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Neuroimaging studies of priming

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Abstract

This article reviews functional neuroimaging studies of priming, a behavioural change associated with the repeated processing of a stimulus. Using the haemodynamic techniques of functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), priming-related effects have been observed in numerous regions of the human brain, with the specific regions depending on the type of stimulus and the manner in which it is processed. The most common finding is a decreased haemodynamic response for primed versus unprimed stimuli, though priming-related response increases have been observed. Attempts have been made to relate these effects to a form of implicit or "unconscious" memory. The priming-related decrease has also been used as a tool to map the brain regions associated with different stages of stimulus-processing, a method claimed to offer superior spatial resolution. This decrease has a potential analogue in the stimulus repetition effects measured with single-cell recording in the non-human primate. The paradigms reviewed include word-stem completion, masked priming, repetition priming of visual objects and semantic priming. An attempt is made to relate the findings within a "component process" framework, and the relationship between behavioural, haemodynamic and neurophysiological data is discussed. Interpretation of the findings is not always clear-cut, however, given potential confounding factors such as explicit memory, and several recommendations are made for future neuroimaging studies of priming.

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Abbreviations: PET, positron emission tomography; fMRI, functional magnetic resonance imaging; BOLD, blood oxygenation level dependent; BA, Brodmann area; SOA, stimulus onset asynchrony; LOC, lateral occipital complex; EEG, electroencephalography; MEG, magnetoencephalography; ERP, event-related potential

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1. Introduction

Priming refers to a change in the speed, bias or accuracy of the processing of a stimulus, following prior experience with the same, or a related, stimulus. Priming is normally measured in "indirect" memory tasks (Richardson-Klavehn and Bjork, 1988), in which no reference is made to the prior experience. Examples include faster reaction times to make a decision about the stimulus, a bias to produce that stimulus when generating responses, or the more accurate identification of a degraded version of the stimulus (e.g. when presented briefly, or in the presence of noise). Priming is one of the most basic expressions of human memory, influencing how we perceive and interpret the world. Indeed, it is likely to be a fundamental form of memory in higher nervous systems.

This review is concerned with PET and fMRI studies of priming in humans. Both imaging techniques rely on changes in the haemodynamic supply to brain regions following changes in local neural/synaptic activity, with a typical spatial resolution of 1–10 mm (for further explanation of the techniques, see Attwell and Iadecola, 2002; Heeger and Ress, 2002; Raichle, 1998). The review is organised around three main reasons for the recent interest in functional imaging studies of priming: as an example of implicit memory (Section 3), as a tool for mapping the stages in stimulus processing (Section 4) and as a domain within which to relate haemodynamic data in the human and single-cell recording data in the non-human primate (Section 5). As such, it is a selective review, focusing on specific paradigms (such as word-stem completion and visual object priming) that have received the most attention in these respects. The three reasons are expanded below.

1.1. Priming as a memory phenomenon

Foremost is the interest in priming as an example of "implicit memory". Implicit memory represents an effect of prior experience on behaviour, in the absence of conscious awareness of the past (Graf et al., 1984). This term arose from studies of amnesiac patients with damage to medial temporal lobe structures, who can show priming even though they appear unaware of any prior exposure to the primed stimulus (i.e. lack "explicit" memory). Warrington and Weiskrantz (1974), for example, showed that amnesiacs were impaired relative to controls on the "direct" memory tests of recall and recognition for previously studied words. On indirect tests however, in which the participants simply tried to identify degraded versions of words, amnesiacs showed an advantage for studied words that was equivalent to that in controls. In another study, Graf et al. (1984) presented word "stems" (the initial three letters of words) at test, and varied the task instructions. When instructed to use the stems to recall studied words ("word-stem cued-recall"), amnesiacs were impaired relative to controls. When instructed to complete the stems with the first word that came to mind however ("word-stem completion", an indirect task), amnesiacs were as likely to complete the stems with previously studied words as were controls, again demonstrating intact priming. Neuroimaging studies of this paradigm are described in Section 3.1.

Findings like these led to the proposal that priming reflects the operation of "non-declarative" memory systems supported by regions outside the medial temporal lobe, as distinct from the "declarative" memory system that is impaired following medial temporal damage (Squire and Cohen, 1984). This proposal has been bolstered by reports of a few patients with more posterior cortical lesions, who show intact performance on direct memory tests but impaired performance on certain indirect tests (Gabrieli et al., 1995; Keane et al., 1995). Priming is usually distinguished from other types of implicit memory that are intact in amnesia, such as skill-learning (Milner et al., 1968), because it can occur after a single stimulus presentation, rather than requiring repeated trials (Hauptmann and Karni, 2002), and because it is normally specific to a particular stimulus or process, unlike a generalised skill (see Gabrieli, 1998; Schacter and Tulving, 1994, for reviews).

The association of priming with implicit memory is further supported by data from healthy individuals, such as functional dissociations between direct and indirect tests as a function of study task (Jacoby and Dallas, 1981) or retention interval (Tulving et al., 1982), and reports of intact priming when the prime is subliminal (Forster and Davis,

1984) or shows no evidence of explicit memory (Stark and McClelland, 2000). Nonetheless, demonstrations that priming *can* occur in the absence of explicit memory do not imply that priming effects measured under normal conditions are a pure reflection of implicit memory. Even though an indirect memory test does not refer participants to previous encounters with stimuli, participants may voluntarily, or involuntarily, recollect such encounters. As a consequence, considerable effort has been devoted to developing methods that dissociate implicit and explicit contributions to memory tasks (e.g. Hayman and Tulving, 1989; Jacoby et al., 1993; Richardson-Klavehn and Gardiner, 1995; Schacter et al., 1989). However, few imaging studies to date have achieved this dissociation. Moreover, even if explicit memory is shown not to affect a concurrent behavioural response, the poor temporal resolution of haemodynamic imaging techniques means that imaging data may include explicit memory processes arising subsequent to that response. That is, on any given trial, both an initial implicit response to the stimulus and an immediately following explicit recognition of the stimulus as having been encountered earlier might occur, but not be separated in the haemodynamic response. Thus, it must be kept in mind that the brain regions discussed below that correlate with a manipulation of "priming" may reflect contributions of either implicit, or explicit, or both types of memory.

1.2. Priming as a tool

Priming can also be viewed in terms of the interface between perception and memory, in that priming effects may be a (beneficial) side-effect of the normal operation of perceptual systems. Indeed, behavioural priming has been used for many years to investigate the different stages in the processing of visual objects or the processing of linguistic stimuli. The same logic has been adopted by neuroimaging studies in order to map out the brain regions associated with those stages. Imaging studies of visual object processing, for example, have tested whether the effect of repeating an object on the response of a brain region generalises across various changes in the visual depiction of that object. If a region shows an equivalent repetition effect for objects depicted from either the same or different viewpoint, then the processes subserved by that region are inferred to operate over view-independent (or object-based) representations. This second reason for an interest in neuroimaging studies of priming—the use of priming as a tool—is exemplified in Section 4.

Moreover, it has been claimed that this approach is particularly useful in neuroimaging because it offers greater spatial resolution (Grill-Spector et al., 1999; Naccache and Dehaene, 2001a). The basic reason for this claim is that the signal from a single voxel (the smallest sampling unit in an image) represents the average response over a large number of neurons. It is possible that this mean signal will not differ between two classes of stimuli, even though one-half of the neurons are responsive to the first class, and the other half are responsive to the second class. If the neurons adapt to repeated presentation of their preferred stimulus though, the signal will differ when one or other class of stimuli is repeated. Thus, repetition effects may reveal a finer level of functional–anatomical specialisation than conventional subtractions of different stimulus classes (see Section 4.2 for further explanation).

1.3. Priming as a model domain

Since priming can be measured simply by comparing repeated versus initial presentations of a stimulus, the haemodynamic correlates of (some simple forms of) priming might be usefully compared with the effects of repeating a stimulus on action potentials recorded directly from neurons in the non-human primate. Indeed, the decrease in the haemodynamic response normally associated with priming (see below) is consistent with the well-established decrease in neural firing observed in inferotemporal (IT) neurons of the Macaque following repetition of visual stimuli (so-called "response suppression", Desimone, 1996). According to some views, this decrease reflects development of sparse perceptual representations, a consequence of gradual long-term learning of the environment (Wiggs and Martin, 1998). Alternatively, the decreases may reflect temporary modifications of existing representations that allow more rapid processing of stimuli that have been perceived recently. Such dynamic tuning of the perceptual apparatus has clear adaptive implications.

Though neurophysiological studies of non-human primates do not typically consider behavioural indices of priming, the similarity of the paradigms used and the potentially fundamental nature of priming suggest important parallels with functional imaging studies in humans. Thus, a final reason for the interest in neuroimaging of priming is to stimulate and test models that relate data across these different levels of neuroscience. Further discussion of these issues is given in Section 5.

2. Definitions and overview

Priming is indexed by differences between a primed stimulus (or "target"), which has been preceded by a "prime", and an unprimed stimulus, which has not. In some cases, the unprimed stimulus is the initial presentation of the same stimulus, perhaps in a separate "study" phase; in other cases, the unprimed stimulus is a different stimulus that was not presented previously (Fig. 1). In the special case of "repetition priming", the primed stimulus is (for all intents) identical to the prime. In other cases, "priming" pertains to a common referent, associate or component of two different stimuli. In semantic priming, for example, the primed stimulus is semantically related to the prime, whereas in word-stem priming, the primed stimulus is the first few

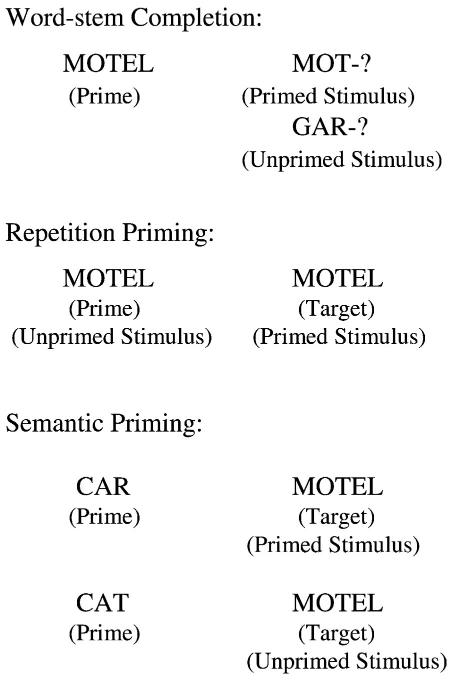

Fig. 1. Schematic of three example verbal priming paradigms.

letters of the prime. In some cases, the same task is performed on the primed stimulus as was performed on the prime. In other cases, the task may differ, potentially causing different responses to, and processing of, the same stimulus.

2.1. *Psychological generalisations: the component process view*

A broad distinction has been made between perceptual and conceptual priming (Roediger and McDermott, 1993). The main differences are that perceptual, but not conceptual, priming is affected by differences in the physical features of the prime and primed stimulus, whereas conceptual, but not perceptual, priming is affected by differences in the degree of semantic processing of the stimuli. Tasks requiring perceptual identification of degraded stimuli are likely to reflect mainly perceptual priming, whereas tasks requiring semantic decisions are likely to reflect mainly conceptual priming. The neural basis of this distinction is supported by dissociations in, for example, Alzheimer's patients, who show intact perceptual priming but impaired conceptual priming, presumably because the early sensory areas believed important for perceptual priming are less affected by the disease than frontotemporal regions believed important for conceptual priming (Gabrieli et al., 1994).

Other tasks, however, like the word-stem completion task, are more difficult to fit into this dichotomy. Priming in this task is affected by variations in some physical properties (Church and Schacter, 1994), yet residual priming can still occur across modalities, even when voluntary explicit retrieval can be excluded (Richardson-Klavehn and Gardiner, 1996). These data suggest separate modality-dependent and modality-independent components. Furthermore, word-stem completion can be unaffected by the degree of semantic processing of primes (e.g. semantic versus phonological), yet be reduced following very superficial (e.g. graphemic) processing of primes (Richardson-Klavehn and Gardiner, 1998), consistent with a contribution from a component at the lexical level (Weldon, 1991). Other dimensions along which indirect tasks differ may also produce behavioural dissociations, such as the distinction between competitive and non-competitive access to semantic information for example (Vaidya et al., 1997).

An alternative perspective is the "component process" view of priming (Tenpenny and Shoben, 1992; Witherspoon and Moscovitch, 1989), according to which there can be several processes involved in a given task that may be facilitated by prior processing. (A "process" in the current context is assumed to be a mapping or transformation between two representations, at least one of which is stimulus-specific.) A behavioural measure like reaction time is likely to reflect the summation of the times taken to perform each process. Indeed, the amount of priming will depend on the degree of overlap between the processes performed on the prime and those performed on the primed stimulus (Postle and Corkin, 1999). This component process perspective is further illustrated in the next section.

2.2. *Functional imaging generalisations: repetition suppression*

As mentioned above, the most common finding in functional imaging studies is a reduced response for primed versus unprimed stimuli (see Schacter and Buckner, 1998, for a review; though see also Section 4.5). For historical reasons, this haemodynamic reduction will be called "repetition suppression" (even though the stimuli themselves may not be repeated), in analogy with the neural phenomenon of "response suppression" (Section 5). It is important to remember that repetition suppression is a descriptive term that may, or may not, in fact, reflect priming, as strictly construed. For example, it may reflect a confounding difference between "primed" and "unprimed" stimuli, such as explicit memory. A few generalisations can be made about repetition suppression.

