The account of priming given in Learning and Complex Behavior is consistent with work published since its last printing. See the following article for a review of recent behavioral, neuropsychological, and neurophysiological findings on the role and mechanisms of priming.

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The experienced learner’s behavior is the joint product of the present environment acting on an organism that has been changed by the effects of past environments. Priming procedures reveal the effects of both environments as they are mediated by the nervous system. (The posted article should not be considered the copy of record.)

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TUTORIAL REVIEW

Where perception meets memory: A review of repetition priming in visual search tasks

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What we have recently seen and attended to strongly influences how we subsequently allocate visual attention. A clear example is how repeated presentation of an object's features or location in visual search tasks facilitates subsequent detection or identification of that item, a phenomenon known as *priming*. Here, we review a large body of results from priming studies that suggest that a short-term *implicit* memory system guides our attention to recently viewed items. The nature of this memory system and the processing level at which visual priming occurs are still debated. Priming might be due to activity modulations of low-level areas coding simple stimulus characteristics or to higher level episodic memory representations of whole objects or visual scenes. Indeed, recent evidence indicates that only minor changes to the stimuli used in priming studies may alter the processing level at which priming occurs. We also review recent behavioral, neuropsychological, and neurophysiological evidence that indicates that the priming patterns are reflected in activity modulations at multiple sites along the visual pathways. We furthermore suggest that studies of priming in visual search may potentially shed important light on the nature of cortical visual representations. Our conclusion is that priming occurs at many different levels of the perceptual hierarchy, reflecting activity modulations ranging from lower to higher levels, depending on the stimulus, task, and context—in fact, the neural loci that are involved in the analysis of the stimuli for which priming effects are seen.

Imagine yourself at a party with someone that you have a crush on or are even in love with. You seem to be constantly aware of where that person is, and your gaze is repeatedly drawn toward the dashing red shirt or dress that he or she is wearing or to their shining black hair, in such fine contrast to their paler face, despite your best efforts to not look *too* eager. This person is an example of a stimulus that is the focus of your attention and matters very much to you. Recent research has unveiled how our attention and gaze seem to be automatically drawn toward those features that we have recently attended to and are important to us, such as the red dress or dark hair of our object of desire. Such *priming* appears to have a very strong effect on what grabs our attention. Recent research on priming in visual search tasks suggests that we possess a primitive memory system drawing our attention to features or objects that we have recently attended to and are important to our goals or to the task that we are performing. We seem to have little or no voluntary control over the workings of this memory system. We review a large body of neurophysiological and neuropsychological evidence with regard to such priming that suggests that activity changes in the neural mechanisms devoted to the analysis of the particular stimuli for which priming effects are seen are the source of the observed priming effects and that these activity modulations occur at a number of different levels of the visual hierarchy.

Basic Characteristics of Priming

Since the pioneering studies of Maljkovic and Nakayama (1994, 1996) and Treisman (1992), a large number of studies have addressed priming effects in visual search. This research has shown that our perception is heavily influenced by what we have seen in the past. As we search for a target of, say, a particular color, detection or discrimination of that target or features of that target (such as its shape, color, or location) becomes easier if we are familiar with it or if we have seen it or acted upon it before. This has been widely investigated by means of controlled lab experiments in which the effects of previously presented displays on performance in the present have been investigated. Such effects, called *perceptual*

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priming, indicate that we possess an implicit memory system that strongly influences how we subsequently allocate our visual attention.

Priming may be described as an altered activation state of particular representations or associations in memory. It can also be described as an experimental procedure by which a stimulus is used to sensitize the subject to a later presentation of the same or a similar stimulus. Priming is normally considered to be an example of implicit memory (Schacter & Buckner, 1998), since it can be dissociated from declarative memory (see below). Asking an observer to remember a color is thus not an example of color priming, whereas an observer's speeded responses to successive targets all having the same color is an example of such color priming. To give another example, if, during a quiz, someone knows the answer to a question, this simply represents the operation of memory; priming would be a triggering of thought processes and associations leading to the identification of the correct response, which the observer did not have available before this activation was triggered by the question.

A number of studies have shown how what has been termed *declarative*, or explicit, memory may be dissociated from *nondeclarative*, or implicit, memory. Warrington and Weiskrantz (1968) tested Korsakoff patients who had lost the ability to retain new memories, presenting them with fragmented pictures of stimuli. The patients became better and better at recognizing the fragmented pictures the more often they performed the task, despite having *no* recollection of performing the task previously (see also Brooks & Baddeley, 1976). Also, severely amnesic patients can exhibit priming in paired associate learning despite having no explicit memories of the learning process (Shimamura & Squire, 1984). In what appears to be the flipside to such findings, Gabrieli, Fleischman, Keane, Reminger, and Morrell (1995) studied a patient who had his right occipital cortex removed because of epilepsy. This patient did not have any problems with declarative memory, whereas he did not show any perceptual priming, since his identification of briefly presented stimuli *did not* improve with repetition. This pattern of results is the exact opposite of the effects observed by Warrington and Weiskrantz and by Shimamura and Squire, and together, these studies show how priming can be dissociated from conscious awareness.

This distinction between declarative and nondeclarative memory has often been focused on different neuroanatomical loci for the different type of memory effects, which is indeed supported by good evidence, but others have argued that, even though the two may be dissociated, this does not always reflect the operation of different neural systems (see, e.g., Berry, Shanks, & Henson, 2008). Turk-Browne, Yi, and Chun (2006) found that attending to a particular stimulus can lead to effects on both implicit and explicit memory, and they found, furthermore, that implicit and explicit memory performance for particular stimuli were positively correlated. Importantly, such a correlation was also seen with regard to the neural patterns involved in the processing, as measured with functional imaging. Berry et al. argued, in part in light of the Turk-Browne et al. finding, that some dissociations between implicit and explicit memory function can be explained without the need to assume that they reflect the operation of "independent memory systems or independent sources of memory" (Berry et al., 2008, p. 371).

The present review of priming in visual search is largely focused on the behavioral manifestations of implicit memory at work in the priming of visual search, which are different from the mechanisms serving explicit memory, as found in studies of neurological populations (Eichenbaum, 1997; Poldrack & Gabrieli, 2001; Poldrack & Packard, 2003; Schacter & Badgaiyan, 2001). In fact, the evidence that we will review suggests that the implicit memory subserving the priming of visual search reflects facilitation of processing through repetition of neural activity patterns associated with a preceding event.

