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Research Report

Behavioral, neuroimaging, and computational evidence for perceptual caching in repetition priming

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ABSTRACT

Repetition priming (RP) is a form of learning, whereby classification or identification performance is improved with item repetition. Various theories have been proposed to understand the basis of RP, including alterations in the representation of an object and associative stimulus–response bindings. There remain several aspects of RP that are still poorly understood, and it is unclear whether previous theories only apply to well-established object representations. This paper integrates behavioral, neuroimaging, and computational modeling experiments in a new RP study using novel objects. Behavioral and neuroimaging results were inconsistent with existing theories of RP, thus a new perceptual memory-based caching mechanism is formalized using computational modeling. The model instantiates a viable neural mechanism that not only accounts for the pattern seen in this experiment but also provides a plausible explanation for previous results that demonstrated residual priming after associative linkages were disrupted. Altogether, the current work helps advance our understanding of how brain utilizes repetition for faster information processing.

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1. Introduction

Repeated encounters of the same item facilitate faster information processing in the brain; as a result a person is able to respond sooner and more accurately. This facilitation is referred to as repetition priming (Roediger and McDermott, 1993; Tulving and Schacter, 1990; Schacter, 1987). Repetition priming has been widely used to study implicit memory—a form of learning that is reflected in the performance of a task without being dependent on conscious awareness of the previous experience (Schacter, 1987). Recent human studies have consistently elicited both behavioral and neural effects

of repetition priming, which includes reduction in response time and reduction in neural activity in specific cortical regions (Henson, 2003; Schacter and Buckner, 1998; Wiggs and Martin, 1998). Repetition-related reductions in single-unit recordings have also been identified in monkeys (Rainer and Miller, 2000). Despite a wealth of studies on repetition priming, there are still many open questions and there remains a lack of consensus on what neural mechanisms are directly responsible for behavioral performance gains.

Several mechanisms have been proposed to account for the performance gains in repetition priming. For example, it has been proposed that repeated presentations of an object could

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result in a “tuned” neural response (Wiggs and Martin, 1998), i.e., neurons that are not essential for object identification or retrieval of task-relevant object knowledge respond less intensely with repetition. Thus, the neural processing becomes more selective, and this “tuning” or sharpening results in a faster and more efficient response.

In a recent series of studies, it has been argued that if repetition priming reflects tuning of object knowledge, then the magnitude of priming should be unaffected by changes at the level of decision orientation (Dobbins et al., 2004; Schnyer et al., 2006). In one of these studies (Dobbins et al., 2004), participants were asked to make size judgments about visually presented objects (“is it bigger than a shoebox?”). After they were exposed to items either once or three times, the decision cue was inverted (“is it smaller than a shoebox?”), a manipulation that should not significantly alter the processes associated with item identification or access to item-related size knowledge. However, inverting the decision cue resulted in a significant disruption of behavioral facilitation, associated with repetitions, and a loss of repetition-related neural signal reductions in critical regions of prefrontal cortex and fusiform gyrus. This finding led to the conclusion that participants were learning their responses to items, and in doing so, they shifted from a resource-demanding analysis of specific object-size information to a more automatic stimulus-response-based strategy (Logan, 1990; Schacter et al., 2004).

Hence, a mechanism of response or decision learning (DL), whereby a particular response or decision becomes associated with an item through repetition, was proposed to account for the portion of observed priming gains that are specific to a particular decision orientation (Schnyer et al., 2006). The typical behavioral signatures of DL, as found in the literature (Dobbins et al., 2004; Schnyer et al., 2006; Horner and Henson, 2008; Race et al., 2008), include increasing reductions in response time with multiple repetitions, robust priming, and a significant disruption in priming gains as a result of inverting the decision cue. Neural signatures of DL include reduced cortical activity with repetitions in regions of left inferior prefrontal cortex (LIPC) and temporal regions, including the fusiform gyrus. Inverting the decision cue also significantly disrupted these neural reductions.

In another set of experiments, DL in amnesic patients, with damaged medial temporal lobe (MTL) structures, was examined (Schnyer et al., 2006). Since amnesic patients can access object knowledge, a tuning model would predict that greater priming should be observed across multiple repetitions. Although significant behavioral priming was observed in amnesic patients, i.e., reduction in response time with repetition, was found, there was no indication that multiple repetitions provide any further gains in facilitation. Further, inversion of the decision cue did not disrupt observed priming gains in these same patients. Altogether, the study indicated that amnesic patients lack the evidence for typical DL signatures, and this led to the conclusion that DL depends on an MTL-based learning mechanism.

Although DL has been demonstrated to be a critical component of repetition-related priming changes, several key issues remain unresolved and should be addressed to fully understand the underlying mechanisms of repetition priming:

1. Scope of decision learning: Previous research on decision learning in repetition priming has utilized commonly known objects or words, each of which have well-established

preexisting representations. Thus, the observed priming gains can be explained through a mechanism of DL, i.e., associating items with previous decisions, thereby bypassing intermediate stages of information retrieval and comparison (Fig. 1, curved solid arrow). However, it remains unclear whether such a linkage requires a preexisting representation or whether a similar association can be formed for novel, never before encountered, visual stimuli (Fig. 1, curved dashed arrow). The answer to this question will indicate the extent to which DL depends on well-structured object knowledge representations and whether the scope of DL could be extended to more flexible levels of automaticity.

2. Explanation for residual priming in healthy population: Although the priming gains associated with DL were significantly disrupted by inverting the decision cue, the response time for repeated items was still found to be significantly lower than for those that were shown for the first time. In addition, neural changes have been associated with these preserved advantages (Race et al., 2008). As previously indicated, such preserved priming may be due to changes at the stimulus level. It is unclear whether these changes rely on preexisting representations or would also be found in repetition of novel visual stimuli.
3. Explanation for intact priming in amnesic patients: DL signatures were not found in repetition priming in amnesic patients, but instead a different pattern of priming gains was observed. One possibility is that these gains are also due to changes in the stimulus level as described in no. 2 above. These changes need to be more clearly specified.

The currently available evidence suggests that repetition priming, even within a single task, may result from multiple mechanisms. This paper integrates behavioral, neuroimaging, and computational modeling experiments to build a more complete and plausible model of repetition priming. First, the dependence of DL on well-established representations was tested with a repetition priming experiment using novel 2-D objects. Any evidence found for DL across repetitions of novel objects would suggest that the systems form associations between transient visual representations and previous decisions. However, if such criterion is not found, it suggests that well-established representations are necessary for DL. Indeed, the results revealed that novel objects result in a short-lived priming effect both behaviorally and neurally and that multiple repetitions did not provide additional facilitations in response times. This pattern does not fit previous explanations based on DL or tuning theory. To test whether this result is only due to the novel stimuli and not due to the experimental design, a control behavioral experiment using common or well-known objects was implemented with the identical design as with novel objects. The results from this common object priming experiment clearly showed the previously demonstrated signatures of DL. Thus, to explain the short-lived priming and to account for the transient stimulus-level changes in case of novel objects, a perceptual memory-based caching system (PCS) is proposed. Behavioral and neuroimaging results reported in the paper support this formulation and establish the characteristic properties of PCS.