Firstly, regions showing repetition suppression are normally restricted to those that are responsive to the type of stimuli used. In other words, the regions are normally activated by unprimed (and primed) stimuli versus a low-level baseline (such as visual fixation). This is illustrated in Fig. 2A, which shows that the regions exhibiting repetition suppression when people repeatedly complete visual word-stems are a subset of the regions activated when word-stem completion is contrasted against fixation (adapted from Buckner et al., 2000). A simple interpretation of this generalisation is that reduced haemodynamic response reflects faster or "more efficient" processing of

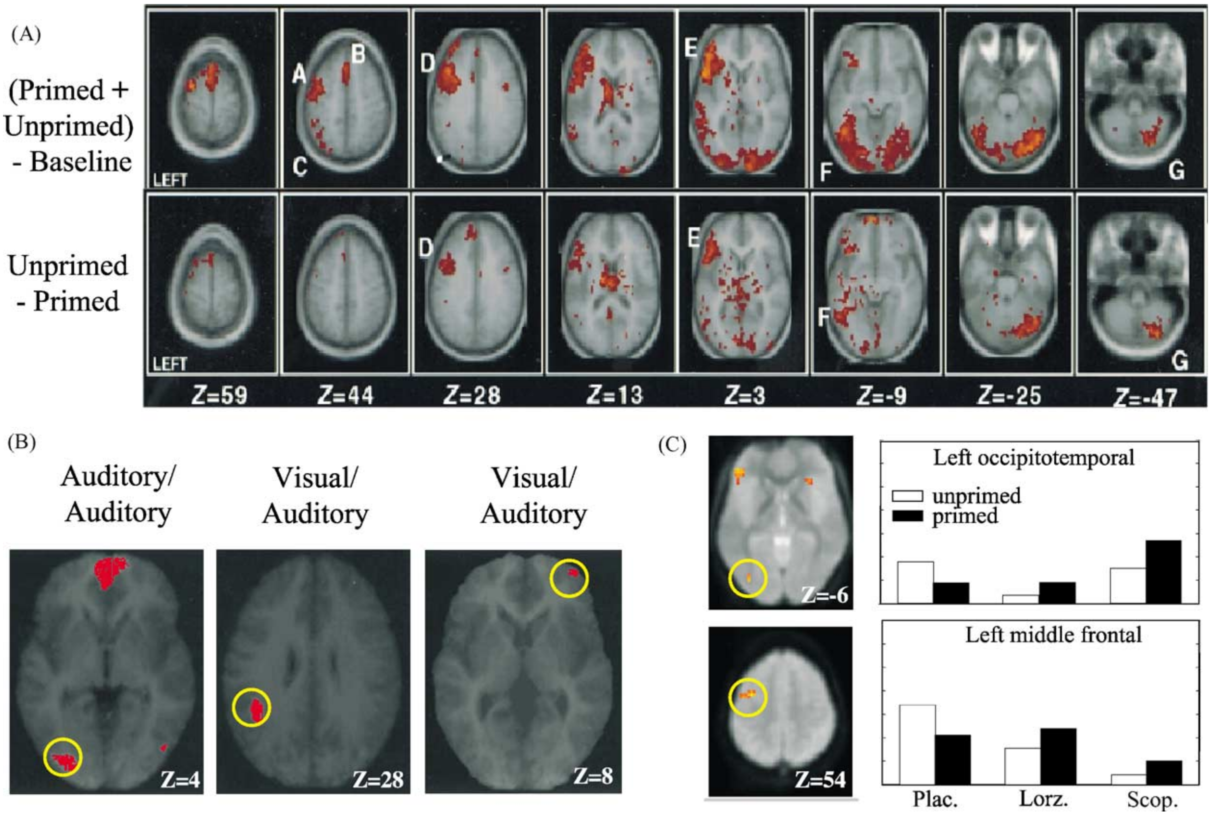

Fig. 2. (A) Transverse sections (Talairach *z*-co-ordinate below) through regions showing significant response increases for visual word-stem completion vs. fixation (upper row) and unprimed vs. primed word-stems (lower row) (adapted with permission of Oxford University Press from Buckner et al., 2000). (B) Regions showing differences between unprimed and primed stems under within-modality (auditory/auditory) and across-modality (visual/auditory) conditions. Circled regions from left to right: left occipitotemporal (more active for unprimed stems), left superior temporal (more active for unprimed stems) and right anterior frontal (more active for primed stems) regions (adapted with permission of MIT Press from Badgaiyan et al., 1999). (C) Left occipitotemporal and dorsal frontal regions (circled) showing repetition suppression from Thiel et al. (2001), together with magnitude of event-related responses (arbitrary scale) for unprimed and primed word-stems vs. fixation in placebo (Plac), lorazepam (Lorz) and scopolamine (Scop) groups.

the primed stimulus, owing to performance of the same processes in the recent past (on the prime)—the so-called “hot-tubes” or “greased tracks” metaphors.

A second generalisation is that repetition suppression can be seen in multiple brain regions, suggesting that several stages in the processing pathway between stimulus and response can be facilitated (all, a subset, or none of which may contribute to the specific behavioural measure of priming). The word-stem completion task, for example, is likely to include orthographic, phonological, lexical and semantic access, each of which might be facilitated to some extent by prior exposure to the prime. This is evident in the multiple brain regions showing repetition suppression during word-stem completion in Fig. 2A. In neural terms, the processing of primes may produce synaptic changes at several stages in the pathway between stimulus and response, which can produce facilitation when parts of that pathway are re-used for the primed stimulus. In other words, as with the component process view introduced above, priming is likely to depend on the degree of intersection of such processing pathways, which is determined by the relationship between the prime and primed stimulus, and the tasks performed on each. This perspective also highlights the potential confusion of attributing priming to a single memory system.

A third generalisation is that repetition suppression is not seen in all regions associated with processing stimuli in a particular task. For example, repetition suppression is not normally seen in early visual regions or late motor regions in visual-motor paradigms. Visual pole activations can be seen for the contrast of primed and unprimed word-stems versus fixation in Fig. 2A, but not for the contrast of primed and unprimed stems. This suggests that not all processes occurring between stimulus and response are facilitated by repetition. The computational properties of a process that determine whether it is significantly facilitated by repetition comprise an important, though as yet unresolved, question (it may reflect, for example, the number of possibilities in a one-to-many mapping). Moreover, though priming may arise at multiple loci in the brain (see above), there may nonetheless be “key” processing stages that are shared by a number of common priming paradigms, and hence contribute to generalisations across those paradigms.

The question thus faced by component process views of priming, and pursued by numerous behavioural studies, is to isolate these key processes. Two main ways to address this question are to manipulate the stimuli or to manipulate the task. The use of each strategy in the imaging literature is illustrated throughout the following sections.

3. Priming as a memory phenomenon

This section reviews imaging studies that focus on priming as an example of implicit memory. The approaches include stimulus manipulations in word-stem completion, task manipulations during semantic decisions about words, comparisons across direct–indirect tasks and masking of the prime.

3.1. Word-stem completion

The word-stem completion paradigm was mentioned in Section 1.1, and has been used extensively with amnesiac patients. It is sometimes viewed as an example of perceptual priming, though is likely to involve several component processes. The task is normally divided into separate study and test phases, with the study phase serving to prime a set of words. Priming is indexed by the probability of completing a word-stem with a word from the study phase, relative to the baseline probability of completing the stem with that word when it had not been studied (the latter often determined by counter-balancing stimuli across participants). One reason for the popularity of the task is that the stimulus can be held constant, while only the instructions are varied, to produce, for example, either a direct task—"complete the stem with a word from the study phase"—or an indirect task—"complete the stem with the first word that comes to mind". This constancy of the stimulus across direct and indirect tasks is a requirement of the "retrieval intentionality criterion" (Schacter et al., 1989), though an important distinction must be made between retrieval volition and conscious awareness (Richardson-Klavehn and Gardiner, 1995). Indeed, the interactions that have been found between test instructions and several experimental manipulations in this task—such as a switch of presentation modality between study and test, or the type of task performed at study—comprise some of the main evidence for functional dissociations between implicit and explicit memory.

One of the earliest imaging studies that included a priming component was the PET study of Squire et al. (1992). In two indirect conditions, the baseline and priming conditions, participants completed three-letter stems with the first word that came to mind (there were at least 10 possible completions per stem). The only difference between the conditions was that one-half of the word-stems in the priming condition could be completed with words that had been studied previously. Approximately, 70% of stems that corresponded to a studied word were completed with that word in the priming condition, compared with a baseline rate of 7% in the baseline condition. The largest difference in blood-flow between the two conditions was in right occipital cortex, which showed a decrease in the priming relative to baseline condition.

Squire et al. also included a direct, word-stem cued-recall task, the memory condition, in which participants used the stems to try to recall studied words. Of the one-half of stems that corresponded to a studied word, 76% were completed with that word. The largest difference between the memory and baseline conditions was in a medial temporal region, which showed greater activity in the memory condition (as might be expected from the typical lesion sites in amnesiac patients). Interestingly, this region also showed greater activity in the priming condition than baseline condition. Furthermore, the right occipital region that showed a decrease in the priming relative to baseline condition, also showed a decrease in the memory relative to baseline condition.

In subsequent PET experiments using similar tasks, Buckner et al. (1995) replicated the reduced occipital responses associated with priming, though found these decreases bilaterally and extending into posterior temporal cortex (see also Schacter et al., 1996; Backman et al., 1997). Like Squire et al. (1992), Buckner et al. attributed these occipitotemporal reductions to "more efficient" perceptual processing, which increased the probability of completing stems with studied words (and reduced the time taken to produce the completion). This more efficient processing might also aid word-stem cued-recall, possibly explaining the occipital decreases for the memory as well as priming conditions in the Squire et al. study (i.e. an implicit memory contribution to a direct memory test). Buckner et al. failed however to find any differences in medial temporal regions, and suggested that the medial temporal activation in the priming condition of the Squire et al. study may have reflected contamination of the indirect task by explicit memory.

The association of the occipitotemporal repetition suppression with visual perceptual priming was based on the location of the regions within the visual processing pathway (in extrastriate cortex, Brodmann area (BA 19) though the precise locations are difficult to localise with PET). In a further manipulation, Buckner et al. (1995) found equivalent levels of repetition suppression for word-stems in which the letter case was either the same or different from that used for the prime words. This suggests that the occipitotemporal responses do not reflect form-specific visual processes, but may operate at a more abstract level (e.g. orthographic or lexical). The relationship between these haemodynamic changes and priming remains unclear however, because the case-change manipulation did significantly reduce the proportion of stems completed with studied words (from ∼70 to ∼50%). This case-sensitivity may reflect a contribution from other components of the task.

However, Badgaiyan et al. (1999) found repetition suppression in bilateral occipitotemporal cortex (Fig. 2B, leftmost) even when both primes and stems were presented auditorily. Buckner et al. (2000) reported similar findings, though in a slightly more anterior inferotemporal region (close to region F in Fig. 2A), when auditory word-stems were completed repeatedly. These data are inconsistent with a purely visual interpretation of occipitotemporal priming effects. Furthermore, Badgaiyan et al. (1999) found no evidence of repetition suppression in these regions in a second experiment involving cross-modal priming from visual primes to auditory stems (despite the fact that, in this particular experiment, behavioural priming did not differ significantly within- and across-modality: within, 54%; between, 48%; baseline, 20%). Complementary findings were reported by Schacter et al. (1999) when comparing within- and across-modality priming with visual, rather than auditory stems. Again, a numerical, but not significant, advantage for within-modality priming was accompanied by an occipitotemporal decrease in the within-modality condition, but not in the across-modality condition (though direct statistical tests of the interaction between modality and priming were not reported in either study). These data suggest a more complex, modality-independent role of the occipitotemporal regions in word-stem completion priming (see Badgaiyan et al., 1999, for further discussion).

In their within-auditory modality conditions, Badgaiyan et al. (1999) also found repetition suppression in other brain regions, namely precuneus (BA 7), right angular gyrus (BA 39/40) and medial anterior frontal cortex (BA 10). Furthermore, in their visual/auditory across-modality condition, they found repetition suppression in a left angular gyrus region (BA 22/39; Fig. 2B, middle), which was also found in the auditory/visual across-modality condition of Schacter et al. (1999). The repetition suppression in this region was attributed to priming of lexical representations (Weldon, 1991), which can mediate across-modality priming. In the anterior frontal cortex however, particularly on the right (Fig. 2B, rightmost), Badgaiyan et al. and Schacter al. found an increased response for primed versus unprimed stimuli in their across-modality conditions. This activation was attributed to involuntary explicit memory, i.e. conscious memory, subsequent to completion of the stem, that the word was studied (Richardson-Klavehn and Gardiner, 1996). This is supported by imaging studies that have associated this region with episodic retrieval (Rugg et al., 1996; Tulving et al., 1994), though it is unclear why this activation was not also seen in the within-modality conditions (unless it reflected voluntary explicit retrieval specifically recruited for the across-modality condition, perhaps owing to the blocked nature of the modality-manipulation, Verfaellie et al., 2001).

A subsequent study by Badgaiyan et al. (2001) explored these issues further. In one experiment, within-modality auditory priming was compared when the primes and stems were spoken in either the same or different voice. Previous behavioural experiments have shown that changes in the fundamental frequency (but not intensity) reduce, but do not eliminate, auditory word-stem priming (Church and Schacter, 1994). Badgaiyan et al. found repetition suppression in a left occipitotemporal region, as well as precuneus, right angular gyrus and medial anterior frontal cortex (as previously, Badgaiyan et al., 1999), in both the same- and different-voice conditions. Repetition suppression in these regions thus appears independent of changes in specific auditory features (though this conclusion is tempered by the failure to find a voice-effect on behavioural priming in this particular experiment). Together with the lack of any effect of letter case in the visual word-stem completion task of Buckner et al. (1995), these data reinforce the conclusion that the occipitotemporal regions are sensitive to changes in modality, but not to changes in (low-level) within-modality features.

In a second experiment, Badgaiyan et al. (2001) compared auditory-to-visual across-modality priming when the prime words were studied under either full or divided attention. Dividing attention at study generally impairs performance on direct memory tests, but not word-stem completion (Debner and Jacoby, 1994). Consistent with this claim, Badgaiyan et al. found no effect of the attentional manipulation on the amount of behavioural priming. The only brain region showing an effect of the attentional manipulation was a medial frontal region (BA 9), which showed greater responses for stems corresponding to words studied under full than under divided attention. As with the right frontal region identified in their previous studies, the authors attributed this frontal increase to explicit memory. The lack of any difference in behavioural priming would then support their previous contention that such explicit retrieval is incidental to task performance. Badgaiyan et al. also found repetition suppression in a left superior temporal/angular gyrus region, which occurred under both full- and divided attention conditions (but again, no repetition effects in the occipitotemporal region in this cross-modal test). This reinforced their proposal that the left superior temporal/angular gyrus region subserves amodal, implicit priming of lexical access. Further study of these hypotheses would benefit from fully factorial investigations of within/between modality, auditory/visual modality and full/divided attention.

One problem with many of the word-stem completion studies described above is that they conform to a “blocked” design, in which haemodynamic activity is averaged over many trials (as is normally necessary for PET). This means that primed and unprimed trials are presented in different blocks, rather than being randomly intermixed (as is conventional in behavioural studies). One potential problem with such designs is that any difference between blocks of primed and blocks of unprimed trials may reflect differences in the participant’s strategies or “mental state”, particularly if the participants detect this blocking (see, for example, Verfaellie et al., 2001). In other words, some of the repetition suppression effects described above may reflect confounding variables that do not pertain to (stimulus-specific) priming per se. The advent of event-related techniques in fMRI eschews these problems, by allowing random intermixing of trial-types. An example of an event-related study of word-stem completion is that of Thiel et al. (2001). The primary aim of this study was to explore the pharmacological bases of priming, via administration of a cholinergic blocker (scopolamine), a GABAergic modulator (lorezapam), or a placebo, to different groups of participants. Cholinergic blockade is believed to impair explicit memory, but not implicit memory (Schifano and Curran, 1994), while GABAergic modulation is believed to impair implicit memory (Vidailhet et al., 1999).