What Are the Manifestations of Priming in Visual Search?

Perceptual priming, such as that seen in visual search tasks, is based on repetition of features such as color, orientation, shape, motion, size, and so on (Becker, 2008b; Campana, Pavan, & Casco, 2008; Fecteau, 2007; Goolsby & Suzuki, 2001; Kristjánsson, 2006b, 2009; Lamy, Carmel, Egeth, & Leber, 2006; Magnussen & Greenlee, 1999; Maljkovic & Nakayama, 1994; McBride, Leonards, & Gilchrist, 2009; Olivers & Meeter, 2006; Wolfe, Butcher, Lee, & Hyle, 2003; see Kristjánsson, 2006a, for a review) but also on repeated position (Campana & Casco, 2009; Campana, Cowey, Casco, Oudsen, & Walsh, 2007; Geng et al., 2006; Geyer, Müller, & Krummenacher, 2007; Kristjánsson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Maljkovic & Nakayama, 1996). More complex forms of priming have also been found in visual search tasks, such as relatively longer term priming for whole stimulus configurations (Chun & Jiang, 1998) and distractor set identity (Geyer, Müller, & Krummenacher, 2006; Kristjánsson & Driver, 2008; Kristjánsson, Wang, & Nakayama, 2002; Lamy, Antebi, Aviani, & Carmel, 2008; Saevarsson, Jóelsdóttir, Hjaltason, & Kristjánsson, 2008; Wang, Kristjánsson, & Nakayama, 2005). Although the original studies of Maljkovic and Nakayama (1994, 1996) were conducted on pop-out visual search, strong priming effects have also been found for more difficult search tasks, such as conjunctive visual search (Becker, 2008b; Becker & Horstmann, 2009; Geyer et al., 2006; Hillstrom, 2000; Kristjánsson & Driver, 2008; Kristjánsson et al., 2002; Wang et al., 2005). Priming has even been seen for the size of the attentional focus (Fuggetta, Lanfranchi, & Campana, 2009), where search is speeded when the size of the search array is kept constant between trials, as compared with when the size changes. Priming has also been found to lead to speeded saccades to predesignated targets in visual search tasks (Becker, 2008b; McPeek, Maljkovic, & Nakayama, 1999; see also Edelman, Kristjánsson, & Nakayama, 2007, for some related findings). The fact that priming is seen for such different forms of stimulus characteristics presents a challenge to any theory of priming in which a single *priming site* is assumed to account for priming in visual search and indicates, furthermore,

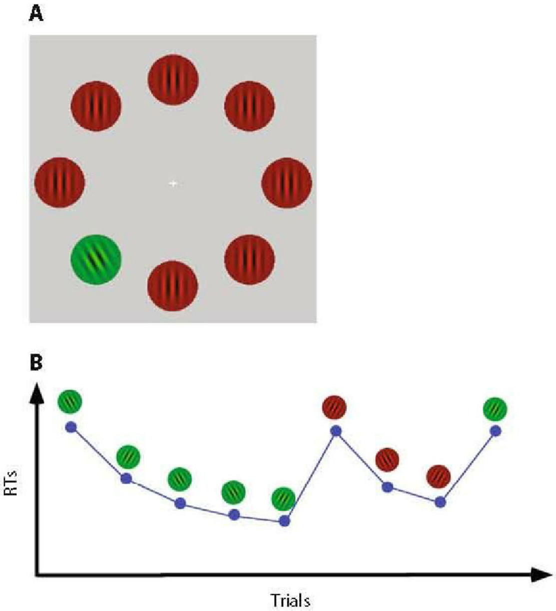

Figure 1. An example of priming in visual search. (A) A visual search task in which the oddly colored Gabor patch is to be found and the task is to indicate whether it is tilted toward the left or right from vertical (paradigm based on Kristjánsson, 2006b). (B) Illustration of how response times (RTs) tend to develop as the target color is repeated across consecutive trials (shown from left to right) or when the target color changes (simulated data).

that priming may reflect modulations of neural activity at a number of different processing levels in the nervous system (see the discussion on neurophysiological mechanisms below).

In a typical visual search experiment, repeating the same target feature or spatial position across trials results in better performance than if the target or feature changes from trial to trial. For example, if the target color on the present trial is red, as it was on the previous trial, search is facilitated, whereas if the target color is green, search is slowed (Figure 1). Similar results have been observed for a number of different visual features, such as the spatial frequency, orientation, or shape of the target. Importantly, though, priming usually occurs more easily for features that are not directly associated with the motor response; it works better in so-called compound tasks (Duncan, 1985), where the response dimension differs from the dimension defining the target. To maximize color priming, observers should, thus, be requested to respond to some other feature of the target, such as its orientation, spatial frequency, or spatial position (e.g., Kristjánsson, 2006b; Olivers & Meeter, 2006). Olivers and Meeter (2006; see also Meeter & Olivers, 2006) also argued that the crucial factor with regard to whether priming effects are seen at all is whether there is inherent ambiguity about the task in terms of the identity of the target.

Two seminal studies by Maljkovic and Nakayama (1994, 1996; see also Treisman, 1992) are crucial to understanding the characteristics of priming in pop-out visual search and have had a large impact on the literature. Their observers searched for a diamond of odd color, relative to two distractor diamonds, and judged whether the target diamond had a notch on the right or on the left (a task originally introduced by Bravo & Nakayama, 1992). The response feature was thus independent of the color of the target (a compound task), so that the effects of repetition of target color could be dissociated from any effects from repetition of the response. Maljkovic and Nakayama (1994, 1996) found that search was speeded by tens of milliseconds (a surprisingly large proportion of the overall response times) if the target color was repeated from one trial to the next. Their results showed that even when search is easy and effortless, as in pop-out search, perceptual priming can strongly influence the speed of the search. This result was quite surprising in light of foregoing theorizing about visual attention, since *pop-out* was assumed in many theories to be entirely stimulus driven (e.g., Treisman & Gelade, 1980; Yantis & Jonides, 1984) and should not be affected by such repetition biases, since the target should simply pop out very clearly from its background.