Second, to formalize and test this postulated caching mechanism, a computational model is developed. The model

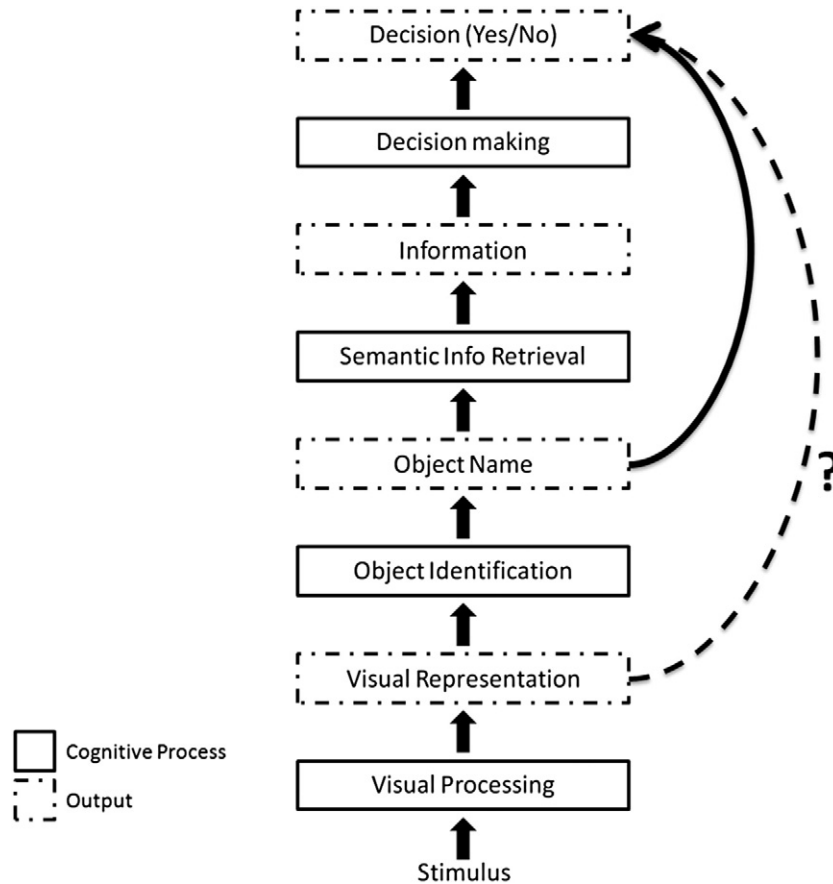


Fig. 1 – A series of cognitive steps required in a classification task with decision learning. When the stimulus is shown for the first time, visual representation is formed, due to initial visual processing. Based on that representation, memory-based search tries to identify the object, returning its name. Given that name, task related information is retrieved, like real-world size information (Schnyer et al., 2006), which in turn helps in comparison and decision making. Finally, a decision, like yes or no, is the output. However, during future encounters of the same visual stimuli, MTL-based decision-learning association (solid arrow) is used to bypass the information extraction and decision-making steps. In the case of common objects, these associations have been shown to account for significant portion of the observed priming gains (Schnyer et al., 2006). However, it is unclear whether similar associations in case of novel objects would develop (dashed arrow), since they lack well-established representations.

is further extended to examine priming using commonly known objects, thereby providing a plausible explanation for stimulus level priming effects such as those seen in case of cue inversion in the healthy population and in case of intact priming in amnesic patients. In addition, the model provides conclusive predictions to shape future research in this area.

Altogether, this paper makes the case for an explicit model for the phenomenon of perceptual memory-based caching and addresses the key issues to provide a more complete theory behind repetition priming.

2. Results

2.1. Behavioral and neuroimaging experiment using novel objects

Dependence of DL on well-established representations was tested by engaging participants in a perceptual classification task with simple 2-D novel objects (Slotnick and Schacter, 2004).

Participants were asked to make size judgments, indicating whether a viewed stimulus should be classified as “fat” (or “slim,” during cue-switching). The design of the experiment and a sample run are provided in Fig. 2. It is important to note here that the repetitions were distributed evenly throughout the run.

A schematic of the cognitive processes that an individual may engage in when making such decisions are shown in Fig. 3. When presented with a visual stimulus for the first time, initial visual processing activates a representation. Based on this representation, task-based perceptual information is extracted, like area or aspect ratio, as would be the case in the current experiment. Following information extraction, a decision is rendered. On successive encounters with the same stimulus, one of the three pathways can be implemented to provide a higher degree of automaticity, and thereby facilitate processing. For example, consider a situation where Pathway 1 is implemented. During successive encounters with the same stimulus, immediately after the perceptual information is extracted, Pathway 1 can activate previous decision made on that perceptual information and thereby bypass the decision-