In fact, both drugs reduced the amount of priming of visual word-stem completion. Moreover, a manipulation of the degree of semantic processing of the prime words in a subsequent experiment did not interact with the amount of priming or drug group, arguing against contamination of the task by voluntary explicit retrieval under these conditions. The imaging data from the placebo group showed repetition suppression in several of the regions identified by the blocked studies described above, as well as in inferior and posterior regions of left frontal cortex (as in Buckner et al., 2000; regions D and E in Fig. 2A). Repetition suppression in three of these regions, namely left occipitotemporal cortex and the two left frontal regions, was reduced or abolished in the scopolamine and lorezapam groups relative to the placebo groups (Fig. 2C). For further discussion of these findings and the pharmacological bases of priming, see Thiel et al. (2001). The relevance of this study to the present context is that event-related methods appear to support the basic findings of previous blocked studies; indeed, they may be more sensitive in detecting regions (such as left inferior frontal cortex) showing repetition effects.

In summary, several imaging experiments have been performed on variants of the word-stem completion task. There is some convergence on distinct processes operating in occipitotemporal, left angular gyrus, left inferior frontal and right anterior frontal cortices. The occipitotemporal process is not well understood, but appears common to visual and auditory modalities, though only when the modality is the same for primes and stems, and independent of the precise within-modality features (at least visual letter case or auditory voice). The left angular gyrus process may relate to an implicit, amodal lexical process, given that it occurs across modalities and appears independent of attention. The left inferior frontal regions may reflect phonological processes, or selection of responses (see Section 3.2). The right anterior frontal activations may relate to explicit memory processes, rather than priming, which are likely to be involuntary, but may be voluntary (and so contaminate measures of priming) in some cases. Many questions remain, however, concerning for example the role of other regions implicated in some word-stem completion studies (e.g. precuneus), and the locus of feature-specific component processes (e.g. for visual letter case or auditory voice) that can modulate behavioural priming. The increasing use of event-related techniques and fully factorial designs is likely to elucidate further these component processes, together with experimental methods for separating voluntary explicit, involuntary explicit and implicit memory contributions on a trial-by-trial basis (e.g. Schott et al., 2002).

3.2. Conceptual indirect tasks

In another indirect memory task that has received much attention, participants make semantic decisions about repeated stimuli (a repetition priming paradigm). The dependent variable is reaction time, with priming reflecting faster responses to repeated presentations (targets) than initial presentations (primes) (Vriezen et al., 1995). This effect is often viewed as a form of conceptual priming, and is normally intact in amnesiac patients (Vaidya et al., 1995).

In the fMRI study of Demb et al. (1995), participants performed one of several tasks on words. In the semantic task, they decided whether the referent of each word was concrete or abstract; in the ("difficult") non-semantic task, they decided whether or not the first and last letter of the word were in alphabetical order. Repetition suppression was seen in left inferior frontal regions (BA 45/47) in the semantic task, but not in the non-semantic task. Furthermore, the overall response of these regions was greater during the semantic than non-semantic task (despite the longer reaction times in the non-semantic task). This is consistent with other imaging studies that implicate left inferior frontal cortex with semantic processing (Poldrack et al., 1998; though see below). These findings suggest that the left inferior frontal repetition suppression reflects repeated conceptual processing of words, and is not a simple consequence of repeated perceptual processing.

In a subsequent study, Wagner et al. (1997) compared frontal responses while participants made living/nonliving decisions on either words or pictures. For both words and pictures, responses to repeated presentations were approximately 50 ms faster than to initial presentations. This priming effect was paralleled by left inferior frontal repetition suppression common to both words and pictures, supporting Demb et al.'s proposal that this region subserves conceptual processes independent of perceptual form. Note that the limited brain coverage of the above two studies (which was restricted to frontal cortex) prevents one from determining whether other posterior regions (such as occipitotemporal cortex, Section 3.1) showed repetition effects common to both semantic and non-semantic tasks performed on words (Demb et al., 1995), or repetition effects that differed for words and pictures (Wagner et al., 1997).

Wagner et al. (2000a) used whole-brain fMRI to compare abstract/concrete decisions on words for which participants had previously made either the same decision, or a different, non-semantic decision (upper/lower case). Reaction times for the targets decreased when same (semantic) task was performed, but not when the different (non-semantic) task was performed. Likewise, a region in left anterior inferior frontal gyrus (as in Demb et al., 1995), as well as a mid-lateral temporal region, showed repetition

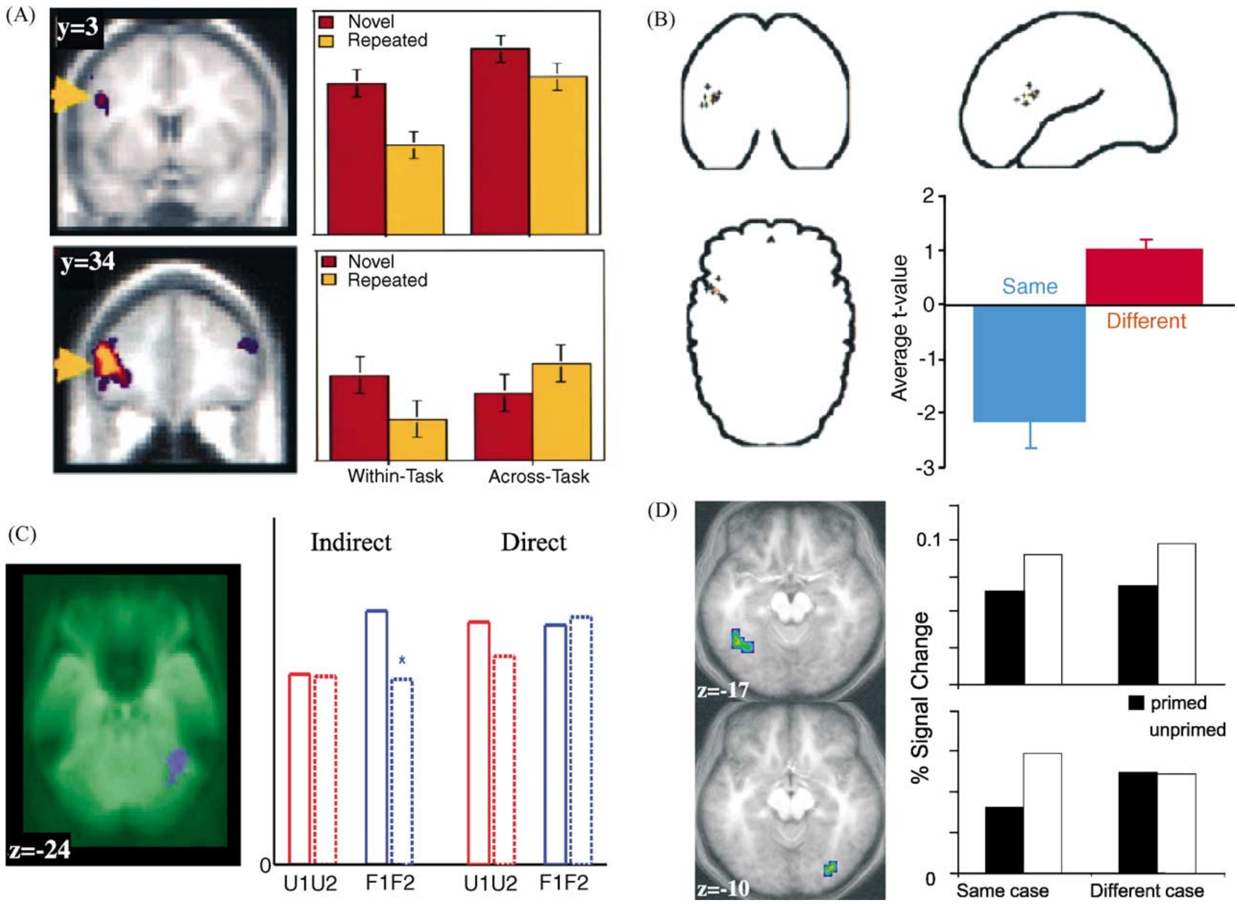

Fig. 3. (A) A posterior left inferior frontal region (upper section) shows repetition suppression both within-task (semantic/semantic) and across-task (visual/semantic), whereas a more anterior region (lower section) shows repetition suppression only within the semantic task (adapted with permission of Oxford University Press from Wagner et al., 2000a). Graphs show percentage BOLD signal change vs. fixation (maximum ordinate value: 1%; red: unprimed; yellow: primed). (B) Individual participant maxima (black dots) for word generation vs. a reading control congregate in left posterior inferior frontal cortex, and show a decrease within a semantic task ("same" attribute for word generation), but an increase across two semantic tasks ("different" attribute for generation), relative to an unprimed control (adapted with permission of Elsevier from Thompson-Schill et al., 1999). (C) A right fusiform (blue region in transverse section) shows repetition suppression for famous faces (F1 and F2, blue lines) in an indirect fame-judgment task, but not in a direct recognition task (bars show magnitude of event-related responses, arbitrary scale). First and second presentations of unfamiliar faces (U1 and U2, red lines) do not differ in this region in either task (Henson et al., 2002). (D) Repetition suppression associated with masked word-priming generalises across letter-case in a left fusiform region (upper section) but not in a right occipital region (lower section). Graphs show average BOLD response at 4.8 and 7.2 s after target stimulus vs. a target-absent baseline (adapted with permission of Nature Publishing Group from Dehaene et al., 2001).

suppression in the within- but not across-task condition (Fig. 3A, lower).

A more posterior, dorsal region of left frontal cortex (BA 6/44) showed repetition suppression in both the within- and across-task conditions (Fig. 3A, upper). Though the size of the decrease was less for the across- than within-task condition, a significant interaction was found between repetition, task and anterior/posterior region of left inferior frontal cortex. This supports a functional dissociation between the two left frontal regions, which has previously been interpreted as a semantic function for the anterior region, and a phonological function for the posterior region (Poldrack et al., 1998). Because phonological access was likely to be automatic (even though it might not aid semantic decision times), repetition suppression would be expected in the posterior frontal region in both tasks. It would be interesting to test whether behavioural priming occurs when a non-semantic task is used on both prime and target (i.e. if semantic/non-semantic task were crossed with within-/across-task repetition in a factorial design).

A different interpretation of left inferior frontal function was proposed by Thompson-Schill et al. (1999). These authors asked participants to produce a semantically-related word in response to a concrete noun. The attribute defining relatedness was either an action (e.g. DOLLAR-spend) or a colour (e.g. DOLLAR-green). In the within-task condition, the defining attribute was the same for prime and target; in the across-task condition the defining attribute was switched. Response latencies showed priming in both conditions relative to an unprimed control condition (though the within-task priming was numerically greater). A posterior inferior frontal region showed decreased responses in the within-task condition, but increased responses in the across-task condition (Fig. 3B). A left inferior mid-temporal region showed decreases for both within- and across-task conditions.

Thompson-Schill et al. attributed the common left mid-temporal decreases to the retrieval of semantic information, which is facilitated in both the within- and across-task conditions. The left inferior frontal differences on the other hand were interpreted in terms of the selection of competing responses. Multiple semantically-related words (presumably retrieved from the mid-temporal region) were assumed to compete for selection in both conditions. When a word with the appropriate semantic relation had been retrieved before (in the within-task condition), it was assumed to be more readily retrieved again, giving it an advantage in the competition, and hence diminishing selection demands. Conversely, when a word with an inappropriate semantic relation had been retrieved before (in the across-task condition), competition and selection demands were assumed to increase (though reaction times might still show priming if the facilitation of semantic retrieval from the left temporal region outweighed the extra selection demands in the inferior frontal region).

The concept of competition has implications for the hot-tubes metaphor described in Section 2.2, which predicts that the brain regions showing repetition suppression are a subset of those that responded to the prime. A brain region involved in selecting amongst competing word candidates might shown faster resolution of this competition for primed items, and hence repetition suppression, that owes to an advantage for primed items in the input to the region (arising from facilitation of earlier perceptual or conceptual processing for example). The same region need not be activated by the prime however, if the task performed on the prime did not engage the same competition. In this case, the prediction is rather that the brain region showing repetition suppression is also activated for unprimed stimuli relative to some baseline.

The selection account of Thompson-Schill et al. (1999) has been contrasted with a more general proposal that left inferior frontal cortex supports “semantic working memory” (Gabrieli et al., 1998), in particular, the control of retrieval of semantic information (Wagner et al., 2001). However, the frontal region identified by Thompson-Schill et al. is closer to the posterior, rather than anterior, frontal region identified by Wagner et al. (2000a), which the latter interpreted in terms of phonological rather than semantic processing. Because the same response word was given in the within- but not across-task conditions of the Thompson-Schill et al. study, the greater posterior inferior frontal decrease in the former could have also reflected priming of phonological processes (though this would not explain the posterior inferior frontal increase for the across-task condition, relative to the unprimed condition).

Wagner et al. (2000b) examined the effect of repetition lag (the time between prime and target) during concrete/abstract decisions on words. Priming after a lag of a few minutes was significantly greater than after a lag of 25 h (57 ms versus 14 ms, respectively, though the long-lag priming failed to reach significance). Collapsing across lag, repetition suppression was observed in left inferior frontal cortex (including both anterior and posterior regions), as expected, as well as left inferior temporal/fusiform and left inferior occipital regions. Direct comparison of the short- and long lags revealed greater repetition suppression in the left anterior and posterior inferior frontal and left inferior temporal regions for short lags. Interestingly, the long-lag condition produced better subsequent recognition memory for the words (tested 48 h after scanning) than the short lag condition (corresponding to the “spaced practice” advantage for explicit memory, Melton, 1967). Furthermore, recognition confidence was inversely correlated with both behavioural priming and left inferior frontal activity. The latter finding suggests that the temporary facilitation of semantic processes enhances priming but impairs encoding for subsequent explicit memory (see Wagner et al., 2000b, for further discussion).

In summary, imaging studies have converged on an important role for left inferior frontal cortex in priming during conceptual tasks, which requires semantic processing of both prime and target, but is independent of the perceptual format of the stimuli. There is still debate about the precise nature of this role, which may reflect distinct functional regions within inferior frontal cortex (e.g. anterior versus posterior regions). Though an interesting inverse relationship has been observed between repetition suppression in left inferior frontal cortex and subsequent explicit memory, this region is unlikely to be sufficient to support explicit memory on its own (given that amnesiac patients generally show intact conceptual priming). One problem with comparisons like those of Thompson-Schill et al. (1999) and Wagner et al. (2000a), however, in which one task is repeated on prime and target, is the increased likelihood of contamination by explicit memory, particularly when the tasks are reasonably difficult and involve long reaction times. The primed reaction times of 900–1000 ms in the within-task condition of the Thompson-Schill et al. study, for example, may have reflected participants’ explicit retrieval of their previous response (e.g. “what did I say last time?”; Section 6.1).