Importantly, Maljkovic and Nakayama (1994, 1996) showed that priming between trials for features such as color, spatial frequency, and spatial position was due to an implicit short-term memory mechanism, and not to stimulus expectancy (see also Becker, 2008c; Sigurdardottir, Kristjánsson, & Driver, 2008). Indeed, responses were significantly slower even when the feature change was completely predictable and occurred on each successive trial than when the feature was also completely predictable but remained constant across trials. This result shows how conscious knowledge of an upcoming target has little or no effect on observed priming patterns.

Note, however, that Fecteau (2007) found that precuing the singleton target on a consequent trial led to modulations of the priming pattern. Wolfe, Horowitz, Kenner, Hyle, and Vasan (2004) showed that even word cues (even if to a lesser extent than picture cues) produced a facilitatory effect that mimicked repetition priming, but this result does not necessarily show that the priming needs *conscious* application of the knowledge provided with the cue. On a similar note, Leonard and Egeth (2008) suggested that prior target knowledge and intertrial priming affect search through different mechanisms—namely, top-down and bottom-up modulation, respectively (see also Müller, Krummenacher, & Heller, 2004, and Müller, Reimann, & Krummenacher, 2003, for some converging findings on this issue).

Maljkovic and Nakayama (1994, 1996) also found that the priming effect from repetition of a particular target stimulus was not confined to the subsequent trial but continued to influence performance on at least seven subsequent trials. Finally, they also found that the effects of priming are cumulative; the greater the number of repetitions of the same feature, the better performance became, with the response times (RTs) following an approximately negative exponential function (Figure 1B). Perceptual priming has, then, been found not only in easy pop-out search, but also in more difficult conjunction search tasks (Becker, 2008b; Hillstrom, 2000; Kristjánsson et al., 2002; Wang et al., 2005), as well as for distractor characteristics or the search context in each case (Geyer et al., 2006; Kristjánsson & Driver, 2008; Lamy, Antebi, et al., 2008; Saevarsson et al., 2008; Wang et al., 2005).

What these findings show is how the presentation of certain stimulus characteristics improves detection or discrimination of subsequent stimuli sharing the same characteristics. Stimulus selection is thus based not only on the current stimulus in its current context, but also on implicit influences from previous trials. What we have recently attended to strongly influences how we subsequently allocate our attention. Note that priming may have important implications for theories of visual attention. Prominent theoretical accounts of attention, such as those of Treisman and Sato (1990) or Wolfe (1994), postulate that attention is drawn to those items in the visual field that are salient (bottom-up guidance) and those that share features with the object of our attention or, as in a visual search task, the target item (top-down guidance). A simple model of this can be envisioned in a visual search task in which an item is found relatively quickly and easily if it stands out against the background (such as a black item among white) or if its feature matches that of the object one is supposed to find; one may relatively easily find a red vertical bar among green vertical and red horizontal items as long as one knows that this is the target that one needs to look for. Kristjánsson et al. (2002) found, however, that priming could account for most, if not all, of the effects of knowledge of the target identity on such a visual search task, which have theoretically been thought to reflect the operation of visual attention (see also Wolfe et al., 2003, for some related findings and a discussion). Although we do not wish to discount the importance of top-down guidance for visual performance, this example shows how powerful priming can be. Note that Wolfe et al. (2003) preferred to refer to this as *implicit* top-down guidance, since there is undeniably some knowledge of the preceding stimulus, even though this knowledge is implicit. Leonard and Egeth (2008) have subsequently argued that top-down knowledge plays an important role in guiding attention, independently of priming, whereas Theeuwes, Reimann, and Mortier (2006) argued that "expectancy-based, top-down knowledge cannot guide the search for a featural singleton" (p. 466). The jury is thus clearly still out on these questions.

Theoretical Accounts of Priming

Attentional, perceptual, or response-related priming? One can think of several ways in which repetition of target characteristics influences performance in a particular visual search. Priming might reflect facilitated perceptual processing of previously attended objects or features, or even processing of whole displays that share properties with previously attended ones. Another possibility is that priming influences the way attention shifts within the visual field, with attention being more likely to shift to, or shift faster to, those features sharing characteristics with previously presented items of interest. In fact, recent results in Sigurdardottir et al. (2008) and Becker (2008c) have indicated that priming affects attention shifts rather than perceptual performance directly. Sigurdardottir et al. found, for example, that although priming resulted in improved detection of a target, priming did not facilitate acuity judgments for that particular target, indicating that repetition has by far the largest effect on attentional guidance, a result in agreement with the findings of Becker (2008c), who observed that priming effects clearly modulated the accuracy and time course of the *first* saccade in the search sequence within a trial during active visual search (where eye movements are allowed). These initial saccades were faster and more accurate when the same target was repeated than when it changed between trials, suggesting that priming affects search at an early stage of attentional guidance, before selection of the first item in the display.

On the other hand, it is also theoretically possible that priming simply affects response selection. Observers could, in theory, speed up their responding as targets or features are repeated, but this has been strongly argued against by Sigurdardottir et al. (2008), who studied priming using signal detection theory measures. They found that repetition of a target feature increased sensitivity (measured with d') to a target in a briefly presented (followed by a mask) visual search display, while having only a minuscule effect on decision criteria (measured with c; see also Becker, 2008c, where a similar point has been argued).

It should be noted that this finding of Sigurdardottir et al. (2008) seemingly contradicts the results of Huang and Pashler (2005), who found only a small priming effect of orientation repetition during feature search of brief displays (there were, however, nonsignificant trends toward such an effect across four experiments!). The task was a relatively coarse localization judgment where observers had to decide whether a target in a search array was on the left or the right of the midline of the array. This task is, of course, quite different from the acuity judgment task *on* the color singleton target that was required in Sigurdardottir et al., which might partly explain the different findings.

Attentional guidance, episodic memory, or dimensional weighting? Some differences in opinion have arisen in the literature as to what part of perceptual processing priming exerts its influence upon. Maljkovic and Nakayama (1994, 1996) argued that the priming patterns they observed reflected altered activation states in response to the recently attended and behaviorally important feature—in their case, the odd color on the preceding trial—so that the primed feature is more likely to grab attention than otherwise. In other words, in their conception, the key effects were upon attentional allocation to single features.