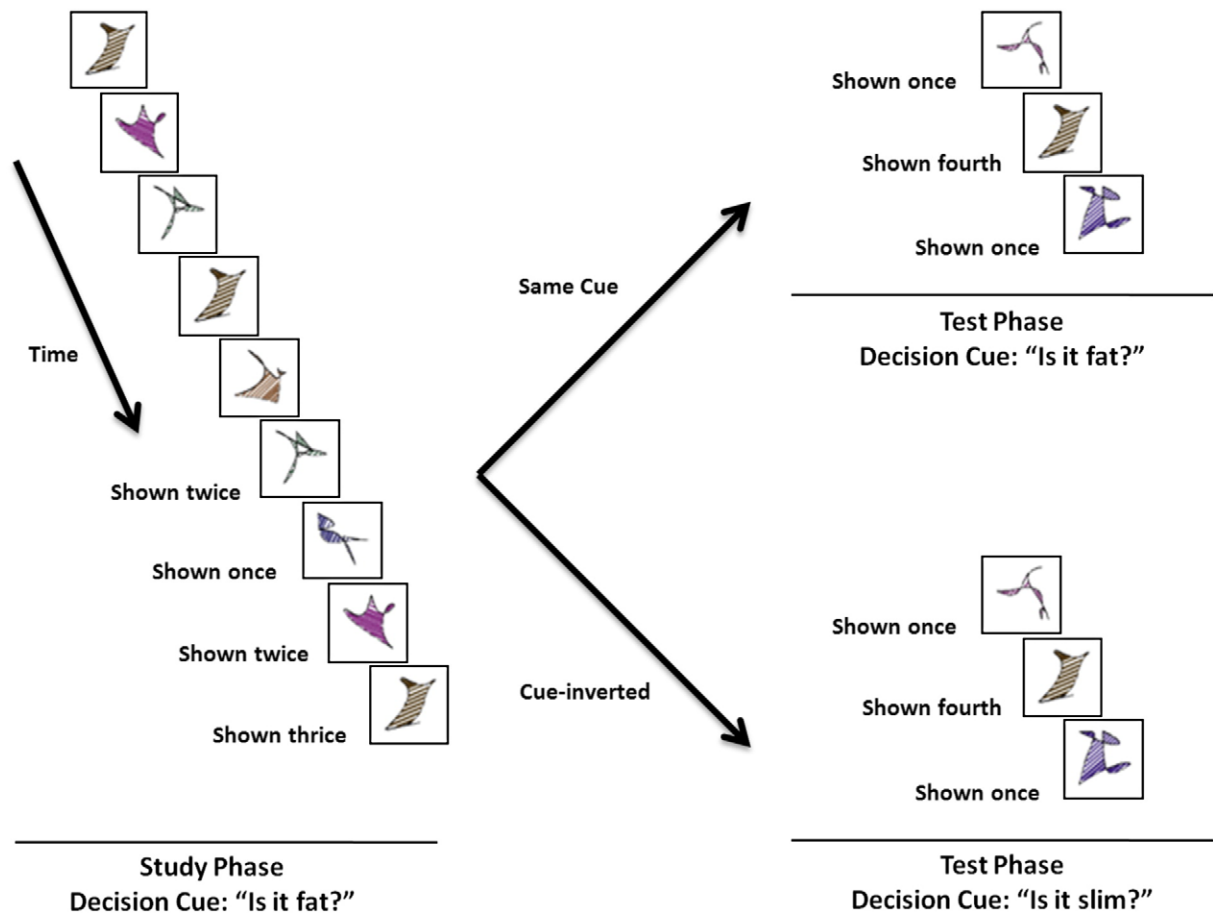


Fig. 2 – Experimental design for repetition priming using novel objects. The participants were shown a stimulus and asked to decide whether the shown stimulus is fat (or slim, during cue inversion). The experiment was divided into four runs; each run was further divided into two phases, a study phase and a test phase. Every study phase had a total of four conditions: no-prime (shown first-time, and repeated later; NPR), low-prime (shown second-time; LP), high-prime (shown third-time; HP) and no-prime items that were never repeated (NPNR). Each condition was presented 20 times. The test phase consisted of 20 high-prime trials from study phase (shown fourth-time; VHP) and 20 trials that were never shown before (NP). Each trial was shown for 3 seconds, except the null trials, where a blank screen was shown. The duration and location of null trials was determined by optseq2 (Dale et al., 1999; Dale, 1999), which generates optimal time and ordering sequences for event-related fMRI designs. The design was kept similar to previous studies of DL so that a fair comparison can be done.

making step. Further, Pathways 1 and 2 correspond to DL by associating previous decisions with either the extracted object knowledge information or a specific visual representation, respectively. On the other hand, additional pathways, such as Pathway 3, can bypass the perceptual information extraction step by linking visual representation with previously extracted perceptual information. This linkage can be achieved by a lower-level perceptual memory-based mechanism.

If, after repetition of novel objects, typical DL signatures are found, it can then be concluded that the priming gains observed likely reflect Pathway 1 or 2. Furthermore, we can conclude that DL does not depend on well-established representations. Alternatively, if DL signatures are not found but priming gains are still evident, then a mechanism similar to Pathway 3 may be responsible.

2.1.1. Behavioral data

Reaction times (RTs) were examined separately for the study phase and the test phase (with the same and inverted cue). In

the study phase, three conditions were included in the analysis: (1) items presented for the first time but repeated later (NPR), (2) the second presentation of an item or a low prime (LP), and (3) the third presentation of an item or a high prime (HP). A fourth condition, shown-once but never repeated (NPNR), was excluded from the analysis because items in this condition were not counterbalanced. These items were included in the study phase to avoid participant perception that all items would be repeated eventually. A repeated-measures ANOVA across the three included conditions revealed a significant effect of condition ($F[2,38]=9.101$, $p<0.0007$). Follow-up two-tailed, pairwise *t*-tests found significant priming between the stimulus shown once (NPR) and the LP items ($t(19)=3.5767$, $p<0.01$), between NPR and the HP items ($t(19)=3.5297$, $p<0.01$), and between NPR and primed (i.e., LP and HP) items ($t(19)=3.9643$, $p<0.01$). However, no difference was found between LP and HP items ($t(19)=-0.3857$, ns), suggesting that RT priming did not interact with the number of repetitions. Thus, repetition of novel items result in a single

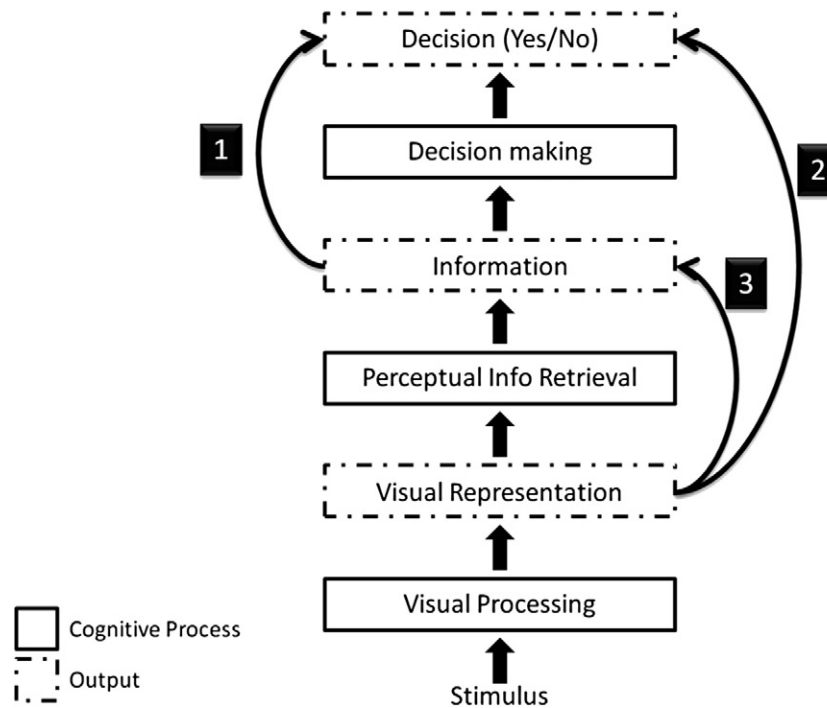


Fig. 3 – A series of cognitive steps required with novel objects. Based on the success of DL theory in explaining priming gains, with common objects, this figure represents three different pathways that could explain any performance gain that would be achieved in the presented experiment with novel objects. Pathways 1 and 2 show associating previous decision with extracted perceptual information, like area or aspect ratio, and visual representation, respectively. Thus, if the signatures of DL are observed, then it could be due to one of these two associations. However, if DL signatures are not found, then any priming gains observed in this experiment could be related to Pathway 3, which bypasses task-based perceptual information extraction during successive encounters of the same item. Further, the results of this experiment would provide characteristics of this previously hidden linkage.

stepwise reduction in reaction times that is not increased with additional repetitions (Fig. 4).

In contrast with the results in the study phase, in the test phase, a repeated-measures ANOVA with condition (fourth presentation (VHP) or shown once (NP)) and cue (same or reversed) revealed a significant effect of the decision cue ($F[1,19]=34.65$ and $p<0.00006$) but no effect of condition ($F[1,19]=0.88$ and $p<0.4$) or any interaction between cue and repetition ($F[1,19]=1.37$ and $p<0.3$; Fig. 4).