3.3. Comparisons across direct and indirect tasks

Another approach to teasing apart implicit and explicit memory is to compare directly stimulus repetition effects across direct and indirect memory tasks. Donaldson et al. (2001), for example, used an abstract/concrete semantic task on initial presentations of words, which were then repeated in either the same task, or a direct recognition memory task. A left anterior inferior frontal region (as in Section 3.2) showed repetition suppression in the within- but not across-task condition. Blaxton et al. (1996) however found repetition suppression in a similar left inferior frontal region for both an indirect and direct task, in which participants were exposed to a word-pair (e.g. SKY–EAGLE) and later given the first word (SKY) for either generation of a semantic associate (indirect test), or cued-recall of the target word (direct test). The divergent findings across the two studies may reflect different component processes engaged by the different direct memory tasks. The recognition task of Donaldson et al. might be performed without appreciable semantic processing, whereas the cued-recall task of Blaxton et al. might involve generation of semantic associates of the cue, prior to recognition, with this generation process being primed by prior semantic processing in the study task.

Blaxton et al. also found repetition suppression in left occipital cortex (BA 17) for both completion (indirect test) and cued-recall (direct test) using word-fragments (e.g. E_G_E), analogous to the right occipital decreases seen by Squire et al. (1992) for both direct and indirect versions of word-stem completion (Section 3.1). Other studies using direct and indirect perceptual tasks have produced different results, however. Schacter et al. (1995) found response increases (rather than decreases, see Section 4.4) in left inferior temporal/fusiform regions associated with repetition of possible object-drawings in both an indirect possible/impossible object task and a direct recognition task. Using random-dot patterns, Reber et al. (1998) found response decreases in occipital regions associated with exemplars of learned versus different categories in an indirect categorisation task, but response increases in nearby regions associated with repeated versus new patterns in a direct recognition task. Henson et al. (2002) found response decreases in a right fusiform area (BA 37) for repeated familiar faces in an indirect familiarity-judgment task, but no significant repetition effects in a direct recognition task (Fig. 3C). A more anterior, medial temporal region, probably in perirhinal cortex, has shown repetition suppression across a number of direct memory recognition tasks (Henson et al., 2003).

These divergent results are difficult to interpret in any simplistic distinction between direct and indirect tasks. They also highlight the danger of assuming that the tasks are "process-pure" (Section 1.3), in that many direct tasks are likely to involve priming of some of the same component processes engaged by indirect tasks, in addition to explicit memory processes presumably subserved by a specialised medial temporal lobe system. However, the added complication of direct tasks is that, by directing the participant's attention towards repetition (by definition), many regional changes may be altered by attentional or target-related effects. For example, participants in recognition memory tasks are likely to treat the repeated stimuli as targets, and neural correlates like the "P300" event-related potential (ERP) are known to be influenced by the "targetness" of stimuli (Johnson, 1988). In addition, the degree to which some cells in the Macaque cortex show response suppression (Section 5) appears sensitive to the task-relevance of the repetitions (Miller and Desimone, 1994).

3.4. *Masked priming*

One way to be more confident that repetition effects reflect priming in the absence of explicit memory is to use masked priming, in which the prime is presented briefly (typically less than 50 ms) and followed by a backward mask. If the prime can shown to be imperceptible, then it cannot be consciously retrieved when the target is presented (nor is there reason for differential attention to primed and unprimed stimuli). The presence of masked priming effects has been used to argue for "unconscious" processing, even to the level of semantics or affective value (Draine and Greenwald, 1998; Marcel, 1983), though this has been a matter of much debate, particularly concerning the measurement of awareness for the prime (see, for instance, Holender, 1986; Merikle and Reingold, 1990). Another potential complication is that masked priming is usually short-lived, tending to last only a few hundred milliseconds and disappearing when other items intervene between prime and target (though see Seamon et al., 1995; Misra and Holcomb, 2003). It may therefore reflect mechanisms quite different from those involved in the supraliminal, long-term priming discussed so far (Forster and Davis, 1984; Humphreys et al., 1988). Nonetheless, masked priming is a interesting phenomenon in its own right.

In an impressive demonstration of masked semantic priming, Dehaene et al. (1998) presented a number for 43 ms, forward and backward masked. After the 71 ms backward mask, another number was presented, and participants decided whether it was larger or smaller than five. Psychometric tests showed no evidence that participants could detect or discriminate the primes. Reaction times to the target however were 24 ms faster when the prime and target were congruent (both larger or smaller than five) than incongruent (one larger, one smaller). A semantic locus for the effect was suggested by the finding that priming did not differ reliably when prime and target number were both words (ONE, FOUR) or numerals (1, 4), than when one was a word and the other a numeral. Because participants indicated their decision with either left or right hands, response-locked EEG from central electrode sites showed evidence of a "lateralised readiness potential" (LRP). The LRP demonstrated a covert priming effect that preceded the overt response by approximately 150 ms. An analogous "lateralised blood oxygenation level dependent (BOLD) response"—the relative magnitude of the haemodynamic response in left and right motor cortices—also showed a congruency effect. These data suggest that the effects of unconscious processing can extend to the level of motor programming (even in the absence of direct stimulus-response mappings, Naccache and Dehaene, 2001b).

In a subsequent study, Dehaene et al. (2001) provided evidence of masked repetition priming for words. Participants made semantic decisions (natural/man-made) about target words that were preceded by masked presentation of the same or different word (for 29 ms, followed by a backward mask of 29 ms), in either the same or different letter case. Priming of 10–15 ms was observed that did not differ significantly across same and different case primes. More spatially-extensive decreases than would be expected by chance were observed in a left fusiform region for primed versus unprimed words. The responses in this left fusiform region did not appear to differ for same versus different cases, in contrast to a right occipital region, which showed a larger repetition effect for same than different cases (Fig. 3D).

However, in another fMRI study of masked word repetition priming (Schnyer et al., 2002), the only repetition effects found were response increases for primed versus unprimed words (i.e. "repetition enhancement" rather than repetition suppression; see Section 4.5). The primes were presented for 50 ms, and followed immediately by the target, presented in a different case (previous studies have suggested that discrimination of the prime is close to chance under these conditions, though no concurrent tests of prime discrimination were made in the scanner). Nine of the 12 participants showed priming, in the form of faster lexical decision times (with an average speed-up of 32 ms), and the fMRI data from only these participants were analysed. Three of the 10 regions implicated in lexical processing (by being more active for words than pseudowords) showed repetition enhancement, including a left occipital region close (though slightly superior and medial to) the homologous occipital region of Dehaene et al. (2001). Schnyer et al. (2002) proposed that, prior to identification of a prime, activation spreads through neural networks that include perceptual/lexical representations of the prime word. When a related target is presented after a masked prime, this activation is added to the response to that target, producing repetition enhancement. Once the prime is identified however, prior to presentation of the target, the spread of activation is terminated, and a different mechanism (e.g. a lowered threshold for activating word representations) produces the repetition suppression associated with supraliminal priming.

In a third study, primes were presented from 16–50 ms, based on subject-specific, forced-choice threshold testing, and followed by a backward mask (Davis et al., 2001). These authors failed to find significant repetition effects under masked conditions anywhere in the brain, despite concurrent evidence of supraliminal word repetition effects. Thus, the results of imaging studies of masked word priming are far from conclusive. The reason for the divergent findings across the studies of Dehaene et al., Schnyer et al. and Davis et al. is unclear, but may relate to inter-participant variability or precise masking conditions. Given that behavioural masked priming effects are typically of the same order as the prime-target SOA, one possibility is that processing of the target simply onsets slightly earlier when primed. The size of this onset difference (e.g. 58 ms in Dehaene et al., 2001) is beyond the typical temporal resolution of fMRI experiments (see Section 5.2), and may be difficult to detect as a change in the magnitude of a haemodynamic response to the target. Note that in the earlier Dehaene et al. (1998) study, the longer prime-target SOA (114 ms), together with the presence of incongruent primes (which may have the opposite effect of slowing down reaction times), may have increased the probability of detecting an effect. Specifically, a combination of increased neural activity for congruent trials and decreased activity for incongruent trials (relative to an unprimed case) during a 114 ms interval between prime and target may be easier to detect as a difference in the haemodynamic response magnitude (Section 5.2).

One intriguing approach was taken by James et al. (2000), who attempted to slow down the time-course of priming by using a gradual unmasking technique. Grey scale images of everyday objects were slowly revealed over 61 s from behind either panel or noise masks. The time taken for participants to identify the object was reduced for those objects presented previously for passive viewing (mean identification times of approximately 25 s versus 30 s for primed versus unprimed objects, respectively, collapsing across mask-type). Regions of interest in bilateral fusiform and parietal cortices showed haemodynamic responses that increased faster for primed than unprimed stimuli prior to the point of identification. After the point of identification, the responses decreased. This pattern resembles that described by Schnyer et al. (2002). However, a problem with this analysis is that the "gradual build-up" of activation could simply be an artefact of averaging over punctuate responses that occurred at different identification times on different trials. Because identification times were likely to comprise two Gaussian-like distributions over trials (with the central tendency of the "primed" distribution simply occurring earlier than that for the "unprimed" distribution), the mean haemodynamic data would have similar profiles, even if the response to any one trial only ever arose immediately after identification. This would not necessitate any build-up in neural activity prior to the point of identification. Nonetheless, if this build-up is a real effect, and it holds for more conventional, brief stimuli, then haemodynamic repetition effects may require more detailed consideration in terms of the latency or duration of underlying neural activity (see Section 5.2).

Other studies have examined situations where the target is masked. Explicit identification of such stimuli is generally improved when primed. This form of "masked priming" of visual objects is associated with response increases in regions including the lateral occipital cortex and fusiform (Grill-Spector et al., 2000). This repetition enhancement correlates directly with the level of conscious identification of stimuli (Bar et al., 2001). In this sense, the response increase is not particularly surprising, since it represents a process occurring on primed but not unprimed stimuli, and so would be expected to reflect the neural correlates of that further cognitive process (see Section 4.5). A potentially more interesting aspect of such "perceptual identification" tasks is the onset of the priming effects in relation to the onset of conscious recognition, as measured by electrophysiological techniques for example (Doniger et al., 2001).

In summary, imaging studies using masked primes are still few in number, and their divergent results in terms of repetition suppression versus repetition enhancement requires resolution. Moreover, the relation between the typically short-lived masked priming and the long-lag priming normally employed in studies of implicit memory (e.g. in amnesia) is unclear; these forms of priming may in fact involve different mechanisms. This limits the potential generalisability of studies that use masked priming as a technique to rule out explicit memory contamination of imaging data: this approach may well eliminate the unwanted influence of conscious recollection, but at the cost of studying a different phenomenon than long-lag priming.

4. Priming as a tool

This section reviews imaging studies that have used repetition suppression as a signature to map the brain regions associated with different stages of stimulus processing, analogous to the use of behavioural priming to inform theories of visual object processing (e.g. Biederman and Cooper, 1991) and language processing (e.g. Forster and Davis, 1984). More generally, the logic of this approach is, if region R shows a reduced repetition effect to a target that only differs from a prime on dimension D, then the processes subserved by region R are sensitive to dimension D. The section concentrates on visual object processing and the inferior temporal lobe, including the concepts of fMRI adaptation and hyper-resolution, but also covers the issues of stimulus familiarity, repetition-related response increases (repetition enhancement), repetition lag effects and semantic priming with verbal stimuli.

4.1. *fMR adaptation*

Priming is used to investigate how people represent visual objects by testing how it transfers across various changes in the depiction of objects. Grill-Spector et al. (1999) combined this approach with fMRI to investigate the representational properties of the “lateral occipital complex” (LOC), which has previously been shown to respond more to objects than to textures with no shape properties (Malach et al., 1995). LOC responses decreased as the frequency of repetitions within blocks of objects increased (Fig. 4A), a technique the authors called “fMR adaptation”. The degree to which this adaptation was sensitive to variations in the repeated objects was used to isolate the representational level of different subregions within LOC. For example, the degree of adaptation in an anterior, ventral region in LOC (in posterior fusiform gyrus and occipitotemporal sulcus) was invariant to the size and position of the object, but not to the illumination or viewpoint of the object, implicating this region in non-retinotopic but view-based (rather than fully object-based) representations.

One problem with the specific approach of Grill-Spector et al., in which repetition frequency is varied across blocks, is that participants are likely to anticipate these different frequencies, and hence any adaptation may reflect corresponding decreases in attention (particularly for blocks in which a single object is repeated). This problem can be overcome with event-related designs in which repeated and non-repeated stimuli are randomly intermixed. Kourtzi and Kanwisher (2000) used event-related fMRI to compare responses to successive trials in which either the same or different object was depicted, in either the same or different format (a line-drawing or grey scale photograph). Repeated objects were associated with decreased responses in LOC, extending into posterior temporal regions, whether they were repeated in the same or a different format (relative to unrepeated objects in the same or different format, which did not differ). These results extend those of Grill-Spector et al. in showing that LOC is involved in extracting object structure from different image cues (though the precise relationship between the format-invariance of Kourtzi and Kanwisher (2000), and the illumination-dependence of Grill-Spector et al. (1999), may need to be determined).

Whether the reductions observed by Grill-Spector et al. (1999) and Kourtzi and Kanwisher (2000) correlate with behavioural priming remains unclear, since they used covert naming or one-back repetition detection (Grill-Spector et al., 1999) and passive viewing (Kourtzi and Kanwisher, 2000), none of which provides a conventional measure of priming. The relationship between the short-lag (i.e. high-frequency) repetition and the longer-lag repetition used in typical priming experiments, also needs to be established (Section 4.6). Indeed, it may be useful to distinguish neural “adaptation”, which is likely under the short lag, high-frequency repetition conditions of the Grill-Spector paradigm, from neural “response suppression”, which occurs after a single presentation and can be long-lasting (Section 5.1).

4.2. *Hyper-resolution*

Grill-Spector et al. proposed that the adaptation technique offers better spatial resolution than conventional, categorical subtractions (in which blocks of one stimulus-type are contrasted against blocks of another stimulus-type). The logic behind this “hyper-resolution” is that a voxel sampled by fMRI or PET may contain a mixture of neurons with different selectivities. Though the spatial distribution of neural firing within that voxel may distinguish two stimulus-types, the mean level of activity may not (Fig. 6A). However, if these neurons adapt or exhibit response suppression following prior presentation of the same stimulus-type, the mean activity levels will differ, and hence be detectable with fMRI or PET.