A challenge to this conception comes from the results of Huang, Holcombe, and Pashler (2004; see also Hillstrom, 2000). They proposed an explanation for priming in visual search that was quite dissimilar from such feature facilitation accounts, on the basis of results from a study in which observers searched for a bar tilted either 45° or −45° from vertical that was of an odd size relative to randomly oriented distractors. The target was either a large target bar among small distractor bars or vice versa. They observed that repetition of both an irrelevant feature (brightness) and the target-defining feature (size) speeded search, whereas repetition of the irrelevant feature, but not of the target-defining feature, slowed the search. Since the feature repetition effect did not seem to be independent of the repetition of other features on the target, Huang et al. argued that priming does not affect processing of single features but occurs at a later stage in the perceptual process. They argued that the speeded performance following repetition of target characteristics reflects an episodic memory representation of the preceding trial and that the behavioral pattern following repetition thus reflects the priming of assembled objects rather than of features. Although these results do not, as such, rule out feature-based priming, Huang et al. argued from "Occam's razor" logic, that the episodic memory account was the most parsimonious explanation of the findings. The between-trial facilitation was assumed to reflect facilitated processing of the whole display through an episodic memory representation of the previous trial. In contrast to the conclusion in Huang et al., a recent study by Kristjánsson (2009) showed very little or no interaction between priming from the repetition of color and motion. Repetition of these two features led to largely independent priming effects, speaking against the episodic retrieval account. Also, Becker (2008b) has shown, with both saccade latencies and manual RTs, that switch costs are due not to delayed shifts of attention to the target (as predicted by the episodic memory account), but to more frequent selections of nontarget items, because of a "wrong" prioritization of nontarget features. The episodic retrieval account also received some support from a follow-up study by Huang and Pashler (2005), in which few effects of repetition were observed when brief, masked displays were used, which, on the surface, would seem to indicate that the priming exerts its effects at a relatively late stage of processing. Huang and Pashler argued that "the measurement of accuracy in processing of very brief displays . . . reveals the character of perceptual-level effects, whereas RT measurements (as in Maljkovic and Nakayama's work) are likely to include contamination from postperceptual effects as well" (p. 153). Note, however, how this conclusion contradicts the findings of Sigurdardottir et al. (2008) mentioned above, who found sensitivity increases with feature repetition for brief displays.

Kristjánsson, Ingvarsdóttir, and Teitsdóttir (2008) conducted experiments that indicated that the level of priming can be modulated by relatively subtle changes to the stimuli used to test the priming effects. They found that whether the priming effects were object based or feature based depended heavily on the type of stimulus tested. They contrasted search for stimuli that had been shown in previous studies to be processed differently, as either whole objects or separate parts (Wolfe, Friedman-Hill, & Bilsky, 1994; Xu, 2002a), in visual search tasks, as well as in visual short-term memory tasks (Vogel, Woodman, & Luck, 2001; Xu, 2002b). In short, Kristjánsson et al. (2008) found that stimuli that the visual system seems more inclined to treat as objects tended to result in object-based priming patterns, whereas stimuli less conducive to object-based processing resulted in feature-based priming patterns (see Figure 2). In this light, it seems quite likely that both the object-based and the feature-based views of priming carry some truth, but the stimuli and the circumstances of the task in each case dictate what sort of priming occurs. This could indicate that priming reflects modulations of neural activity at multiple levels of visual processing, a view that is also supported by the results of Campana et al. (2008).

Campana et al. (2008) found that when a priming stimulus and the probe for priming were of the same type (either first- or second-order motion stimuli; see, e.g., Cavanagh & Mather, 1989; Chubb & Sperling, 1988; Kristjánsson, 2001), motion priming was modulated by a target's spatial position, indicating retinotopic processing at lower levels of the visual hierarchy, whereas when the prime and the probe were of different types (alternatively first- and second-order motion stimuli), priming was position insensitive, suggesting modulations of activity at higher levels of visual processing following repetition. McBride et al. (2009) also found evidence indicating that "flexible tar-

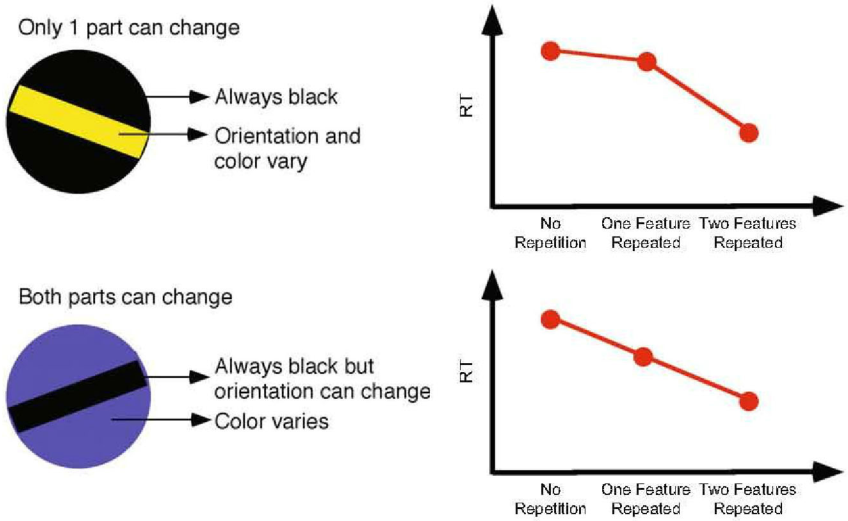

Figure 2. Object-based versus feature-based priming patterns dependent on stimulus type. In the upper panel, only one part of the object can change (the orientation or color of the central bar). In the lower panel, either the background of the circle can change color or the central black bar can change orientation. Stimuli like the one in the upper panel tend to lead to object-based priming patterns, where priming is seen only if both features are repeated, whereas repetition of only one feature is sufficient to cause priming for the stimuli in the lower panel (as can be seen by the response times [RTs] as a function of repetition of number of features, shown on the right; based on Kristjánsson, Ingvarsdóttir, & Teitsdóttir, 2008).

get representations" underlie the priming effects, since repeating the same feature (orientation) had different consequences on RTs, depending on the task context. This issue is discussed in more detail below, in the section on the neural mechanisms involved in priming.