There was no evidence for a decision-same advantage or decision-switch cost during the test phase. However, one additional way to assess for evidence of DL would be to examine the response consistency across task switches. If the error rate increases significantly with cue switches relative to the same cues, then that would provide some evidence for memory of the previous decisions that was not revealed in RTs. To examine this question, correct classifications for any given item were computed by selecting the response that was selected by 85% or greater participants. This assessment was performed for the first presentation of repeated items during the study phase and then the test of response consistency was performed for the test phase only. Using repeated-measures ANOVA, with cue (same or switch) and condition (no-prime or fourth-presentation) as factors, the only significant finding was a main effect of cue ($F[1,19]=5.499$, $p<0.05$). The main

effect of condition and the interaction were not found to be significant (condition, $F[1,19]=0.073$, $p<0.8$ and cue \times condition, $F[1,19]=2.002$, $p<0.2$). The mean percentage of errors for the conditions was as follows, no-prime items (or NP): 10.68% in same-cue and 12.58% in switched-cue condition, and fourth-presentation items (or VHP): 8.47% in same-cue and 14.04% in switched-cue condition. Thus, this analysis supports only a nonspecific increase in error rates for the switch condition.

However, examining the between condition effects with a two-tailed paired t-test, it was found that the number of errors recorded for NP items was similar in both same- and switched-cue condition ($t(19)=-0.885$, $p<0.4$). However, the number of errors recorded for VHP items were significantly lower in the same-cue condition than in the switched-cue condition ($t(19)=-2.856$, $p<0.05$). This finding is a weak evidence for memory of decisions, associated with respective items, such that participants made more errors when classifying highly primed items during a cue-switch relative to a cue-same condition. However, in the current experiment, this signature of DL was weak and unreliable.

In sum, the commonly seen behavioral signatures of DL were not observed with the repetition of novel objects. Instead, a single stepwise reduction in response time was found, in the study phase that is relatively short-lived, as it did not transfer to the test phase.

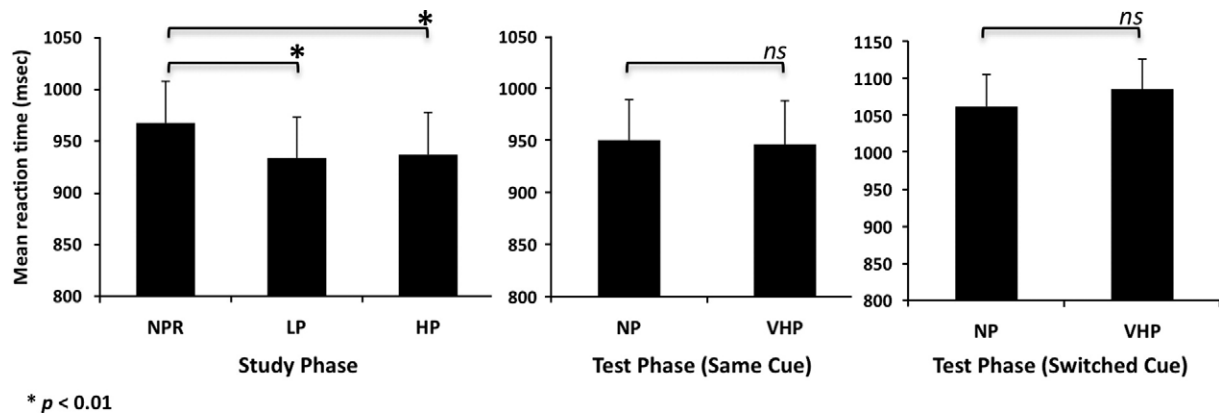


Fig. 4 – Behavioral results (experiment I). Reaction times in study and test phases (with and without cue inversion) in the novel object priming experiment. Significant priming was found only in the study phase, between shown-once (NPR) and primed conditions (LP and HP), and as a stepwise reduction. However, no significant difference in reaction times was found between stimuli that were shown once (NP) and those shown four times (VHP) in either the same cue or switched cue condition during the test phase. Further, overall increase in response time, in the phase, was evident with cue switching. This pattern of response facilitation does not fit the established characteristics of DL.

2.1.2. Functional imaging data

When the neural responses during the study phase for LP and HP items were compared to that of items that were shown once (NPR), reduced cortical activity was found in fusiform gyrus, superior parietal lobule, temporal–occipital cortex, and lateral occipital cortex regions. In addition, significant reductions in cortical activity were found in right inferior frontal gyrus for HP condition, i.e., items shown thrice, compared to NPR items (Fig. 5). Table 1 shows the neural regions where reduced activity was found during LP and HP conditions relative to NPR. (Z, Gaussianised T/F, statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = 0.05$; Worsley, 2001.)

During the test phase, there were reductions in cortical activity in the left lingual and occipital gyrus in cue-switch condition only, when corrections for multiple comparisons were applied. No cortical activity reductions were found during same-cue condition (Table 2). Examining the results of the test phase with a more liberal uncorrected statistical threshold ($p < 0.01$) revealed reductions, with NP > VHP, in occipital, temporal, and frontal gyrus during the same decision cue and in occipital, temporal, and parietal regions during the switched decision cue condition (Table 3).

In previous studies, the left prefrontal cortical regions were reliably found to reflect DL. In the current study, reduced activity, with priming, in the right inferior prefrontal cortex during the study phase and reduced activity in frontal gyrus, during same-cue condition in test phase, could potentially reflect weak DL.

To determine whether response time reductions correlate with the regional activity reductions, MR signal was extracted from specific regions of interest (ROIs). The regions that were focused on were those implicated in previous priming studies (Dobbins et al., 2004) that demonstrated reduction in cortical activity with repetitions, namely the prefrontal cortex and ventral–temporal cortex—in particular, the fusiform gyrus. As shown in Fig. 6, in the study phase, significant reductions

(two-tailed pairwise t-tests) in the cortical activity for primed items relative to items shown for the first time were found in both right inferior frontal ($t(3) = 3.580$, $p < 0.05$) and bilateral occipital–fusiform gyrus ($t(3) = 3.693$, $p < 0.05$). Both ROIs depicted a similar pattern of stepwise reduction as found in behavioral response time data. Further, significant correlations were also found between the mean MR signal from ROIs and the response time data ($r = 0.577$, $p < 0.05$ for right inferior frontal and $r = 0.504$, $p < 0.05$ for bilateral occipital–fusiform gyrus).

Only weak priming was seen in the test phase, both in the behavioral and neuroimaging results. This result contrasts with priming studies using familiar stimuli. There are a number of possible explanations including the possibility of interference between novel objects and temporal decay of activation with time. To investigate temporal decay, reductions in reaction time associated with repetition were examined with respect to the distance from the first presentation (NPR) of an item. Distance was measured in terms of the number of items between the NPR and the specific priming condition. The results in the study phase indicate that reduction in RT after the second presentation (LP) and the distance between the first and second presentations follows a log relationship ($F = 5.473$, $p < 0.05$). Thus, as the distance between the presentations is increased, priming gains were reduced, i.e., reduction in RT was lower, until the gains die-off after a distance of about 15 items or so (Fig. 7). Furthermore, while not significant, a similar relationship was found between NPR and HP items ($F = 1.699$, $p < 0.2$). This log relation provides evidence for a relatively rapid temporal decay of priming effects for these novel objects, which no doubt is the basis of the lack of significant RT priming effects in the test phase.