Empirical evidence for hyper-resolution was provided by Naccache and Dehaene (2001a), in a further analysis of the masked priming data of Dehaene et al. (1998) described in Section 3.4. They compared a “priming” subtraction

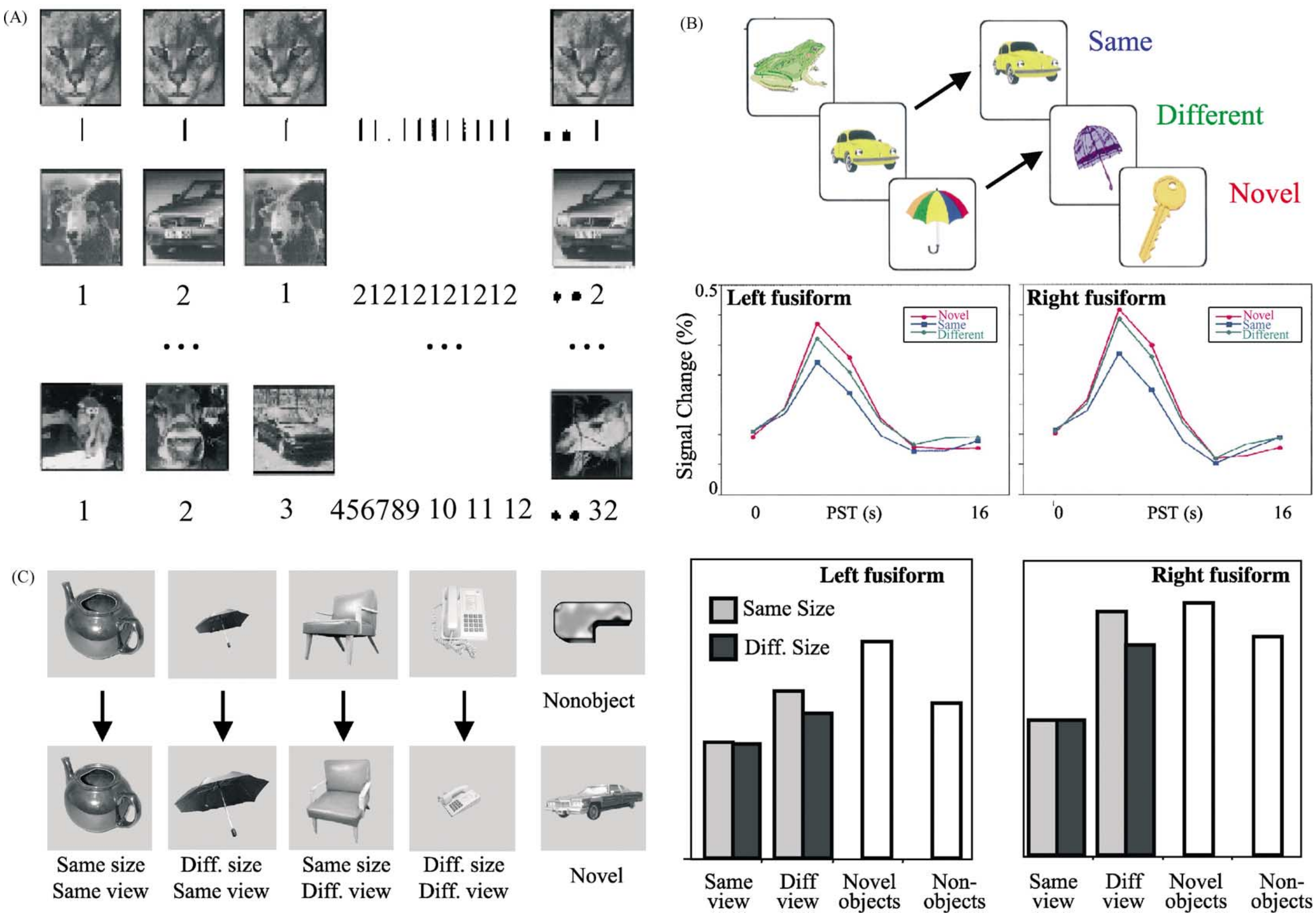

Fig. 4. (A) "fMR adaptation": blocks that contain different frequencies of repetition (numbers in sequences represent distinct stimuli) can be contrasted parametrically (adapted with permission of Elsevier from Grill-Spector et al., 1999). (B) Objects that were repeated from a prior study phase ("same"), that were different from, but exemplars of the same category as, an object appearing in the study phase ("different"), or that were previously unseen ("novel"), produced different patterns of event-related response in left and right fusiform (adapted with permission of Elsevier from Koutstaal et al., 2001). Graphs show percentage BOLD signal change vs. fixation as function of post-stimulus time (PST). (C) Across two experiments, objects in a study phase were repeated in either the same or different size, and from either the same or different view, together with novel objects and non-objects (Vuilleumier et al., 2002). Graphs show magnitude of event-related responses (arbitrary scale) vs. fixation in left and right fusiform regions for same and different views of repeated objects, together with novel objects and nonobjects.

(e.g. prime-target pairs of ONE–1 or FOUR–4 versus ONE–4 or FOUR–1) with a "categorical" subtraction of large versus small targets (e.g. ONE–4 or FOUR–4 versus ONE–1 or FOUR–1). The former subtraction revealed repetition suppression in bilateral intraparietal sulci (i.e. when prime and target were the same quantity), suggesting that these parietal regions represent numbers at an abstract level. The categorical subtraction did not reveal any significant difference in the intraparietal regions however. Naccache and Dehaene (2001a) therefore promoted the priming approach; in particular, the use of masked priming to minimise potential confounding effects such as attention (Section 3.4).

4.3. *Higher-level object priming*

In the event-related study of Buckner et al. (1998), participants made semantic decisions on pictures of everyday objects (deciding whether or not each object moved). The same task was performed on a subset of pictures presented six times prior to scanning, producing a robust RT speed-up for these pictures during scanning. Decreased responses to primed pictures were observed in bilateral inferior temporal/occipital regions, including fusiform (BA 37) and bilateral middle occipital (BA19) gyri, as well as left posterior frontal cortex, anterior cingulate, SMA and left cerebellum. The occipitotemporal decreases were close to those reported by Grill-Spector et al. (1999), anterior to retinotopic visual areas. The left frontal decreases may have reflected automatic, covert naming of the objects.

Koutstaal et al. (2001) used a similar event-related paradigm in which participants made size-judgments to the same or different exemplars of a repeated object-category (i.e. objects with a common name, Fig. 4B). Relative to novel (unprimed) objects, reaction times were faster for both same (by 134 ms) and different (by 66 ms) exemplars of a repeated category, though this priming was greater when the same exemplar was repeated. Several occipitotemporal and frontal regions showed repetition suppression to both types of primed objects. Direct comparison of same versus different exemplars showed greater repetition suppression for same exemplars in regions including bilateral posterior inferior frontal and midfusiform cortices. A regions of interest analysis across left and right midfusiform showed a greater effect of exemplar change in right than left fusiform. This interaction reflected an apparent decrease relative to unprimed objects for both same and different exemplars in the left fusiform, but a decrease only for same exemplars in the right fusiform (Fig. 4B).

Koutstaal et al. interpreted the fusiform laterality effect in terms of a hemispheric specialisation hypothesis (Marsolek, 1995). In a number of split-visual field experiments (e.g. Marsolek et al., 1992), greater modulation of priming by perceptual changes has been observed when prime and target are presented to the left than to the right visual hemifield (i.e. right versus left hemisphere, respectively). These findings have been attributed to the hypothesis that the right hemisphere retains visual-form representations, whereas the left hemisphere retains more abstract (e.g. lexical) representations. This is consistent with Koutstaal et al.'s findings of right fusiform decreases specific to particular object pictures, but generalisation across exemplars of the same category in left fusiform. It is also consistent with the proposal that perceptual priming impairments are more common after right posterior regions (Gabrieli et al., 1995, though this right-lateralisation has been questioned, Yonelinas et al., 2001).

A similar fusiform lateralisation was found by Vuilleumier et al. (2002). These authors simultaneously examined effects of exemplar-, viewpoint- and size-changes while participants decided whether stimuli depicted "real" or "nonsense" objects (Fig. 4C). The real objects were familiar, everyday objects; the nonsense objects were unfamiliar (though structurally possible) objects. Behavioural priming was found for real objects in all conditions (priming of nonsense objects was not of primary interest, since it was only measured in one experiment, without size/view changes, and was potentially confounded by time and by the task; see Section 4.4). The amount of priming for real objects was independent of size-changes, but was bigger for objects repeated in the same than different view (Tarr et al., 1998). Indeed, size-changes did not interact with repetition effects in any brain region, even though early retinotopic regions showed a main effect of greater responses to large than small objects, as expected.

Lateral occipital regions showed repetition suppression for both real and nonsense objects, consistent with a general role in shape extraction, prior to object recognition (Malach et al., 1995). Midfusiform regions however showed greater repetition suppression for real than nonsense objects, consistent with a role in object recognition (Section 4.4). Like Koutstaal et al. (2001), the pattern of fusiform responses showed greater generalisation in left than right fusiform (Fig. 4C): the left fusiform decreases were independent of view-changes, whereas the right fusiform decreases were greater for same than different views (matching the pattern of behavioural priming). Unlike Koutstaal et al. however, the fusiform decreases did not generalise across different exemplars of an object-category (with the same name). The only region that showed repetition suppression that generalised across exemplars was in left inferior frontal cortex, which may have reflected priming of covert naming. One possibility is that the left midfusiform generalises over visual features of objects (that vary with view), and that the different exemplars used by Koutstaal et al. possessed a greater overlap of visual features than those used by Vuilleumier et al.

Another fMRI study examined repetition effects across view-changes of objects rotated in depth (James et al., 2002). A subregion within the LOC, close to the fusiform regions identified by Vuilleumier et al. (2002), showed comparable levels of repetition suppression for identical and depth-rotated objects (though the extent of concurrent behavioural priming was unknown, given that participants viewed the stimuli passively). Unlike Vuilleumier et al., there was no apparent lateralisation, since the same pattern was found for both left and right LOC subregions. Repetition suppression across views was also observed for nonsense objects. A region in the caudal intraparietal sulcus however only showed repetition suppression for identical views (close to a region showing a similar pattern in the Vuilleumier et al. study). This intraparietal region may be part of a dorsal object processing stream that subserves the visuomotor transformations associated with mental rotation and required, for example, when grasping an object (Goodale and Milner, 1992). The facilitation of such transformations by prior exposure is likely to be view-specific.

In summary, imaging studies are converging on a hierarchical perspective of visual object processing in which object representations become more abstracted from posterior to anterior occipital/temporal regions, and possibly more abstracted in left than right hemispheres. Early retinotopic regions do not appear to show repetition effects. Rather, lateral occipital regions appear to support the earliest stage at which repetition effects emerge, and these appear to arise from size-invariant, but not view-invariant, representations that are independent of long-term object knowledge (i.e. are equivalent for familiar and unfamiliar objects). More anterior fusiform regions appear to support long-term knowledge of familiar objects (Section 4.4), which may be view-independent in the left fusiform and view-dependent in the right fusiform (though see James et al., 2002). Later stages of object naming can also show repetition effects in regions associated with the language system, including left inferior frontal cortex, while object-sensitive regions within parietal cortex may aid in extrapolating across views.

4.4. *Familiar versus unfamiliar object priming*

By comparing repetition effects for familiar stimuli (e.g. words, known faces) with those for unfamiliar stimuli (e.g. non-words, unknown faces), it may be possible to identify regions in a processing pathway where stimuli make contact with pre-existing, long-term memory representations—i.e. at the interface between perception and memory. Such regions should show repetition effects for familiar, but not unfamiliar, stimuli ("familiarity" here referring to pre-experimental familiarity). This relates to a debate in the psychological literature between "modification" (or "abstractionist") and "acquisition" (or "episodic") theories of priming (Bowers, 1996; Tenpenny, 1995). According to modification theories (Bruce and Valentine, 1985; Morton, 1969), priming reflects some modification, such as lowered thresholds of, or residual activity in abstract, pre-existing representations. According to acquisition theories however (Jacoby, 1983; Roediger and Blaxton, 1987; Schacter et al., 1990), any exposure to a stimulus can, in principle, leave some residual trace of its processing. Thus, an important difference between the two theories concerns whether unfamiliar stimuli, with no pre-existing representations, can be primed. According to acquisition theories, they can; according to modification theories, they cannot.

Several behavioural studies have found priming only for familiar stimuli, supporting modification theories. However, several factors may confound these findings. Firstly, some of the studies have confounded stimulus familiarity with the task, for example using familiarity judgments to famous and unknown faces (Ellis et al., 1990), or lexical decisions to words and pseudowords (Forster and Davis, 1984). In such tasks, any increased fluency with which unfamiliar stimuli are perceived (owing to priming) may be erroneously attributed to pre-experimental familiarity, interfering with the judgment. Secondly, few of these studies controlled for explicit memory, which may interact with stimulus familiarity. Thirdly, the definition of "familiarity" can be troublesome, since the priming that is found for some types of unfamiliar stimuli (e.g. pseudowords) could reflect partial modification of pre-existing representations of similar stimuli (e.g. related words) or familiar sub-components of the stimulus (e.g. familiar sublexical letter/phoneme chunks).

Other studies have found priming for unfamiliar stimuli when these factors are controlled, such as (a) unknown faces in a sex-decision task (Goshen-Gottstein and Ganel, 2000), performance of which is (in principle) orthogonal to face familiarity; (b) non-words in an incremental perceptual threshold task, in the absence of concurrent explicit memory (Stark and McClelland, 2000); and (c) illegal non-words in a perceptual identification task (Bowers, 1994), which is difficult to explain in terms of familiar sublexical components. These findings support acquisition theories. Nonetheless, priming effects are generally greater for familiar than unfamiliar stimuli, and demonstrations of equivalent priming across physical changes between prime and target are difficult to explain by acquisition theories alone (in which priming effects generally depend on the overall similarity between prime and target, Bowers, 1996). Moreover, amnesiac patients appear to have impaired priming for unfamiliar stimuli, relative to controls (Gooding et al., 2000), which might be expected if amnesiacs cannot acquire new representations (in contrast with their intact priming for familiar stimuli, which might reflect modification of pre-existing representations). The above considerations suggest a compromise position that allows for contributions from modification of pre-existing representations and from newly acquired representations. The priming of familiar items can then benefit from both components.