In fact, as we will see in the next section, neurophysiological and neuropsychological findings on priming suggest that it may be severely problematic to think of behavioral priming effects as reflecting the operation of a single perceptual process exerting its effects at a single level of the perceptual hierarchy. The results from such studies seem, on the other hand, to be most consistent with conceptions of priming in visual search where priming is assumed to reflect activity modulations at several different levels of the perceptual process.

A single mechanism for priming is thus not well supported by the findings from neurophysiology, neuropsychology, or neurology or by the behavioral results reviewed above. In fact, the results seem to suggest that priming reflects activity modulations at the very neural loci that are connected with processing of the aspects of the display that the behavioral priming effects are observed for. This view is consistent with the ideas put forward by Tulving and Schacter (1990; see also Magnussen & Greenlee, 1999), that priming of perceptual attributes depends on a more general perceptual memory system (called the *perceptual representation system* [PRS]) that is largely nonconscious and consists in a series of subsystems, each dedicated to a particular aspect or feature of the primed object or visual scene. These subsystems are placed at different levels of processing, from higher level structural description systems that compute information about the global form and structure of visual objects (Tulving & Schacter, 1990), to lower level dimension-dedicated systems computing sensory information (Magnussen & Greenlee, 1999).

Ivry and Cohen (1990) found that variation in irrelevant feature dimensions interferes with visual search, demonstrating that it is impossible to fully inhibit bottom-up information. This point was embodied in the Guided Search 2.0 theory of attention (Wolfe, 1994), which states that attention is guided to the task-relevant feature dimensions. This basic idea is encapsulated in an influential account of repetition-priming effects in visual search that stems from the *dimensional-weighting* account of visual search, proposed originally by Müller, Heller, and Ziegler (1995; for related results, see also Cohen & Magen, 1999; Found & Müller, 1996; Müller et al., 2003). The core idea of the dimensional-weighting account is that a change in the feature dimension that defines the target results in a cost in terms of visual search performance. As an example, search times are slower if the target changes from being the oddly *colored* item in the scene to being the oddly *shaped* item than when the target changes but the target-defining dimension remains unchanged, such as when the target changes from being the red item in the display to being the green item from one trial to the next. Müller et al. (1995) found that such dimensional uncertainty adds a constant factor (as a function of set size) to the RTs in a visual search task (see Cohen & Magen, 1999, however, for some exceptions to this that may apply under certain conditions). Found and Müller investigated repetition priming in visual search in light of the dimensional-weighting account. The targets in their study were defined along two feature dimensions (orientation and color) within a block of trials. They directly compared the effects of changes between dimensions (e.g., from red to leftward tilted) and within-feature changes (from left-tilted to right-tilted or from red to green, etc.). Their conclusion was that the largest between-trial repetition effects could be attributed to dimension changes, rather than to feature changes. This is indeed quite consistent with the dimensional-weighting account (Found & Müller, 1996; Müller et al., 1995; Müller et al., 2004), where attention is assumed to be weighted toward the target-defining feature dimension in a particular visual search task. The largest repetition priming effects should thus be observed for those features that receive the largest weighting—in this case, the ones that define the target within each block of trials. In another twist to this, Lamy, Bar-Anan, and Egeth (2008) found that search for a particular singleton target was speeded up if the preceding target stimulus was a singleton on the same dimension as the current target, rather than a nonsingleton.

Olivers and Meeter's (2008) study investigated this dimensional-weighting account of between-trial priming effects and observed that the effects from changes in a feature value (such as from one color to another or from one orientation to another) were quite comparable in spite of whether they occurred within a feature block (where the target-defining dimension remained constant) or a dimension change block (where the target-defining dimension varied unpredictably, from trial to trial within a block, between being orientation or color). In other words, it did not seem to make a large difference to the pattern of results what the particular dimensional context within a trial block was on a given trial (see also Kristjánsson, Bjarnason, Hjaltason, & Stefánsdóttir, 2009, for converging results for priming of search for motion and color). Note, however, that there was nevertheless a cost of dimensional change in terms of RTs, but this could not at all be described as the *major* determining factor for the effects of between-trial changes. This is in basic agreement with the recent results of Becker (2008a), who argued that feature priming speeds up the search for the target, whereas target dimension changes affect processes that follow the selection of the target.

To sum up, it seems that the evidence indicates that priming can operate at multiple levels of perceptual processing, on feature representations or whole objects, and is also weighted by the dimensional context in each case. What is perhaps less clear are the relative contributions of each to the priming, and it is, of course, quite possible (and consistent with some available evidence) that this will vary depending on the nature of the particular task and the context in each case.

Neurophysiological and Neuropsychological Studies of Priming in Visual Search

A number of neurophysiological and neuropsychological studies have followed up on the original behavioral findings for priming in visual search. What these studies have revealed is that priming in visual search is related to activity modulations as a function of repetition at various sites in the nervous system, again arguing against accounts that focus on any single level in the perceptual hierarchy as a critical locus for priming. These studies have indicated, instead, that priming reflects the fact that the neural activity patterns that occur when a particular stimulus is presented are facilitated with repetition. Neural processing of a particular color, for example, is thus facilitated when it is repeated.

Bichot and Schall (1999, 2002) found that single neurons in the frontal eye fields of macaque monkeys performing visual search tasks that required them to make saccades to oddly colored targets discriminated target properties more quickly and more accurately when the same features distinguished the target as on the last trial and showed an enhanced response to distractors that had previously been the target (see, e.g., Fecteau & Munoz, 2003, for a review). Interestingly, such response patterns accord well with results from neuroimaging studies reviewed later in this section.