Overall, behavioral and functional neuroimaging revealed relatively weak and short lived repetition-related effects during the study phase, while there were no reliable priming changes that continued into the test phase. Also, the behavioral facilitation that was evident with repetition did

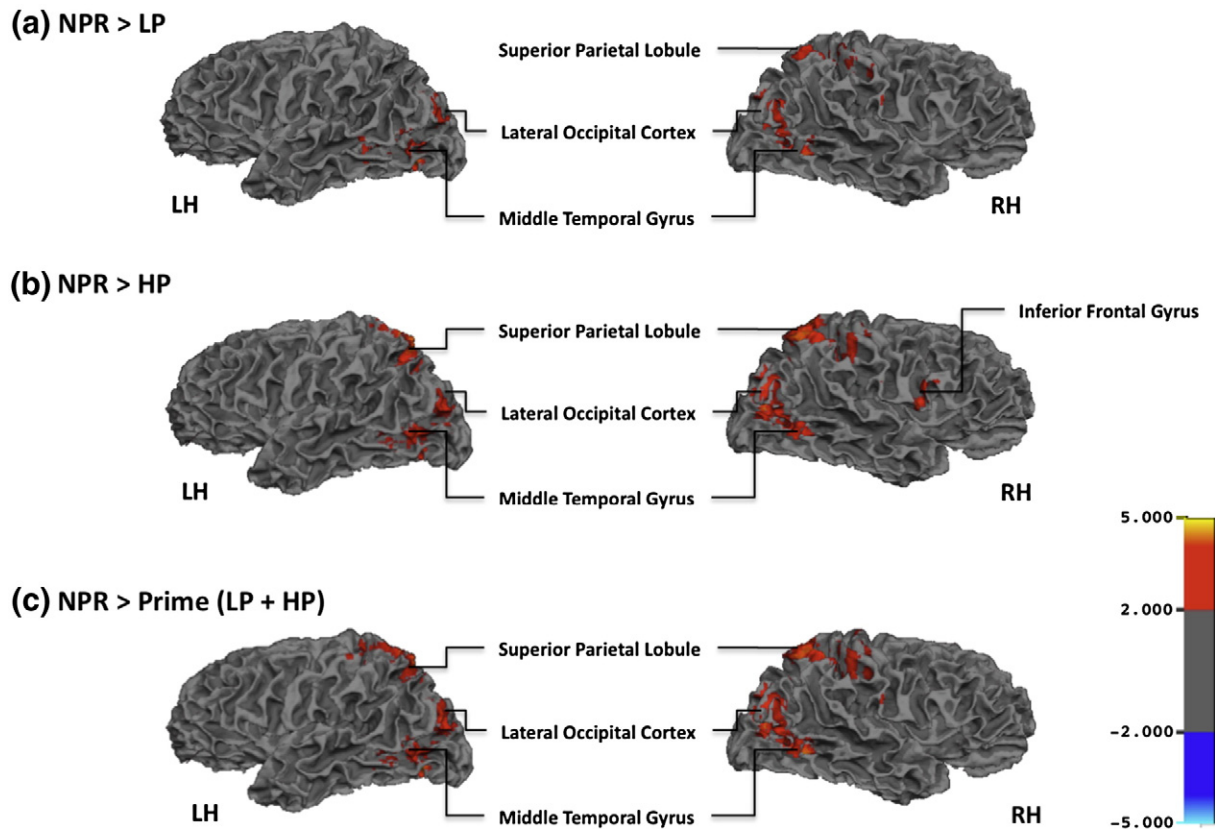


Fig. 5 – Functional neuroimaging results (experiment I). Significant comparisons were found in the study phase. Regions revealed by comparing conditions, where the stimulus was shown only once (NPR) and shown (a) twice (LP), (b) thrice (HP), and (c) average of LP and HP, are shown. Repetition related reductions in cortical activity were found in superior parietal lobule, lateral occipital, temporal–occipital–fusiform cortex, and medial temporal regions. In addition to reductions found in regions revealed by (a), reduced cortical activity was also found in right inferior frontal gyrus when NPR was compared with HP items.

not gain additional benefit from multiple repetitions in the study phase. These two results are not consistent with a DL mechanism being responsible for RP with novel objects. This suggests that well-established representations are required for DL. It is possible that given DL is reliant on an episodic memory-based association system, such a system would be overwhelmed by multiple novel objects that are highly similar. Given lack of evidence for DL in this novel object priming experiment and the fact that previous experiments examining DL in common objects did not utilize exactly the same parameters of experimental design, a behavioral experiment was conducted to demonstrate the nature of DL in this design for common objects.

2.2. Behavioral experiment using non-novel or common objects

To examine the pattern of DL with common objects, a control experiment was conducted where the design was kept exactly identical to the previous experiment using novel objects. The only difference was the stimulus material. In this task, a different set of participants were engaged in a classification task using common objects or well-known objects (as used in Schnyer et al., 2006). Participants were 12 young adults (mean age = 18.5 years, 6 females) and were asked to make size judgments, indicating

whether a viewed stimulus should be classified as “bigger” than a shoebox (or “smaller” than a shoebox, during cue-switching).

If, after repetition of common objects, typical DL signatures are found, it can then be concluded that the priming gains observed are likely due to the stimulus material employed. Furthermore, it can be concluded that lack of DL in case of novel objects should also be due to the stimulus material and not due to the design of the experiment.

2.2.1. Behavioral data

Reaction times were examined separately for the study phase and the test phase (with the same and inverted cue). In the study phase, three conditions were included in the analysis: (1) items presented for the first time but repeated later (NPR), (2) the second presentation of an item, or a low prime (LP), and (3) the third presentation of an item, or a high prime (HP). A fourth condition, shown-once but never repeated (NPNR) was excluded from the analysis. These items were included in the study phase to avoid participant perception that all items would be repeated eventually. A repeated-measures ANOVA with condition as a within-subjects factor, revealed a significant effect of condition ($F[2,22]=98.89, p<0.0001$). Follow-up two-tailed, pairwise *t*-tests found significant priming between the stimulus shown once (NPR) and the LP items ($t(11)=10.458, p<0.0001$), between NPR and the HP items ($t(11)=12.144,$

Table 1 – Regions where reduced cortical activity (cluster-corrected) was found in study phase with priming. Table shows Brodmann area (BA) and Talairach coordinates (x, y, and z).

Region	BA	x	y	z
<i>(a) NPR > LP</i>				
Right cerebellum culmen	*	21.51	-49.7	-12.51
Left cerebellum culmen	*	-20.16	-51.58	-7.46
Left cerebellum declive	*	-27.79	-70.24	-12.34
Right fusiform gyrus	19	25.25	-59.45	-9.5
Left fusiform gyrus	37	-44.8	-62.62	-10.14
Left lingual gyrus	19	-18.33	-66.88	-6.63
Right lingual gyrus	19	28.99	-65.63	-2.64
Left middle occipital gyrus	19	-24.13	-88.84	10
Left middle temporal gyrus	37	-44.81	-61.19	-2.81
Right parahippocampal gyrus	36	27.24	-34.59	-11.49
Right postcentral gyrus	2/3	49.84	-23.21	45.49
Right posterior cingulate	30	8.13	-66.26	9.86
Right precentral gyrus	6	49.92	-14.47	27.96
Right precuneus	7	25.09	-57.7	52.14
Left precuneus	31	-22.21	-70.71	23.86
Left superior occipital gyrus	19	-31.72	-84.02	24.74
Right superior parietal lobule	7	25.1	-61.03	44.68
<i>(b) NPR > HP</i>				
Right cuneus	17	23.23	-79.55	7.28
Left cerebellum declive	*	-27.77	-64.55	-11.97
Left fusiform gyrus	19/37	-25.85	-55.32	-7.74
Right inferior frontal gyrus	9	50	6.38	29.32
Right inferior parietal lobule	40	51.72	-27.02	45.25
Left middle occipital gyrus	18/37	-35.49	-86.96	11.86
Right postcentral gyrus	2	49.84	-26.77	41.64
Left precuneus	7	-20.35	-69.76	38.41
Right precuneus	7	23.21	-57.45	48.52
Right superior parietal lobule	7	9.92	-63.49	55.29
Left superior parietal lobule	7	-24.15	-70.08	43.79

$p < 0.0001$), and between LP and HP items ($t(11) = 4.175$, $p < 0.003$), suggesting increasing facilitation in RT with repetition. A pattern of multistepwise reduction in reaction times across multiple repetitions is clearly revealed in the current experiment and will serve to inform the computational model (Fig. 8).