Schacter et al. (1995) examined priming of 2D drawings of abstract objects that either could or could not exist in 3D ("possible" or "impossible" objects). These unfamiliar stimuli are unlikely to have pre-existing representations (or familiar sub-components), yet previous behavioural studies have shown that they exhibit priming effects, at least for "possible" objects (Cooper et al., 1992). Indeed, such findings have been used to support the "perceptual representation system" (PRS) theory (Schacter, 1990), in which pre-semantic structural representations (of possible objects) can be established following a single exposure. In the Schacter et al. (1995) study, priming was evident as increased accuracy of possible/impossible decisions to possible objects following a prior judgement task in which participants decided if the object appeared best suited for use as a tool or for support. Contrary to previous imaging studies however, Schacter et al. found repetition-related increases, rather than decreases, in left inferior temporal/fusiform regions. This repetition enhancement, like the behavioural priming, was only observed for possible objects. One reason why most other imaging studies find repetition suppression may be that they tend to use familiar stimuli (such as words, or everyday objects), which have pre-existing representations.

An event-related fMRI study by Henson et al. (2000) directly compared repetition effects for familiar and unfamiliar stimuli. Using an indirect target-monitoring task, the authors identified a right midfusiform region that showed different repetition effects for familiar and unfamiliar stimuli (Fig. 5A). For familiar stimuli (famous faces or meaningful symbols), the more common repetition suppression was observed. For unfamiliar stimuli (unknown faces or meaningless symbols), repetition enhancement was observed. In a preliminary study, Henson (2001) found a similar interaction for words and non-words, but in a more anterior left fusiform region. Henson et al. (2000) offered an explanation of their results in terms of both modification of pre-existing representations (for familiar stimuli), associated with repetition suppression, and acquisition of new representations (for unfamiliar stimuli), associated with repetition enhancement. This explanation is generalised in Section 4.5. Interestingly, in a subsequent study, Henson et al. (2002) identified a left occipital region that showed repetition suppression for both familiar and unfamiliar faces, which may reflect acquisition of representations earlier in the visual processing pathway that are common to both types of face.

In summary, both behavioural and imaging evidence suggest that, while priming can occur for unfamiliar stimuli without pre-existing representations, it can interact with stimulus familiarity. This interaction is not well captured by

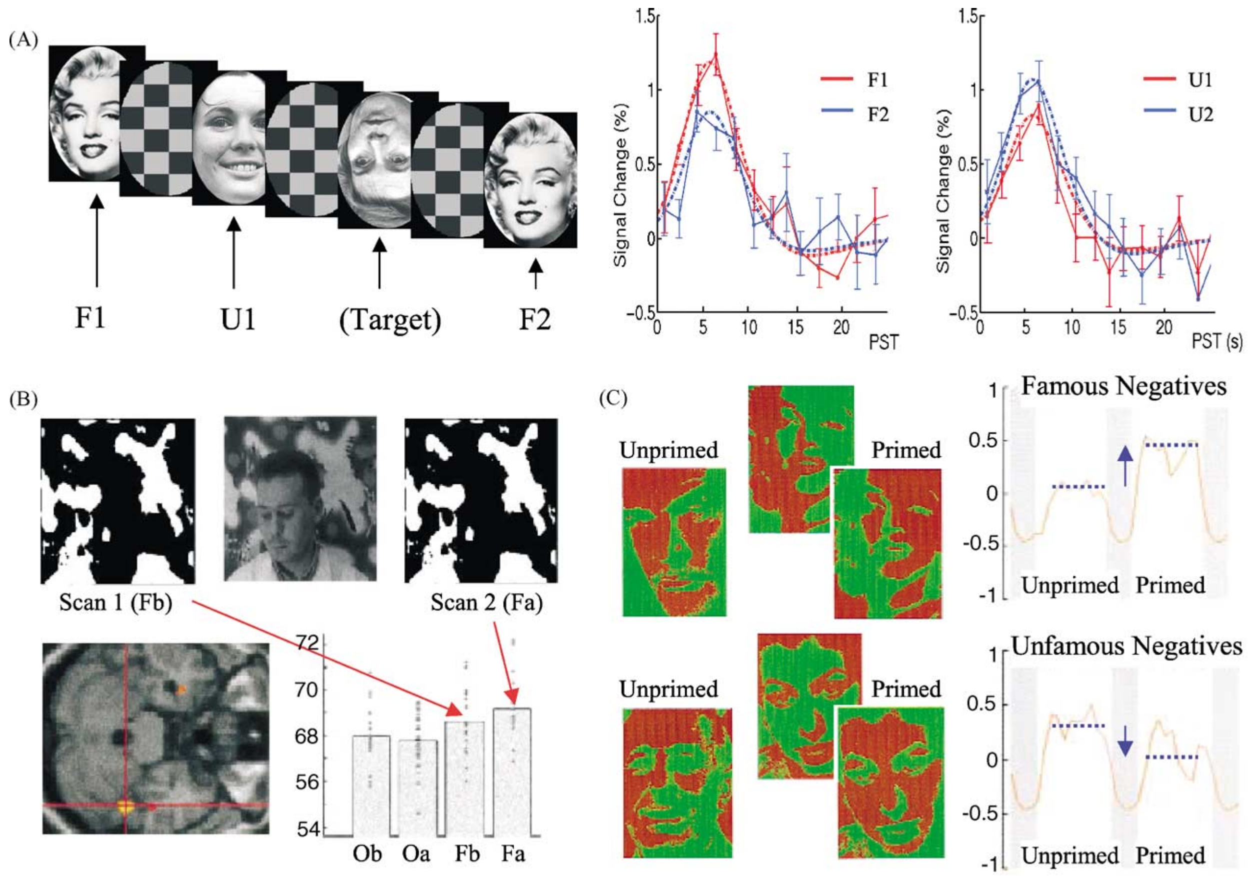

Fig. 5. (A) First and second presentations of famous (F1 and F2) and unfamiliar (U1 and U2) faces occurred while participants monitored for an inverted target face (Henson et al., 2000). Graphs show percentage BOLD signal change vs. fixation from a right fusiform region. (B) Initially ambiguous binarised images of faces (Fb) were disambiguated on repetition (Fa) after intervening presentation of intact images (adapted with permission of Nature Publishing Group from Dolan et al., 1997). Graph shows adjusted PET rCBF vs. a global value of 50 in a right fusiform region (for objects, Ob and Oa, as well as faces). (C) Negative-contrast images of famous faces (top) and unfamiliar faces (bottom) either were, or were not, primed by prior presentation of positive-contrast versions (adapted with permission of Nature Publishing Group from George et al., 1999). Graphs show mean percentage BOLD signal change (against fixation periods in grey) during blocks of famous negatives (top graph) and unfamiliar negatives (bottom graph).

either modification or acquisition theories alone. The interaction is however compatible with a "component process" view of priming that allows multiple contributions from different levels of stimulus representation. Thus, behavioural priming may include contributions of form-specific representations acquired temporarily in "early" object-sensitive regions, common to both familiar and unfamiliar stimuli, and modification of more abstract representations of familiar stimuli in higher object regions.

4.5. *A theory of suppression versus enhancement*

At least two other imaging studies have reported repetition enhancement with faces (Dolan et al., 1997; George et al., 1999). Participants in the Dolan et al. (1997) study viewed binarised images of either faces or objects, which were difficult to perceive as such on their initial presentation (only ∼10% of object images and ∼50% of face images were reported to give a percept). When these degraded images were repeated following intervening presentation of an intact version of each image (Fig. 5B), a greater number was recognised (∼90% in both cases, though not when irrelevant images intervened, indicating an item-specific rather than general practice effect). Greater fusiform responses to repeated than initial presentations were observed, on the left for objects and on the right for faces, in addition to common increases in medial and lateral parietal regions.

Participants in the George et al. (1999) study viewed two-tone images of either famous or unfamiliar faces (Fig. 5C). For the "positive images", the shading provided by the light/dark tones was sufficient to recognise the famous faces. For the "negative images", the contrast polarity of the tones was reversed, producing faces that were difficult to recognise (only ∼20% were identified in a behavioural experiment). Recognition of negative images was made easier (∼45% identified) when they were preceded by positive versions. Using an indirect target-monitoring task during fMRI, greater bilateral fusiform responses were observed to negative images of famous faces when they were preceded by positive versions than when they were not. In contrast, these regions exhibited decreased responses when negative images of unfamiliar faces were preceded by corresponding positive images. The former increase was attributed to recognition for the negative images (which the authors termed "active" priming); the latter decrease was attributed to facilitation of low-level processes common to positive and negative images (which they termed "passive" priming).

Prima facie, the results of George et al. (1999) conflict with those of Henson et al. (2000) discussed in Section 4.4: repetition enhancement and repetition suppression was seen for familiar and unfamiliar faces, respectively, in the former, but the opposite pattern was seen in the latter. However, the results of all three "face priming" studies (Dolan et al., 1997; George et al., 1999; Henson et al., 2000) can be interpreted parsimoniously by the following assumption. Regions that show repetition enhancement are those that subserve a process that occurs on primed but not unprimed stimuli (i.e. when an additional process operates on the target), whereas regions that show repetition suppression are those that subserve a process that occurs for both primed and unprimed stimuli (i.e. the "hot-tubes" metaphor described in Section 2.2).

In the above examples, these regions are within fusiform cortex, and the specific processes are likely to relate to some form of visual object recognition (see Section 4.3). It is worth distinguishing at least two types of recognition: "categorical recognition" (recognition that a face, rather than say a car, is present in an image) and "exemplar recognition" (recognition that a particular face, say that of Marilyn Monroe, is present). Both types of recognition may be associated with an increased fusiform response (evidence for the latter includes the greater response to unprimed positive than unprimed negative images of famous faces in the George et al. study and the greater response to initial presentations of famous than of unfamiliar faces in the Henson et al. study).

In the Dolan et al. (1997) study then, the additional process following priming was the categorical recognition of an object or (unfamiliar) face in an otherwise ambiguous image, producing repetition enhancement. In the George et al. (1999) study on the other hand, such categorical recognition was possible for both positive and negative images (i.e. even the negative images were perceivable as faces, unlike the binarised images in Dolan et al.). For unfamiliar faces therefore, the same process occurred for both primed and unprimed negative images, producing the fusiform repetition suppression. For the famous faces however, additional exemplar recognition was possible for primed but not unprimed negative images, producing the fusiform repetition enhancement.

In the Henson et al. (2000) experiments, which used undergraded faces, categorical recognition was possible in all cases. Additional exemplar recognition was also possible for famous faces. The repetition suppression for famous faces then reflected the repetition of the same exemplar recognition process. However, if one assumes that a single presentation of an (undergraded) unfamiliar face is at least sufficient to begin the formation of a new perceptual representation (Section 4.4), then the repetition enhancement for unfamiliar faces reflected an exemplar recognition process occuring on repeated but not initial presentations (this new perceptual representation would be sufficient at least to detect that the face was seen before, even though it may not have the same status as representations of famous faces).

The assumption that initial presentations of unfamiliar stimuli can, under some conditions, form a new structural representation is consistent with the PRS hypothesis of Schacter (1990) mentioned in Section 4.4. Indeed, the above explanation can also be extended to the Schacter et al. (1995) study, if one assumes that object recognition (and hence fusiform activation) is only possible for 2D drawings for which a 3D representation can be formed. Impossible objects therefore do not activate the fusiform and hence do not show fusiform repetition effects. Initial exposure to a 2D drawing of a possible object however may be sufficient to form a new 3D representation that allows exemplar-level recognition when that drawing is repeated, producing repetition enhancement (analogous to unfamiliar faces). Note, however, that repetition enhancement has not always been found in fusiform cortex for unfamiliar stimuli such as faces (Henson et al., 2002) or possible objects (Section 4.3, e.g. Vuilleumier et al., 2002). This may reflect additional sensitivity of repetition effects to the task (Henson et al., 2002) or the repetition lag (Henson et al., 2000; Section 4.6).

In summary, a few imaging studies have reported repetition enhancement in indirect memory tasks. These findings may be explained by the simple hypothesis that repetition suppression occurs whenever the same process is performed on prime and target, whereas repetition enhancement occurs whenever priming causes a new process to occur on the target that did not occur on the prime. Note that, if this account is correct, it also means that the (common) association of implicit memory with repetition suppression, and explicit memory with repetition enhancement, is too simplistic; both increases and decreases associated with stimulus repetition might reflect either implicit or explicit memory processes.

4.6. *Longevity of priming effects*

Some priming effects are long-lived, lasting at least a year in the case of object-naming latencies for example (Cave, 1997). Other priming effects are only short-lived, sometimes not surviving an intervening item, as is typical of masked priming (see Section 3.4). The longevity of priming is likely to depend on the nature of the component processes involved, and will thus vary across stimuli and tasks (Bentin and Moscovitch, 1988). The facilitation of processes that are engaged frequently (such as early stages of visual object processing for example) may be less noticeable with the passage of time, given that stimulus-specific effects are likely to be attenuated by similar processing of intervening stimuli.

The issue of repetition lag (the interval between prime and target) is relevant to the use repetition suppression as a tool because some studies have used immediate repetition (with no intervening stimuli, e.g. Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2000), whereas others have used long-lag repetitions (with many intervening items, e.g. Koutstaal et al., 2001; Vuilleumier et al., 2002). Such procedural differences may cause discrepancies in their conclusions. Immediate repetition, in particular, may be a special case (Bentin and Moscovitch, 1988; Humphreys et al., 1988; Nagy and Rugg, 1989), potentially including, for example, the influence of a visual iconic store. It may even have different underlying neural mechanisms, reflecting short-term rather than long-term potentiation (LTP) of synapses.

A few imaging studies have explored the effect of repetition lag. The fusiform repetition suppression and enhancement in the Henson et al. (2000) study, for example, were found to attenuate with the lag between repetitions (which ranged from approximately 10 s to 20 min, or from 2 to approximately 140 intervening stimuli). It was not possible to distinguish whether this lag effect reflected passive decay with time, or active interference from intervening stimuli. Henson et al. (in preparation) presented a sequence of pictures of everyday objects, one every few seconds, in which some pictures were repeated immediately, some after one intervening picture (“short” lags) and some after tens of intervening pictures (“long” lags). The longevity of repetition suppression within inferior occipital/temporal cortices tended to increase from posterior to anterior regions (though with exceptions). Furthermore, the addition of a single intervening picture appeared to have a greater effect than a doubling of the interstimulus interval associated with an immediate repetition, suggesting that interference may be a more important factor than time (at least for such short lags).