The results from studies using transcranial magnetic stimulation (TMS) and studies of lesioned neural systems have suggested that a number of different cortical areas mediate priming effects, depending on the primed feature or stimulus characteristic in each case. For instance, by applying TMS during the interval between two search trials (thus affecting not the encoding of stimulus features, but only their storage), Campana et al. (2007; Campana, Cowey, & Walsh, 2006) found a double dissociation of between-trial priming effects: Whereas TMS over area V5/MT abolished priming of motion direction (see Figure 3), it had no effect on priming of spatial position. On the other hand, TMS over the left frontal eye field strongly reduced priming of spatial position, but not of motion direction (Figure 3; see also O'Shea, Muggleton, Cowey, & Walsh, 2007, for some converging results). Moreover, whereas area V5/MT in humans has been shown not to be involved in color priming (Campana, Cowey, & Walsh, 2002), the ablation of areas V4 and TEO in monkeys has been found to eliminate color priming despite normal color discrimination (Walsh, Le Mare, Blaimire, & Cowey, 2000). These studies suggest that the areas involved in the processing of a given perceptual attribute (feature or spatial position) also show activity modulations that may account for priming for that attribute. This is consistent with the PRS hypothesis put forward by Tulving and Schacter (1990) and Magnussen and Greenlee (1999), in which perceptual memory is assumed to reflect lingering activity in early visual areas. In agreement with all this, V5/MT is known to be strongly involved in the processing of motion stimuli (Tootell et al., 1995), areas V4 and TEO have a primary role in color processing (Bartels & Zeki, 2000; Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998), and the frontal eye fields are involved in visuospatial atten-

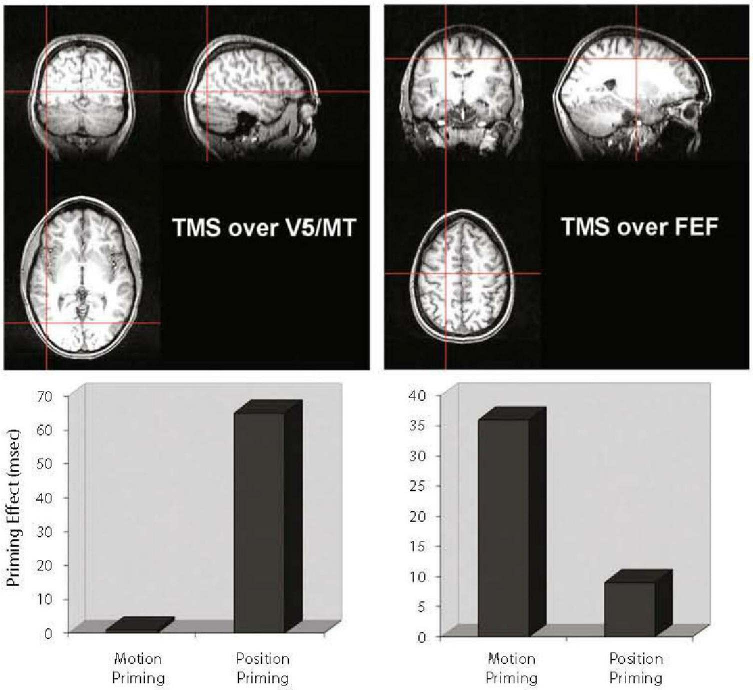

Figure 3. **Double dissociation of the effects of transcranial magnetic stimulation (TMS) over two different cortical sites on visual priming. TMS over area V5/MT (left panels) abolishes priming of motion direction, but not priming of spatial position (left column). On the other hand, TMS over the left frontal eye field (FEF) (right panels) strongly reduces priming of spatial position but has virtually no effect on the priming of motion direction. Data are replotted from Campana, Cowey, Casco, Oudsen, and Walsh (2007) and Campana, Cowey, and Walsh (2006).**

tion, even in the absence of saccadic programming (Muggleton, Juan, Cowey, & Walsh, 2003).

Priming in visual search tasks has also been investigated in humans with fMRI. Reduced activity of brain areas selectively coding for the stimulus properties (also called *repetition suppression*) has been widely found for many different types of stimuli as they are repeatedly presented (e.g., Buckner et al., 1998; Horner & Henson, 2008; Kourtzi & Kanwisher, 2001; Schacter, Wig, & Stevens, 2007). Despite the fact that the relationship between behavioral priming and repetition suppression is still under debate and is not completely understood (Grill-Spector, Henson, & Martin, 2006; Henson & Rugg, 2003; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008) and that various factors seem able to influence repetition suppression (Henson, Shallice, & Dolan, 2000), repetition suppression has been widely demonstrated to be the main neural signature of repetition priming (Geng et al., 2006; Kristjánsson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007; Vuilleumier, Schwartz, Duhoux, Dolan, & Driver, 2005; Wig, Grafton, Demos, & Kelley, 2005; Yoshida, Tsubomi, Osaka, & Osaka, 2003). Kristjánsson et al. (2007) speculated that this reflected the fact that less effort is required to find and/or process a repeated search item or feature when it is repeated. Summerfield et al. argued that repetition suppression reflects perceptual expectancies (which are fulfilled), since they found that repetition suppression was attenuated when repetitions were improbable. Note that there is no reason to believe that these two accounts are mutually exclusive.

In order to investigate the neural substrates responsible for repetition priming in visual search, Kristjánsson et al. (2007) recorded variations in the BOLD signal while observers performed a pop-out search task similar to the one used by Maljkovic and Nakayama (1994; see also Bravo & Nakayama, 1992). One of their findings was that activity modulations (i.e., repetition suppression) were correlated with priming in frontal and parietal areas that have been shown to be involved in the operation of visual attention (Corbetta & Shulman, 2002; Ruff, Kristjánsson, & Driver, 2007), as shown in Figure 4. This clearly suggests that priming reflects activity modulations in the attentional