In the test phase, a repeated-measures ANOVA with condition (fourth presentation (VHP) or shown once (NP)) and cue (same or reversed) entered as within-subject factors revealed a significant effect of the decision cue ($F[1,11] = 13.786$, $p < 0.004$), effect of condition ($F[1,11] = 11.931$, $p < 0.006$), and a significant interaction between cue and

Table 2 – Regions where reduced cortical activity (cluster-corrected) was found in the test phase with priming. Table shows Brodmann area (BA) and Talairach coordinates (x, y, and z).

Region	BA	x	y	z
<i>(a) NP > VHP (Same same cue)</i>				
—	—	—	—	—
<i>(b) NP > VHP (cue-switched)</i>				
Left lingual gyrus	18	-25.95	-76.64	-1.89
Left middle occipital gyrus	19	-24.12	-86.95	10.12

Table 3 – Regions where reduced cortical activity (uncorrected at $p < 0.01$) was found in the test phase with priming. Table shows Brodmann area (BA) and Talairach coordinates (x, y, and z).

Region	BA	x	y	z
<i>(a) NP > VHP (Same same cue)</i>				
Left brainstem	*	0.82	-8.04	-6.3
Right anterior cingulate	32	1.01	45.04	-2.85
Left anterior cingulate	32	-14.17	38.9	5.71
Right caudate (tail)	*	29.09	-33.87	6.67
Left caudate (tail)	*	-27.71	-33.72	11.75
Left caudate (body)	*	-20.08	-9.6	20.61
Left cingulate gyrus	24	-1.17	-10.35	29.72
Right cingulate gyrus	31	21.44	-30.2	39.43
Left cuneus	18	0.45	-86.2	24.8
Right insula	13	29.04	-33.13	24.81
Left lentiform nucleus (putamen)	*	-27.64	-11.08	15.04
Right lentiform nucleus (medial globus pallidus)	*	14.08	-8.04	-8.03
Left middle frontal gyrus	46	-46.43	26.88	19.2
Right middle frontal gyrus	10	35.03	38.24	9.59
Left middle temporal gyrus	*	-52.4	-63.25	0.63
Left paracentral lobule	5	-5.13	-36.82	56.93
Right parahippocampal gyrus	28	23.51	-19.39	-10.52
Left parahippocampal gyrus	28	-23.79	-15.06	-12.34
Right postcentral gyrus	43	48.07	-10.2	20.99
Right posterior cingulate	29	8.2	-45.64	14.82
Right posterior cingulate	30	27.06	-69.99	6.11
Left precentral gyrus	4	-59.89	-15.87	34.43
Right precentral gyrus	6	49.93	-5.57	37.59
Left precuneus	7	-3.3	-55.56	52.1
Right precuneus	7	2.47	-36.19	46.16
Left subcallosal gyrus	11	-12.29	24.65	-9.69
Left supramarginal gyrus	40	-48.63	-51.41	23.14
Left thalamus (lateral posterior nucleus)	*	-22.02	-22.86	19.73
<i>(b) NP > VHP (cue-switched)</i>				
Right anterior cingulate	32	19.83	30.21	18.02
Right caudate body	*	17.76	-12.18	26.1
Left caudate body	*	-4.88	1.87	17.83
Left cingulate gyrus	24	-14.45	-10.81	38.66
Right cerebellum culmen	*	15.85	-42.18	-10.24
Left cerebellum culmen	*	-10.6	-28.68	-9.53
Right cuneus	18	23.21	-78.23	16.41
Right fusiform gyrus	19	27.11	-67.05	-9.98
Left fusiform gyrus	37	-37.13	-36.15	-8.37
Left inferior occipital gyrus	18	-37.32	-82.11	-4.12
Right insula	13	49.86	-34.98	21.2
Left insula	13	-42.9	-39.85	20.31
Right lentiform nucleus (lateral globus pallidus)	*	17.88	-0.73	-3.91
Right lingual gyrus	18	21.35	-80.96	-0.07
Left lingual gyrus	19	-31.58	-65.22	-1.18
Left middle occipital gyrus	19	-29.83	-87.48	19.1
Left middle temporal gyrus	37	-52.38	-59.23	-2.73
Left paracentral lobule	31	-6.89	-11.23	44.11
Right paracentral lobule	4	15.68	-38.89	56.92
Right parahippocampal gyrus	19	29.07	-42.88	-1.16
Left parahippocampal gyrus	30	-18.28	-44.94	7.46
Left postcentral gyrus	5	-33.54	-42.25	56.4
Right posterior cingulate	30	28.95	-68.34	9.85
Left precentral gyrus	4	-29.71	-27.35	61.01
Right precuneus	7	23.24	-53.31	43.37
Left precuneus	31	-22.2	-70.6	22.06
Right superior parietal lobule	7	-27.94	-66.72	51.23
Left superior parietal lobule	7	17.54	-44.95	61.97
Left uncus	28	-23.71	2.58	-20.24