A study by van Turennout et al. (2000) examined short lag (30 s) and long-lag (3 days) priming of object naming under conditions that were unlikely to differ in terms of intervening stimuli (line-drawings). Priming was larger after 30 s (137 ms) than after 3 days (54 ms). In a covert naming version performed during fMRI, repetition suppression was observed in bilateral occipitotemporal regions (including fusiform) and a left inferior frontal region, for both short- and long lags. This suggests that some priming-related neural changes can last several days. Though direct, voxel-wise comparisons of the two lags were not reported, the spatial extent of the occipitotemporal decreases appeared less for the long-lag condition, mirroring the behavioural priming effects. (Repetition suppression was also observed for nonsense objects in occipital, but not fusiform, regions, even though such stimuli could not be named, consistent with the occipital repetition suppression for both familiar and unfamiliar faces found by Henson et al. (2002).) Interestingly, the magnitude of the left inferior frontal repetition suppression for real objects was greater for the long than short lag. Turennout et al. suggested that this time-dependent change reflected the strengthening of links between novel pictorial representations in occipitotemporal cortex and their lexical representation (the object name) in inferior frontal cortex, and that this strengthening takes time (i.e. more than 30 s) to become established. A lag effect was also seen in a left insula region, which showed repetition enhancement that increased with lag. This reciprocal relationship between inferior frontal and insula regions could reflect direct inhibitory or competitive interactions. More generally, these data reinforce the possibility of multiple mechanisms associated with priming, operating over different timescales.

4.7. *Semantic priming*

The use of priming as a tool is beginning to be applied to imaging studies of the language system, in particular the lexcial-semantic system. The case of “semantic priming”, in which a response to a stimulus is facilitated when preceded by a semantically-related stimulus, tends to be restricted to short-term priming (though for evidence of longer-term semantic priming following extensive semantic processing, see Becker et al., 1997). At least two potential contributions to short-term semantic priming have been proposed: automatic spreading of activation in a semantic network (Collins and Loftus, 1975) and strategic/attentional effects (Posner and Snyder, 1975).

Strategic effects are assumed to increase as the proportion of related prime-target pairs increases (Neely, 1991). Mummery et al. (1999) used this manipulation in a PET study of semantic priming within a lexical decision task. The target for lexical decision was immediately preceded by a related or unrelated prime (presented for 50 ms). Across scans, the proportion of related pairs varied from 0 to 100%. There was a trend for priming to increase (up to 90 ms) as the proportion of related prime-target pairs increased, consistent with a contribution of strategic effects. Two regions were identified that covaried with the proportion of related pairs: left anterior temporal lobe (BA 38) and anterior cingulate. Both regions showed response decreases as the proportion of related pairs increased, though the anterior temporal region showed an apparent increase from 75 to 100% related pairs. The anterior cingulate decrease (which was particularly large for the 100% condition) was interpreted as the task becoming more routine as the strategic expectation of relatedness increased. The more complex anterior temporal pattern is difficult to interpret unambiguously, but might reflect a combination of automatic processes (producing the decrease) and a strategic effect at the highest proportion of related pairs (producing the increase). Such interpretations are particularly difficult to make on the basis of blocked designs.

Automatic processes in semantic priming are also assumed to dominate at short prime-target SOAs (<250 ms), whereas strategic effects are assumed to become more important at longer SOAs (Neely, 1991). Rossell et al. (2003) used event-related fMRI to compare prime-target SOAs of 200 ms versus 1000 ms in a lexical decision task. The only region showing repetition suppression was in left anterior temporal cortex, close to that observed by Mummery et al., for both short and long SOAs. The size of this reduction did not interact with SOA however, leaving its precise role in terms of automatic versus strategic processing unclear. Interestingly, an ERP experiment performed under the same conditions did show a difference between the short and long SOA conditions, with the priming effect onsetting 60 ms earlier for the long SOA. It is possible that the strategic contribution to semantic priming affects the latency rather than magnitude of neural activity in anterior temporal regions, which is beyond the temporal resolution of typical event-related fMRI experiments (see Section 5.3). It must also be remembered that, with such SOAs, the event-related haemodynamic response is still an aggregate response to both the prime and target, so that repetition effects could reflect differences in the processing of the prime.

An event-related fMRI study by Kotz et al. (2002) examined prime-target pairs that were either categorically-related (e.g. “duck”–“chicken”), based on word-meanings, or associatively-related (e.g. “coat”–“rack”), based on word-usage. An auditory lexical decision task revealed priming in both cases, with SOAs and relatedness proportions conducive of automatic priming. A main effect of priming was found in several regions within the left inferior frontal gyrus, and in a posterior middle temporal region (a restricted field of view may have prevented detection of priming effects in the anterior temporal regions of Mummery et al., 1999). The frontal regions exhibited a reduced response for primed versus unprimed words, close to those showing repetition suppression in the long-lag semantic decision tasks described in Section 3.2. The posterior temporal region however showed an enhanced response for primed words. This pattern may reflect selection processes in inferior frontal regions that operate over semantic information retrieved from temporal regions (Section 3.2). Greater responses to categorically than associatively primed targets were found in posterior medial parietal/cingulate regions, though interpretation for these regions is less clear. Given that the primes were not subliminal in this or the Rossell et al. (2003) study, one possibility is that some of the haemodynamic repetition effects reflect conscious evaluation of the prime-target relationship, subsequent and independent of the behavioural response to the target.

In summary, imaging studies are beginning to use priming as a tool to investigate language systems, at least at the level of lexical-semantics. Future imaging studies are likely to investigate prime-target relationships in terms of, for example, orthography, phonology and morphology. They may also consider using masked priming, or long-term repetition priming.

5. Priming as a model domain

A potential neural analogue of the repetition suppression observed with fMRI and PET is the phenomenon of “response suppression” (Desimone, 1996) or “decremental responses” (Brown and Xiang, 1998). These terms refer to a decrease in the firing rate of neurons, typically recorded in inferior temporal regions of the non-human primate, on repetition of a stimulus. The decreased firing rate is not non-specific habituation, because it occurs after a single exposure to a stimulus, and does not affect the firing rate to other stimuli for which the neuron is responsive. Moreover, it can last hours/days and across numerous intervening stimuli, though its lifetime tends to decrease from anterior to posterior regions (e.g. 24 h in perirhinal cortex, 10 min in area TE, but often not surviving a single intervening stimulus in occipitotemporal cortex, Brown and Xiang, 1998).

5.1. Sharpening theory

Based on the ideas of Desimone (1996), Wiggs and Martin (1998) extrapolated the neural phenomenon of response

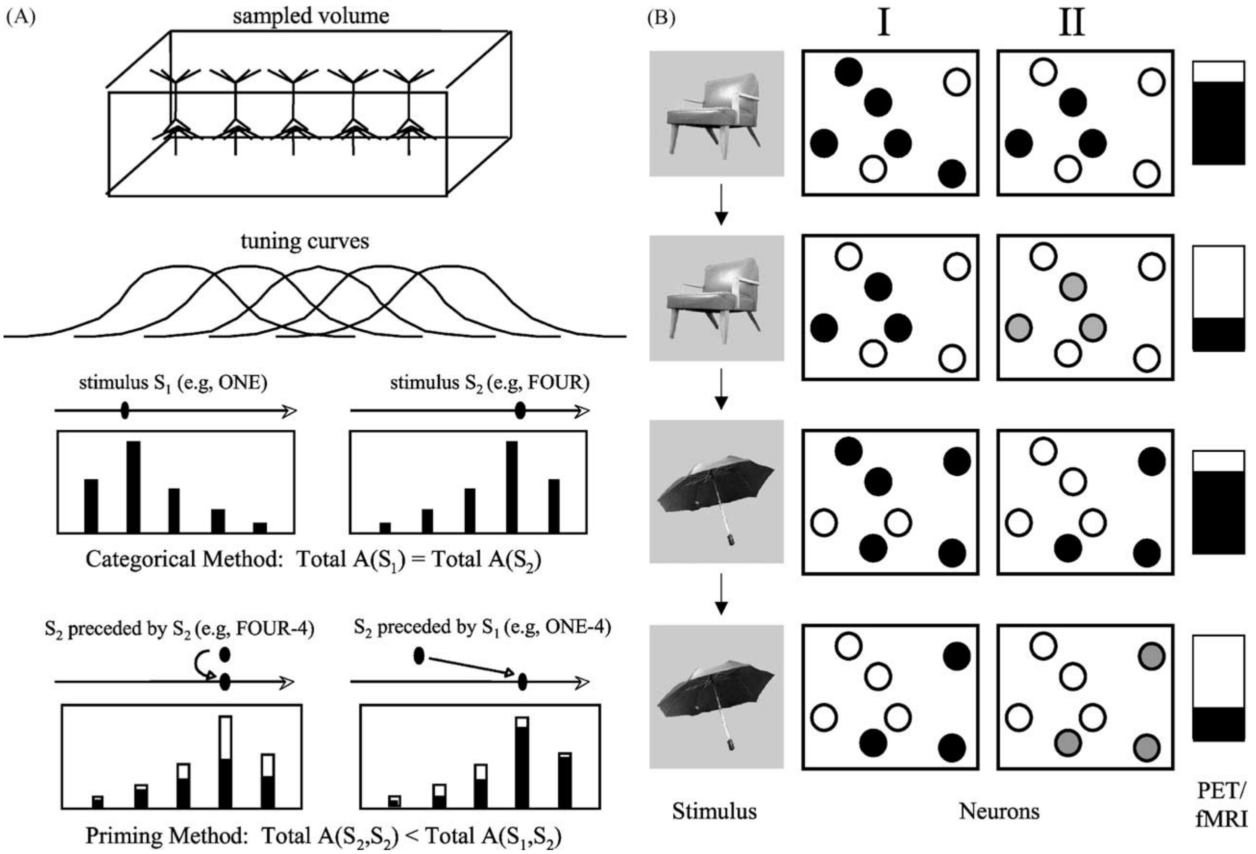

Fig. 6. (A) Schematic of "hyper-resolution" afforded by fMR adaptation (modified from figure provided by Stan Dehaene). (B) Schematic of the "sharpening" theory (I) and fMR adaptation (II) for a sequence of objects (leftmost column), the number of responsive neurons (middle columns, higher firing rates with darker grey levels) and the magnitude of the expected haemodynamic response (rightmost column). See text for more details.

suppression to human imaging findings on perceptual priming. They proposed that repeated processing of a stimulus produces a "sharpening" of its cortical representation, whereby neurons coding features unnecessary for processing that stimulus respond less (exhibit response suppression), which results in a decrease in the mean firing rate of a population of neurons, hence a decrease in the haemodynamic response from that region of cortex (Fig. 6B(I)). This "sparser" representation was then proposed to allow faster/more accurate behavioural responses.

Note that this "sharpening theory" is a slightly different conception of the neural basis often assumed for fMR adaptation (Section 4.1; Fig. 6B(II)). In the former case, the stimulus is assumed to be coded by the neurons that continue to fire vigorously (i.e. do not exhibit response suppression); whereas in the latter case, it is the neurons that show reductions in their firing rates that are assumed to code the stimulus. Moreover, neurons that show response suppression in the sharpening theory can show normal firing rates when a different stimulus is presented (i.e. the neurons themselves are not adapted). In other words, the firing rate reductions in the sharpening theory are stimulus-specific, whereas those in the adaptation theory are neuron-specific. The question of whether response suppression or adaptation is responsible for haemodynamic repetition effects may depend on the repetition lag (Section 4.1).

Though offering an attractive link between different levels of neuroscience, there are potential problems with the sharpening theory. Firstly, the association of neuronal response suppression with behavioural priming is yet to be established, since priming is not normally measured in non-human primate studies (though see Rainer and Miller, 2000). Indeed, the same neural phenomenon (at least in perirhinal regions) has been interpreted in terms of explicit, recognition memory (Brown and Xiang, 1998). The same phenomenon may signal different things in different brain regions (Habib, 2001). Secondly, no mechanistic account is offered as to why sparser representations necessarily allow faster/more efficient processing of stimuli. How a sparse (or distributed) representation affects the speed with which a neural network can recognise a stimulus would appear to depend on the dynamics of the network. Thirdly, the occipitotemporal regions that have been implicated in human perceptual priming lasting minutes/multiple intervening stimuli (Section 4.6) generally show only a limited duration of response suppression in the non-human primate (Baylis and Rolls, 1987). Fourthly, the "sharpening" theory would appear unable to explain the repetition enhancement discussed in Section 4.5. In the case of stimulus familiarity for example (Section 4.4), the theory would seem to predict a greater response decrease for unfamiliar than familiar stimuli (since the latter are likely to have already converged on sparse representations, Li et al., 1993), contrary at least to haemodynamic face repetition effects observed in the fusiform (Henson et al., 2000), a likely candidate for the locus of such representations. Another potential puzzle concerns the effect of the cholinergic drug scopolamine on haemodynamic repetition effects (Thiel et al., 2001), but not neural response suppression (Miller and Desimone, 1993). Finally, Wiggs and Martin state that "sharpening" happens automatically in the cortex. If such perceptual learning were automatic, repetition suppression might be expected regardless of the specific cognitive task, and yet studies have shown that repetition-related responses in perceptual regions do vary with the task (Section 3.3). None of these issues necessarily refutes the "sharpening" theory, but they do suggest that it is insufficient to account for the range of priming-related effects across space, time and task (see Henson and Rugg, 2002, for further discussion).

5.2. *Limitations of haemodynamic techniques*

There are also issues regarding the physiological relationship between the action potentials recorded from single-neurons and the haemodynamic changes observed with PET and fMRI. For example, the blood oxygenation level dependent signal measured by fMRI appears to correlate better with local field potentials than action potentials (Logothetis et al., 2001), raising the logical possibility of decreased rates of action potentials leaving a region from long-range excitatory neurons (for which electrode recordings tend to be biased) to be accompanied by an *increased* haemodynamic response within that region by virtue of increased pre-synaptic activity from short-range inhibitory interneurons. Note also that repetition effects are normally measured in terms of the neural dynamics that are time-locked to stimulus presentation, yet changes in those dynamics are most probably the consequence of synaptic changes. In other words, synaptic changes are likely to be the "real" cause of long-term priming. Synaptic changes (e.g. long-term potentiation) are likely to occur over protracted periods during the interval between the prime and target, and so are not directly observable in typical PET or fMRI experiments.

Furthermore, even with event-related fMRI, it must be remembered that the haemodynamic response effectively integrates over several seconds of neural/synaptic activity. One consequence of this is that a decrease in the magnitude of the haemodynamic response may arise from a shortened duration of neural/synaptic activity, without any necessary change in instantaneous firing rates. Henson and Rugg (2001) found that repetition of famous faces not only decreased the peak magnitude of the event-related haemodynamic response in a right fusiform region, but also its peak latency (though not onset latency), by approximately 240 ms. The most parsimonious account of this combined change in response magnitude and latency is that repetition reduced the duration of underlying neural/synaptic activity (assuming a linear convolution model of the relationship between neural/synaptic activity and fMRI signal, though non-linearities in the fMRI signal, e.g. Vazquez and Noll, 1998, suggest such a reverse inference may not be so simple). The relevance of this observation is that it raises at least one alternative neural mechanism of priming, namely a decreased "settling" time in attractor neural networks following synaptic-changes associated with processing of the prime (e.g. Becker et al., 1997).