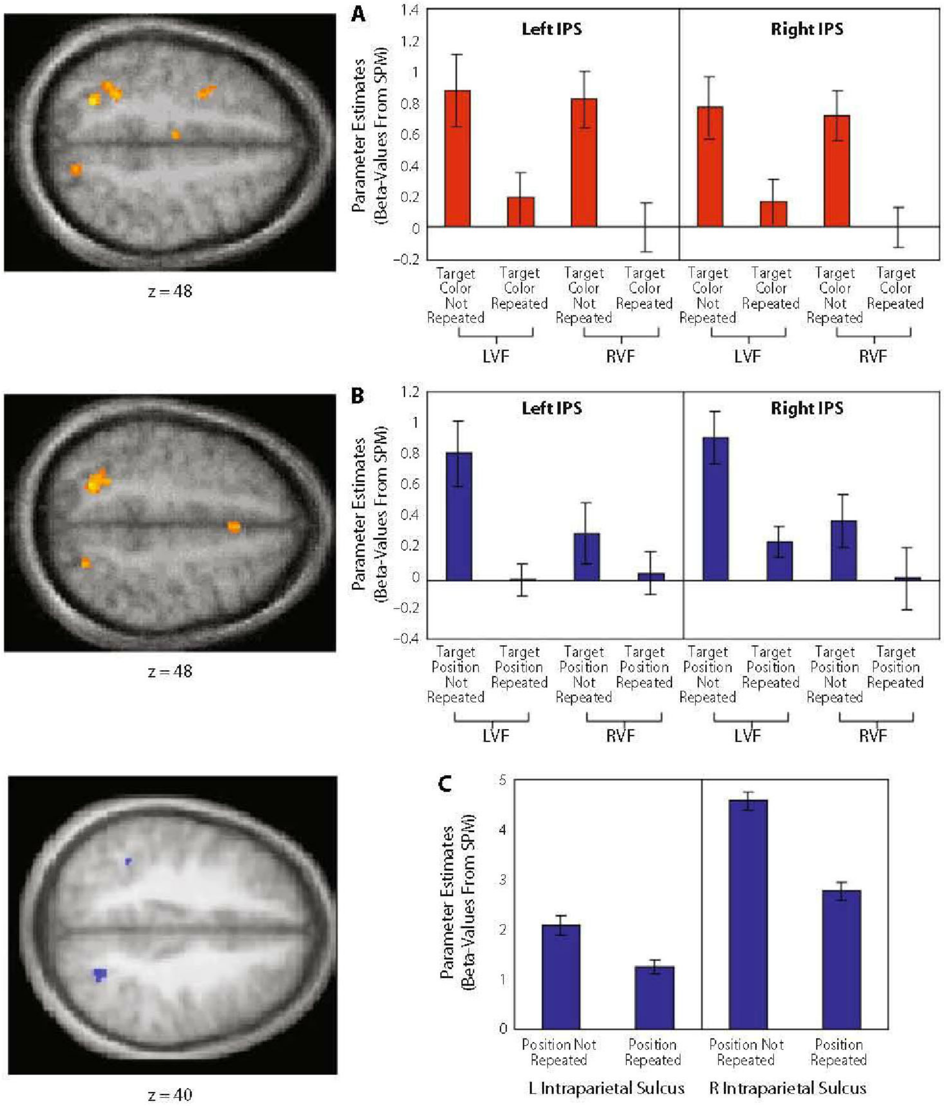

Figure 4. Repetition suppression of BOLD signal as a function of repetition of the color of the target in pop-out visual search (A) and the position of the target (B and C). The left panel shows regions in the intraparietal sulcus (IPS) showing significant repetition suppression, and on the right are shown parameter estimates as a function of whether the color or position is repeated or changed. Panels A and B are replotted from Kristjánsson, Vuilleumier, Schwartz, Macaluso, and Driver (2007), and panel C is replotted from Geng et al. (2006).

system in the brain, which is consistent with proposals that priming affects attention deployments toward the target, as was argued originally by Maljkovic and Nakayama (1994) and by Kristjánsson (2006a) and Kristjánsson and Nakayama (2003) since. There were also strong activity changes in the early visual cortex correlated with priming (Figure 4). Finally, strong modulations of activity were found in the anterior fusiform cortex but, interestingly, were seen only when the whole-display characteristics remained constant or, in other words, when the same target was presented in the same position. This indicates that this region is connected to priming when the whole *Gestalt* of the display is repeated, when the same types of stimuli are found in the exact location as on the preceding trial. Also found were differences in activity dependent on whether color or position (see also Geng et al., 2006) was repeated. There were thus activity modulations correlated with color priming in "color" areas such as V4, which is quite consistent with the TMS and lesion studies reviewed above.

Especially important in this respect is that Geng et al. (2006; for some related results, see also Goolsby & Suzuki, 2001; Vuilleumier et al., 2005) found that the size of priming effects for repeated positions was modulated by the need for attentional selection on the previous trial, a result that strongly strengthens the argument that the priming effects under discussion here lead to faster and more efficient attention shifts toward repeated targets, features, or locations. All in all, these fMRI results argue strongly against any proposals that the behavioral priming patterns reflect activity modulations of a single unitary mechanism of perceptual processing and, at the same time, strongly support the hypothesis that priming involves facilitation of attention shifts toward the primed element.

Pollmann, Weidner, Müller, Maertens, and von Cramon (2006; Pollmann, Weidner, Müller, & von Cramon, 2000) have studied the neural patterns associated with dimensional changes, in light of the dimensional-weighting account of priming in visual search (Found & Müller, 1996; see the discussion above). They observed that the frontopolar cortex, along with the anterior cingulate, is strongly activated during dimension switches within a block of search trials, as well as some parts of the well-known attentional networks (see, e.g., Corbetta & Shulman, 2002; Ruff et al., 2007), activity that may reflect the dimensional repetition effects observed by Found and Müller and by Olivers and Meeter (2008).

In contrast to the neurophysiological findings discussed above, findings from studies of patients suffering from hemispatial neglect are not quite as unequivocal. Marangolo, Di Pace, Rafal, and Scabini (1998) found an overall preserved priming of both color and position in parietal-damaged patients. However, neither color nor position priming was present when probes appeared on the contralesional field. From this finding, the authors concluded that the parietal cortex is involved not just in position priming, but also in color priming, pointing at this area as a possible *priming site*. It should be noted, however, that the absence of color priming when the probes (the primed, not the priming stimuli) were presented in the contralesional field could be due to a more general difficulty of processing probe items in that hemifield, rather than a specific impairment of color priming. The results of Kristjánsson et al. (2005) support this view. They studied priming in visual search in neglect patients, again using a task similar to the one in Maljkovic and Nakayama (1994, 1996), and found that during a brief (200-msec) presentation of the search array, the patients sometimes did not notice a target presented in their neglected hemifield (they missed the priming stimulus). Priming from the target's color (detecting the probe stimulus) was nevertheless unaffected, whereas priming from repeated position occurred only when the patients were consciously aware of the target. On the other hand, Kristjánsson et al. (2005) found relatively normal position priming for the patients with search displays with unlimited search time. These findings accord well with the aforementioned TMS (Campana et al., 2007; Campana et al., 2006) and fMRI (Geng et al., 2006; Kristjánsson et al., 2007) studies and suggest that priming of color and spatial position are, at least partly, mediated by distinct brain areas, perhaps corresponding to the well-known distinction between the dorsal and ventral processing streams of visual information (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Finke et al. (2009) also investigated priming in visual search for neglect patients and found that for a subgroup of neglect patients, inhibitory effects of distractor nonrepetition in a pop-out task like the one used by Maljkovic and Nakayama (1994) were mostly absent. From these results, they speculated that the neural mechanisms involved in target and distractor repetition priming do not overlap completely.