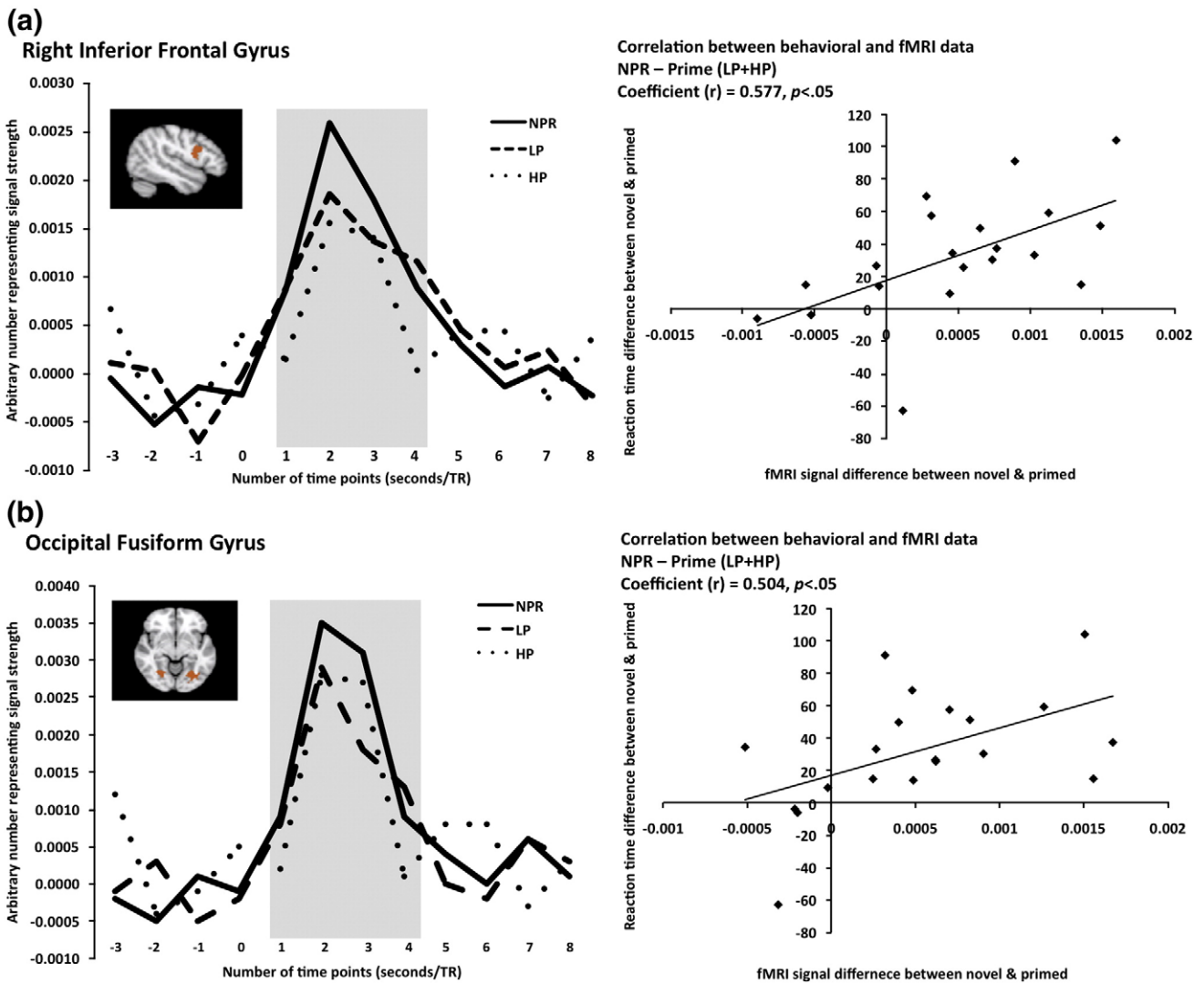


Fig. 6 – Behavioral and neural response reduction correlations in the study phase (experiment I). The regions of interest were those implicated in previous priming studies namely the prefrontal cortex and ventral-temporal cortex (Dobbins et al., 2004). Time series data was derived across a specific time window, starting from 6 seconds before the presentation to 16 seconds after the presentation. Respective ROIs their averaged time series are plotted in the left column for the different conditions. The x-axis depicts time frame in terms of volumes acquired (number of seconds/TR). With zero representing the time at which stimulus was presented. Similar to the behavioral data, significant stepwise reductions in regional signal were found between shown once and repeated conditions (for grayed region). The right column shows correlation analysis between behavioral response time data and mean ROI-based cortical signal for shown once minus prime condition. High correlation values were found for both right inferior frontal gyrus and occipital fusiform gyrus.

condition ($F[1,11]=11.026, p < 0.008$; Fig. 8). Follow-up two-tailed, pairwise t-tests found significant priming in same cue condition between NP and VHP ($t(11)=3.925, p < 0.003$) but no priming in switched cue condition between NP and VHP ($t(11)=1.911, ns$).

In sum, the commonly seen behavioral signatures of DL, i.e., increasing facilitation in RT across multiple repetitions and a subsequent disruption of priming gains with cue inversion, were observed with the repetition of common objects in an experiment that utilized the same design setup as that used with novel objects. The results from this experiment further strengthen the claim that the lack of DL in novel objects is due to the novel stimulus rather than the experimental design setup.

The priming effects seen for novel objects cannot reflect a binding of previous decisions with earlier stages of processing. Therefore, an alternative mechanism must be considered to account for the current results. One possibility is the perceptual memory-based binding system shown as Pathway 3 in Fig. 3, which represents the linking of a visual representation with previously extracted task-specific perceptual information. This link allows bypassing the computational intensive feature extraction phase during successive encounters with the same item. Since much of the previous research and theories of repetition priming have focused on common, well-known objects, the gains achieved by bypassing higher cognitive functions, as in DL, could have potentially

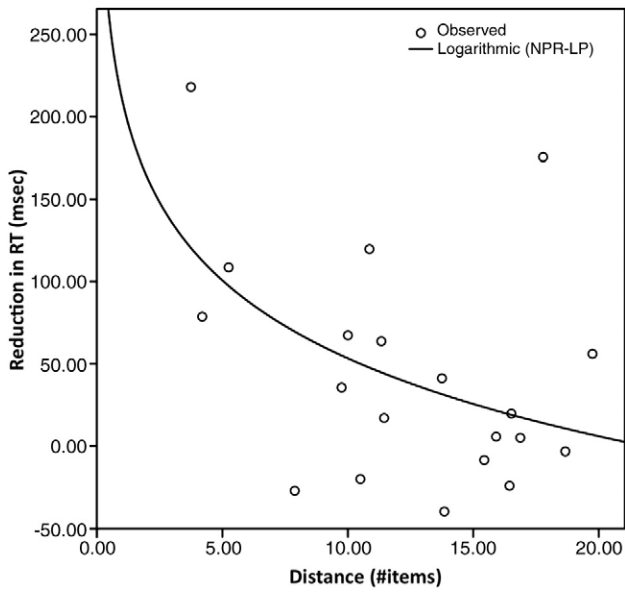


Fig. 7 – Effect of distance between repetitions over priming gains (experiment I). To investigate temporal decay of priming gains, reductions in reaction time associated with repetition, was examined with respect to distance from the first presentation (NPR) of an item. The x-axis denotes the distance between conditions and the y-axis denotes the difference in RT between conditions. Distance was measured in terms of number of items between the NPR and the second presentation (LP). The results in the study phase indicate that reduction in RT for LP items and the distance between first and second presentation follows a log relationship.

overshadowed the ones achieved from a low-level perceptual memory-based systems. However, because the current experiment was based on novel objects, such gains may have been exposed.

The next question, then, is how to formulate the low-level perceptual memory-based binding, which is mechanistically

different from the episodic memory-based DL? In addition, how do these two systems integrate and to what extent do they depend on the stimulus specificity? Finally, it would be interesting to test whether such a perceptual memory-based binding can be used to characterize some of the residual priming that was previously not attributable to DL, such as preserved priming after cue inversion in the healthy population as well as intact priming in amnesic patients. To answer these questions, a computational model was developed, as discussed in the next section.

2.3. Computational modeling experiments

Computational modeling is an effective tool in cognitive science for mathematically formalizing a theory, evaluating, and comparing existing theories and for making novel experimental predictions. In contrast to the loose formulation of traditional verbal theories, computational models include explicit implementation details and can produce highly detailed simulations of human performance (Zorzi et al., 2005). To understand the role of perceptual memory-based linkage in repetition priming, a computational model was developed based on the behavioral and neural results from the experiments above. The sequence of cognitive processes, as in Fig. 3, was modeled along with the Pathway 3 (Fig. 9-R). Further, the model was extended to common object priming by including an episodic memory-based DL component (Fig. 9-L).