Finally, there is the question of whether the haemodynamic correlates of priming are the cause or effect of behavioural priming. Repetition suppression observed in occipital regions might, for example, simply be a consequence of reduced looking times or diminished attention to a primed visual stimulus. In other words, such changes might be the effect rather than cause of the behavioural priming (the cause arising elsewhere in the brain). It is noteworthy in this context that repetition effects, associated with faster reaction times for example, are not normally observed in early sensory regions or late motor regions (Section 2.2), yet effects of visual attention have been observed in regions as early as V1 (Gandhi et al., 1999), and if haemodynamic changes were a simple function of reaction time, one might expect the largest effects in motor regions. Nonetheless, the question of cause and effect cannot be fully resolved with correlational techniques such as fMRI and PET. Such inferences require evidence from other techniques, such as priming-related deficits in patients with lesions to corresponding brain regions (Gabrieli, 1998), or following temporary disruption of those regions using transcranial magnetic stimulation (TMS). Alternatively, one could use haemodynamic data to help localise extracranial electrophysiological (MEG/EEG) effects (see Section 5.3), and argue for cause or effect on the basis of temporal precedence in the time course of repetition effects inferred in a given region.

5.3. *Latency of priming effects*

A final question concerns the onset latency of repetition effects. Neural response suppression is rapid, with an onset latency in perirhinal neurons that equals their visual response latency (70–80 ms), and estimates of the mean population latency as short as 150 ms (Ringo, 1996). These estimates have been used to argue that response suppression (even in anterior temporal regions) is too fast for "top-down" influences (Brown and Xiang, 1998). However, these latencies are considerably shorter than the latencies of priming-related effects measured with ERPs in humans, which typically onset 250–300 ms (Rugg and Doyle, 1994) (effects onsetting 100–150 ms have been reported, but usually for immediate repetition, Nagy and Rugg, 1989, though see George et al., 1997; Tsivilis et al., 2001, for exceptions). Human intracranial ERPs recordings in inferior temporal regions for example show early object-specific (e.g. face-specific) potentials, onsetting 150–200 ms post-stimulus, but little evidence that these potentials are sensitive to prior experience with the objects; such effects only emerge 250–300 ms post-stimulus (Puce et al., 1999). These ERP data therefore raise the possibility that repetition effects in humans involve later (e.g. re-entrant) effects. Indeed, in an exciting study that used fMRI data to constrain the source of MEG repetition effects in a semantic decision task to words, Dale et al. (2000) inferred that an initial wave of activity had spread to temporal, parietal and frontal regions by 185 ms. The earliest repetition effect however emerged in a left anterior inferior temporal region at 250 ms, and was strongest at 385 ms. Furthermore, a second peak in the repetition effect emerged in these regions at 540 ms post-stimulus, raising the possibility of multiple, temporally-separated priming effects, which will simply be averaged by haemodynamic techniques.

These data reinforce the possibility that priming effects do not necessarily arise in a "first-pass" through the neural circuitry, and that effects in posterior regions may include "top-down" influences from more anterior (e.g. frontal) regions. In other words, priming may not arise during the initial volley of "sensory" potentials. One possibility is that repetition effects in a region reflect changes in the prediction error fed-back from higher levels in a processing pathway (Friston, 2002). According to this model, stimulus processing modifies the strengths of recurrent synaptic connections between different levels of a neural hierarchy, which in turn affect the dynamics of each level in settling on an interpretation (e.g. recognition) of a stimulus. In the case of repetition suppression, an increase in the synaptic efficacy of feedforward and feedback connections between two layers, following initial presentation of a stimulus, decreases the error in the lower-level between its bottom-up (stimulus-related) and top-down (prediction-related) inputs when that stimulus is repeated. This reduced error may result in more rapid stimulus recognition, and a reduced haemodynamic response in the lower region. An important perspective offered by this model is that priming reflects interactions between different brain regions (and so is not necessarily "localised" at any one region).

In summary, simple experiments on stimulus repetition, using comparable stimuli such as visual objects or faces, offer an attractive domain within which to compare neurophysiological data in the human and non-human primate. There are certainly parallels in the sense of response reductions following repetition. Some theories, particularly the "sharpening" theory of Wiggs and Martin (1998), have tried to make the reasons for these parallels more explicit. This is certainly a worthy endeavour. However, several issues concerning the precise relationship between neural firing rates, haemodynamic changes and behaviour still need to be resolved.

6. Conclusions

Three main reasons were given for an interest in functional imaging studies of priming. In each case, imaging studies are only just beginning to untangle the interpretational issues surrounding the observed haemodynamic repetition effects. Preliminary conclusions regarding each case are discussed below, together with recommendations for future imaging studies. First however, a general picture of the neural bases of priming is rehearsed.

Priming effects are likely to arise from the same neocortical regions that are responsible for perceptual/conceptual processing of stimuli in a given task (with the presumed exception of medial temporal lobe regions, which may be specialised for explicit memory). This "neural" component process view acknowledges the difficulty of generalising across priming effects: behavioural priming may not be a consequence of any one specialised (implicit) memory system, but depend on the multiple processes engaged by the specific stimuli and task, and therefore requires detailed task-analysis (Tenpenny and Shoben, 1992; Vaidya et al., 1997). Nonetheless, the component process view allows for the possibility that some processes make the dominant contributions to behavioural priming effects, and that these processes may be common to several types of indirect memory tests. Neuroimaging offers a novel means by which to identify these "key" processes, which complements behavioural approaches to the same problem. If repetition effects are consistently observed in a certain brain region across different indirect memory tests (e.g. left anterior inferior frontal cortex in tests involving semantic decisions), and the same region is implicated in a particular process by other non-priming studies (e.g. comparisons of semantic versus non-semantic judgments), then the common anatomical basis supports that process playing an important role in the behavioural priming effect. That is, it is a process particularly prone to facilitation when it has been engaged in the recent past. Note that, though neuroimaging may aid the identification of the key component processes in various priming effects, it does not address the question of *why* some processes can be primed, but others can not. Moreover, though convergent evidence may implicate a region in a general type of process, the presence of item-specific priming effects would seem to necessitate item-specific representations or sub-processes within that region. There is also a need to relate repetition effects to other types of implicit memory, in particular, skill-learning (or "procedural memory"), given that it has been suggested that they share common mechanisms (Logan, 1990) and neural bases (Poldrack and Gabrieli, 2001). These remain important questions for theoretical accounts of priming.

6.1. *Priming as a memory phenomenon*

Researchers with an interest in implicit memory require concurrent behavioural measures of priming in order to make contact with the psychological literature, and to compare their imaging results with the brain regions intact or damaged in patients showing normal or impaired priming. Moreover, such researchers must address the recurring issue of explicit memory contamination. Surprisingly, few of the studies reviewed in Section 3 have addressed this question satisfactorily. This prompts the specification of a number of desirable features in the design of priming studies.

Ideally, explicit memory would be assessed concurrently with the priming measure on a trial-by-trial basis. For example, the indirect task assessing behavioural priming could be followed by a direct task (such as recognition memory), and priming trials restricted to those stimuli not recognised (Schott et al., 2002; Spencer et al., 2001). One problem with this approach is contamination between the two tests: there is always the danger that the initial indirect/direct test results in another exposure to the stimulus that affects the subsequent direct/indirect test (in addition to the unbiquitous problem of different response criteria and test sensitivities, Shanks and St. John, 1994). A related approach is to use a direct memory task (such as recognition), but focus on repeated stimuli that the participants miss, i.e. fail to identify as being presented previously. This approach has been used successfully with ERPs (Rugg et al., 1998), though it does not provide a concurrent behavioural measure of priming. One could even use neuroimaging data to test for explicit memory contamination, by looking for repetition effects in medial temporal regions, for example (a failure to detect such effects arguing against contamination, particularly if the medial temporal signal changes were large enough to be detected in the same experiment under a different condition associated with explicit memory retrieval).

Without a concurrent measure of explicit memory, steps should be taken to minimise explicit memory. For example, as long as the task performed on the prime engages processing to the level of interest, it should be kept as “shallow” as possible, to minimise encoding into explicit memory (Craik and Lockhart, 1972). Alternatively, a secondary manipulation can be introduced that is known to affect explicit encoding—such as the degree of semantic elaboration—and shown not to affect the degree of priming or its neural correlates (Schacter et al., 1989), as in the study of Badgaiyan et al. (2001) described in Section 3.1. Furthermore, behavioural responses to the primed stimulus should be speeded, in order to minimise contributions of explicit retrieval (though haemodynamic repetition effects could still reflect processes operating subsequent to the behavioural response, including incidental recollection of the prime). Explicit memory could also be reduced by administration of pharmacological agents known to impair explicit memory, as in the study of Thiel et al. (2001) described in Section 3.1. Alternatively, subliminal primes can be used to rule out explicit memory, though such priming effects may constitute a special case (see Section 3.4). A final and potentially important approach is to scan amnesiac patients in priming paradigms, for which explicit memory contamination of repetition effects could perhaps be more confidently ruled out (Buckner and Koutstaal, 1998).

Other desirable precautions include a switch in the task performed on prime and target, to minimise uninteresting response contingencies. Ideally, the task performed on the prime should be orthogonal to that performed on the target, such that the only component processes common to the two tasks are those of interest. Orthogonal response requirements also mean that, when responding to a target, there is no reason for participants to explicitly retrieve the response previously made to the prime. This will also minimise the establishment of direct stimulus-response mappings (Naccache and Dehaene, 2001b). Furthermore, response contingencies in the target task should be orthogonal to any stimulus manipulations (to avoid the confounds present when, for example, priming effects for familiar and unfamiliar stimuli are compared in a familiarity-judgment task; Section 4.4).

There are also priming paradigms that have yet to be studied with imaging techniques. Foremost is associative priming, in which decisions about a target are affected by whether it occurs in the same or different context as the prime (and which poses problems for modification theories of priming; Section 4.4). This form of priming is particularly interesting given that it has been claimed that medial temporal structures are necessary for binding together relational information (Chun and Phelps, 1999; Eichenbaum and Otto, 1992). If so, amnesiac patients might be expected to show impaired associative priming despite intact item-specific priming (Moscovitch et al., 1986; Musen and Squire, 1993). Contrary to this hypothesis, Goshen-Gottstein et al. (2000) used a simultaneous lexical decision task on two words to compare associative priming (when both words had been primed together) with item-specific priming (when both words were primed, but in different pairs), and found that associative priming was no smaller (in fact slightly bigger) in amnesiac patients than controls. These data are consistent with the hypothesis that the amnesiac deficit is one of explicit memory rather than of relational information per se (though see Yang et al., 2003). Thus, it would be interesting to test whether associative (but not item-specific) repetition effects are seen in medial temporal regions with neuroimaging (in situations where explicit memory contamination can be ruled out), and whether such priming generalises to associations across different types of information (e.g. verbal-spatial, Mayes et al., 2001). Another approach that may prove informative is to compare haemodynamic responses to primes as a function of the degree of subsequent priming, in other words to concentrate on processes occurring the first time a stimulus is processed (analogous to the subsequent memory paradigm used in studies of explicit memory, e.g. Wagner et al., 1999).

6.2. *Priming as a tool*

Section 4 illustrates that researchers have had considerable success in using repetition effects to make inferences about the brain regions associated with different stages of stimulus processing, particularly in the case of visual objects (applications to other domains, such as language processing, lag somewhat behind in this respect). Many of the potential problems of confounding factors such as explicit memory and differential attention are shared with studies of implicit memory discussed above, and would benefit from the same precautions. As suggested by Naccache and Dehaene (2001a), one powerful solution to many of these problems is the adoption of masked priming paradigms (Section 3.4). If participants can be shown not to be aware of the prime, there is no reason for differential attention or conscious memory for primed versus unprimed targets. Unlike the case for studies of implicit memory described in Section 6.1, it does not matter, in principle, that priming under these conditions may differ from priming for supraliminal stimuli. However, the generally small effect size of behavioural masked priming may be mirrored by problems of sensitivity in imaging studies. Moreover, the short-lived nature of masked priming means that imaging techniques cannot separate potentially complex interactions between processing of the prime and processing of the target (Section 4.7). Nonetheless, if masked priming is used only as a tool, these issues do not necessarily matter (a concurrent behavioural measure of priming is not even required), provided that haemodynamic repetition effects are detected.

One caution concerns the assumption, often implicit in studies of visual object priming, that repetition suppression is an obligatory consequence of stimulus presentation, so will not depend on the particular task used (i.e. that haemodyanmic changes reflect pure “bottom-up”, stimulus-driven responses). This may not be the case however, particularly given that haemodynamic response integrates over several seconds of neural activity (Section 5.2), so that, even if neural activity is initially reduced, this reduction may be swamped by subsequent “top-down” task-dependent effects. The presence of repetition suppression for familiar faces when using an indirect task, but not when using a direct task, even though the stimuli are equivalent (Henson et al., 2002), would lead to different inferences regarding the role of the fusiform cortex for example. This suggests that choice of task, particularly regarding the task-relevance of repetitions (e.g. Miller and Desimone, 1994; Jiang et al., 2000), should be considered as carefully as the stimulus manipulations themselves.

6.3. *Priming as a model*

The is a clear need to develop theories that relate the different types of data collected by neuroscientists, particularly single-cell recording data in the non-human primate and haemodynamic imaging data in the human. Priming is a potentially useful domain for this, and initial verbal theories have attempted to do so (Section 5). The next step is to develop computational models that make these relationships explicit. Several examples exist in the form of artificial neural networks that relate, for example, neural firing rates to the mean population response measured by haemodynamic techniques (Chawla et al., 1999), response suppression in inferior temporal neurons to explicit memory (Bogacz et al., 2001), response suppression to cholinergic manipulations (Sohal and Hasselmo, 2000), and network output or settling times to behavioural measures (Becker et al., 1997; Stark and McClelland, 2000). However, there would seem to be few models that simultaneously relate neuronal firing rates, synaptic plasticity, haemodynamic population measures, behavioural (and electrophysiological) measures of priming, and specific parts of the brain.

Further experimental data are also necessary, particularly data derived from concurrent measurement of neural and haemodynamic activity, as with monkey fMRI (Logothetis et al., 2001). This may be supplemented by pharmacological manipulations that modulate neural/synaptic activity, and so provide insights into the physiological mechanisms underlying haemodynamic repetition effects. Important methodological developments include the combination of haemodynamic techniques with EEG and MEG, as illustrated by the Dale et al. (2000) study described in Section 5.3. Such spatiotemporal “movies” of priming effects across the brain are likely to provide rich data for models of priming. This combination of different approaches and different imaging modalities promises an exciting future.

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