Overall, the neurophysiological and neuropsychological results strongly suggest that the priming patterns simply reflect activity modulations of brain regions responsible for the analysis of these primed stimuli and their selection through the operation of visual attention. What this may entail is that priming effects in visual search reflect altered representational states for a given feature, feature combinations, or objects that then lead to facilitated processing of that property. This leads to the conclusion that there is no need to assume a particular neural mechanism whose operation is revealed in these effects, a view that is consistent with accounts of priming in other paradigms (see, e.g., Schacter et al., 2007). Rather, the very neural mechanisms that are involved in the analysis of the stimuli for which priming is seen are the mechanisms that show activity modulations correlated with behavioral priming.

Taking Stock

The experimental results discussed in this review show that it would, most likely, be a mistake to focus on any one single mechanism or brain module to account for priming effects in visual search. The results cannot be accounted for by assuming that priming in vision is always based on features or, alternatively, always on episodic representations of what has gone before that involve features assembled into objects, although the relative contribution of each to the pattern is still open to debate. Facilitated processing of features is consistent with the majority of results for priming, although a minority of studies do indeed suggest that priming effects can, in some cases, be based on objects rather than features (Campana et al., 2008; Hillstrom, 2000; Huang et al., 2004; Kristjánsson et al., 2008). Note, however, that Ásgeirsson and Kristjánsson (2008) have recently presented evidence that the episodic retrieval account as presented by Huang et al. probably explains priming on only a very limited subset of visual search tasks, and Becker's (2008b) findings that switch costs are due to more frequent selections of nontarget items (implying that priming modulates the attentional priorities of the target and nontarget features), and not to delayed shifts of attention to the target on switch trials, cast serious doubt upon the explanatory power of the episodic retrieval view. Finally, repetition effects can also be dimensional rather than featural, as is shown in the results of Found and Müller (1996), in addition to the results of Olivers and Meeter (2008), although the latter results show that dimensional changes cannot account for large portions of feature repetition effects (see also Becker, 2008a; Kristjánsson et al., 2009).

The most parsimonious account of between-trial priming in visual search could be one in which the implicit memory producing visual priming is assumed to operate locally on feature or object representations, or even both, depending on the task circumstances. According to this view, priming is assumed to reflect activity modulations in multiple sites along the visual pathways, subserving multiple types of representations, from the simplest ones involving separate features, such as color, motion, spatial frequency, or position, in lower level functionally specialized visual areas, to higher level areas holding compound representations involving objects or parts of objects. These activity modulations involve activity changes at the very sites that are involved in the analysis of these aspects of the display. This view is supported by evidence from single-cell neurophysiology studies (Bichot & Schall, 1999, 2002), lesion studies (Walsh et al., 2000), TMS studies (Campana et al., 2007; Campana et al., 2002, 2006; O'Shea et al., 2007), fMRI studies (Geng et al., 2006; Kristjánsson et al., 2007), behavioral studies (Campana et al., 2008; Kristjánsson et al., 2008), and findings from neuropsychology (Finke et al., 2009; Kristjánsson et al., 2005; Saevarsson et al., 2008), all of which indicate that multiple levels of the stream of perceptual processing can show activity modulations correlated with priming, depending on the task or the particular feature involved.

Moreover, stimulus specificity effects (smaller changes in activity the more the probe stimulus is changed with respect to the prime stimulus) of repetition suppression during behavioral priming have been found to be most pronounced in early visual regions (coding simple stimulus features), as compared with higher level structures, coding more complex aspects of the visual environment, such as whole objects or whole visual scenes (Schacter et al., 2007). This adds further support to the idea that priming can be based on multiple representations, from more specific ones occurring in low-level visual areas to more general, feature-invariant representations occurring at higher levels of the visual hierarchy. The specific level of representation triggering the priming effect might then, in the end, depend on the specific stimulus, task, and context in each particular case. Consistent with this, Campana et al. (2008) and Kristjánsson et al. (2008) found that relatively small changes in the stimulus or task demands can shift the level of representation at which priming occurs (such as changing feature-based priming into object-based priming). From the evidence presented above, we can speculate that feature priming is based mainly on the activity of low-level visual areas functionally specialized for the processing of that specific feature, whereas object-based priming reflects activity changes at higher levels of the hierarchy. Position priming is based mainly on the activity of areas specialized in spatial cognition in parietal areas and frontal eye fields, whereas the frontoparietal attentional network plays a crucial role in the development of priming effects and in the attention-grabbing effect of the primed element. This is quite consistent with recent views of priming more generally. Schacter et al. argued that dispersed networks across the brain underlie priming—for example, object priming. Schacter et al. claimed 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" (p. 171), which is a view quite consistent with what the findings on priming of visual search reviewed here seem to indicate.

The research reviewed here has allowed us to make progress toward a better understanding of priming effects in visual search that seem even to affect basic levels of processing, as well as higher processing levels. It also allows us a better understanding of what circumstances lead to which types of priming. But it may, more broadly, have the potential to yield important insights into visual function at the behavioral and neural levels. Some critical unanswered questions remain, however. For one, we do not have a clear understanding of the interactive dynamics between the various brain areas involved in determining the priming effects. For example, one might ask what the nature of the functional dynamics between the parietal lobe and lower level visual areas is in terms of priming. A related question is, What are the specific factors that determine at which level of processing these effects occur? One possibility is that the parietal lobe simply focuses attention on a given feature or object and, then, priming occurs locally at the level determined by the attended feature or object in each case, whereas another possibility is that the parietal lobe plays a more central role in priming. We believe that the answers to these and other related questions will best be answered through the application of a multidisciplinary experimental approach, similar to the one used here, integrating evidence from behavioral, neurophysiological (e.g., fMRI, TMS, and single-cell recordings), and neuropsychological studies, either on their own or in conjunction with one another.

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