despite the global decrease) could explain the faster processing of repeated stimuli.

### 3.12.4.3 Facilitation Model

At its simplest, this model predicts that repetition causes faster processing of stimuli, that is, shorter latencies or shorter durations of neural firing, and thereby may explain faster response times observed during priming. One example is the 'accumulation' model of James and Gauthier (2006), in which stimulus information is accrued faster following repetition. Given that the hemodynamic signal measured by fMRI integrates over several seconds of neural activity, a shorter duration of activity results in a decreased amplitude of the fMRI signal. A shorter duration of neural activity is also consistent with earlier peaking of the fMRI response (Henson et al., 2002a) and might explain why decreases in firing rate can appear to arise after the initial visual response (Ringo, 1996): The neurons initially fire robustly to both first and repeated presentations, but this firing stops sooner for repeated presentations.

An extension of the Facilitation model assumes that the cause of this faster processing is synaptic potentiation between neurons following an initial stimulus presentation, and that this potentiation can occur at many levels in the processing stream. As a consequence, information flows through the stream more rapidly, and hence processing of a repeated stimulus occurs faster. In terms of attractor neural network models, synaptic potentiation might be viewed as deepening the basin of attraction, resulting in a shorter time for the network to settle on a stable pattern corresponding to identification of the stimulus. An example of such a dynamical network model is sketched by Friston (2005). The key idea behind this model is that the firing rate of the long-range excitatory (output) neurons in a population codes 'prediction error' (Rao and Ballard, 1999), which is the difference between bottom-up input ('evidence') and top-down input ('prediction'). The dynamics of the network are such that prediction error decreases

over time after stimulus onset, and synaptic changes serve to accelerate this decrease when the stimulus is repeated (i.e., repetition improves prediction).

This emphasis on recurrent activity between many levels of the processing stream is consistent with the spatiotemporal pattern of repetition effects emerging from MEG/EEG data. Moreover, if inter-regional interactions require an initial volley of activity through the network (Sugase et al., 1999), this model could further explain the relatively late onset of long-lag repetition effects recorded with EEG/MEG. However, such a model would not explain why much earlier repetition effects have been observed in some neurons (e.g., 75–100 ms, which is thought to be too early for feedback; Xiang and Brown, 1998), and further, this model does not necessarily predict decreases in the peak firing rate of individual neurons.

Each of the above models would clearly benefit from further elaboration, including instantiation as detailed computational models. It is possible that different models may apply in different brain regions and under different experimental conditions (e.g., different paradigms/tasks). Nevertheless, specific neural mechanisms matter, because the interpretation and design of experiments depend on the nature of the underlying neural model. For example, models differ as to whether RS reflects quantitative or qualitative changes in representations. One important possibility is that there are multiple models that vary in their relevance across space, time, and task, which may parallel the multiplicity of potential neural/synaptic mechanisms. Finally, it is yet unknown whether the same or different mechanisms operate in different brain regions.

### 3.12.4.4 Distinguishing the Neural Models

There are three main directions in which these models can be distinguished: (1) examining the relationship between RS and stimulus selectivity, (2) examining the effect of repetition on the tuning of cortical responses along a stimulus dimension, and (3) examining the temporal window in which processing occurs for new and repeated stimuli.

#### 3.12.4.4.1 Examining the relationship between RS and stimulus selectivity

The models differ in their predictions on whether RS is strongest for the preferred stimulus or for nonpreferred stimuli. The Sharpening model predicts that neurons showing little or no RS to a repeated

stimulus are highly selective for that stimulus. In contrast, both the Fatigue and Facilitation models predict that RS is proportional to the initial response. Thus, neurons that respond optimally for a stimulus should show the largest suppression. These hypotheses can be tested with single-cell recording.

#### **3.12.4.4.2 Examining the effect of repetition on neural tuning**

Another way to distinguish the models would be to find a single dimension (e.g., motion, orientation) along which stimuli differ and examine the effect of repetition on the tuning curves of different neurons along that dimension. The models differ in their prediction of how repetition will change the shape of neuronal tuning. According to the Fatigue model, repetition reduces the response in proportion to the initial response, but the tuning width does not change. Most likely, the reduction will be maximal for tuning curves centered on the location of the repeating stimulus along the stimulus dimension, and lesser for tuning curves centered farther away. This is consistent with adaptation of V1 neurons to orientation (Dragoi et al., 2002), spatial frequency (Movshon and Lennie, 1979), and motion direction (Kohn and Movshon, 2004). In contrast, according to the Sharpening model, repetition sharpens tuning curves. This is consistent with studies of learning-related changes in IT cortex and V4 (Baker et al., 2002; Sigala and Logothetis, 2002; Rainer et al., 2004). Finally, the Facilitation model does not suggest any particular effect on tuning curves. Indeed, even a widening of the curves might be possible if repetition enlarged the attractor basin in an attractor network model.

#### **3.12.4.4.3 Examining the temporal window of processing for new and repeated stimuli**

The models may also be distinguished in the temporal domain. In particular, the Facilitation model suggests that the latency and/or duration of the response to repeated items will be shorter than to first presentations. The Fatigue and Sharpening models do not suggest a difference in the temporal processing window for repeated stimuli. The latency and duration of processing might be examined via single-cell recordings and/or EEG/MEG techniques.

### **3.12.5 Conclusions and Directions for Future Research**

Visual priming is one of the most studied cognitive processes, as it is a window to understanding the underlying representations and mechanisms of rapid implicit learning and memory in the human brain. Progress has been made using priming to infer the nature of representations in different cortical regions or as a marker for increased processing efficiency, without a complete understanding of its neural basis. Nevertheless, specific neural mechanisms matter, because interpretation of experimental data depends on the nature of the underlying neural mechanisms.

Clearly, many questions remain regarding the neural basis of visual priming. For example, how do the Fatigue and Sharpening models account for improved performance during priming? Do different mechanisms occur in different timescales (e.g., immediate priming vs. priming with many intervening stimuli)? Do fundamentally different mechanisms underlie RE and RS? How does the specificity of priming correlate with particular representations in different visual regions? Are there different mechanisms underlying subliminal and suprathreshold visual priming?

Notably, any empirical data relevant to the models presented here is likely to depend on other factors, such as the lag between repetitions. One of the central outstanding questions is whether different models apply at different timescales. One possibility is that the mechanisms related to the Fatigue model operate during immediate repetitions of a stimulus within a few hundred milliseconds and reflect transient stimulus-specific effects that onset rapidly, whereas the effects of repetition across many intervening stimuli may be more consistent with the Sharpening or Facilitation models and reflect long-term learning that leads to changes in the spatial pattern of stimulus-selective responses and/or dynamics of those responses. Also models differ as to whether priming is associated with quantitative or qualitative changes in cortical representations. One possibility is that there are multiple mechanisms that vary across space, time, and task. Finally, it is yet unknown whether the same or different mechanisms operate in different brain regions.

Progress will be aided by integrating data using a combination of behavioral and neuroimaging methods such as fMRI and EEG/MEG (provided important differences between these measurements

are kept in mind), linking between electrophysiology data in animals and neuroimaging data in humans, and improvements in the spatial resolution of fMRI (Beauchamp et al., 2004; Schwarzlose et al., 2005; Grill-Spector et al., 2006b). Future experiments will yield important empirical data that will validate (or refute) current theoretical predictions. Understanding the neural bases of priming will be critical for understanding whether priming reflects quantitative or qualitative changes in the brain and will allow a fundamental understanding of implicit learning and memory in the adult brain.

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