2.3.1. Computational experiment I: Repetition priming with novel objects

Results from the fMRI experiment characterized the low-level perceptual memory-based binding system and thus form the basis for modeling. Key characteristics include (1) one-shot learning, i.e., significantly reduced response time after a single repetition, (2) no further decrease in response time with multiple repetitions, and (3) lack of transfer of learning from study phase to test phase, reflecting a rapid decay. These characteristics were captured in the computational model by implementing a caching mecha-

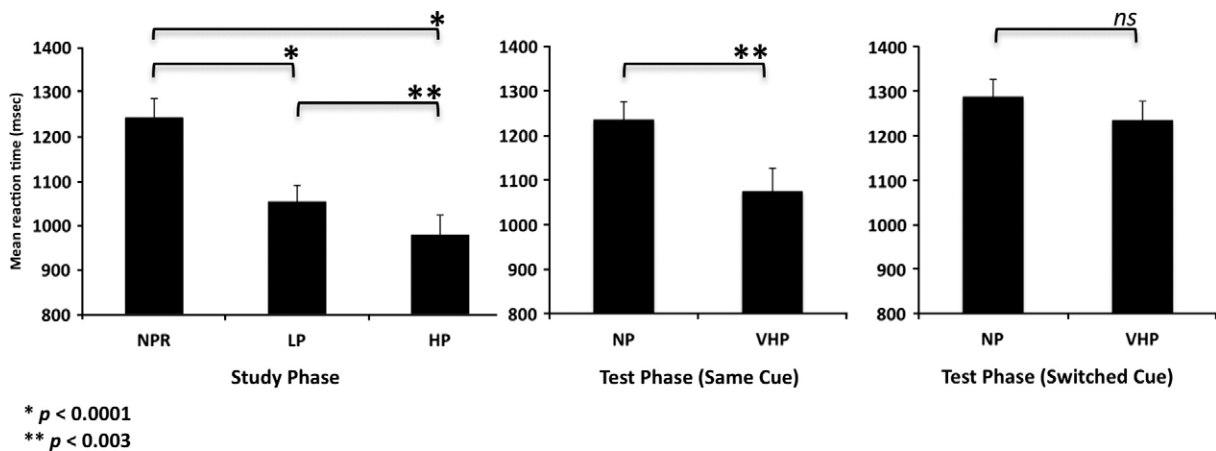


Fig. 8 – Behavioral results (experiment II). Reaction times in study and test phase (with and without cue inversion) in the common object priming experiment. The commonly seen behavioral signatures of DL, i.e., increasing decrease in RT with repetition and disruption of priming gains with cue inversion, were observed.

* $p < 0.0001$
 ** $p < 0.003$

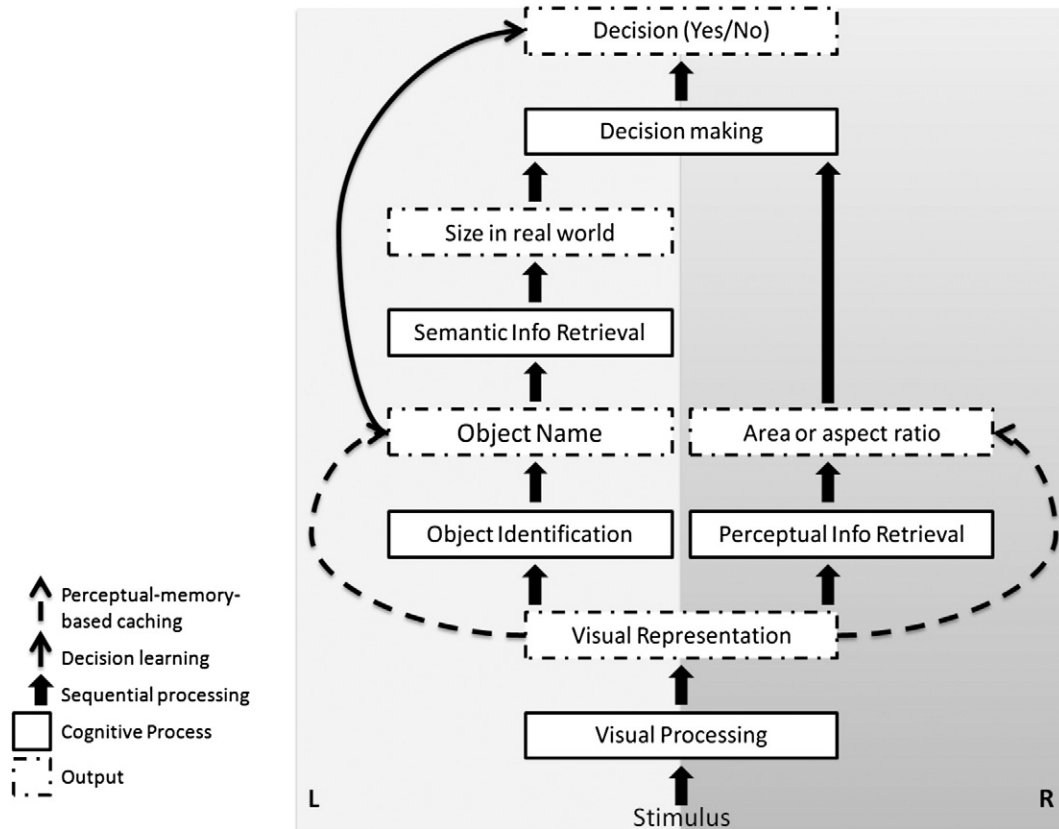


Fig. 9 – Model architecture. Processing objects encountered for the first time is similar for both common (L) and novel objects (R), shown using straight solid arrows. These sequential pathways are computationally intensive and are engaged whenever an item is seen for the first time. There are two alternative processing pathways that can be brought online with repetition. First is the episodic memory-based decision-learning pathway that reflects the previously formulated decision learning process; it exists only for common objects, and shown as solid curved arrow. A second alternative pathway is that of the proposed low-level perceptual memory-based binding, shown as dashed curved arrows. Upon successive encounters with the same visual stimulus, this pathway helps bypass perceptual information extraction (in case of novel objects) or object identification step (in case of common objects). Further, it does not involve associative learning, thus the response time reduction happens in a single stepwise manner and does not benefit from multiple repetitions. For more details, see the [Section 4](#).

nism. By definition, caching is a method of temporarily storing frequently accessed information, to speed up processing. Thus, during the first encounter with a novel item, task-related perceptual information, which is extracted from the visual representation, is cached. During successive encounters with the same item, the cached information can be used directly in decision making (Fig. 9-R). Hence, the computationally intensive perceptual-information-extraction step can be bypassed, leading to faster response after a single repetition. However, caching does not result in associative learning, i.e., multiple repetitions do not increase the synaptic strength of link, and thus, there are no further decreases in response time with multiple repetitions. In addition, because cache is a low-level temporary storage, it needs to regularly flush previously stored information to make room for new information, and hence, it provides only short-term gains. Altogether, the formalized perceptual memory-based caching system (PCS) successfully models the characteristics of priming gains observed in the current RP experiment using novel objects (Fig. 10a).

The computational model is then tested in an experiment that integrates DL with PCS to see if PCS can help resolve the issues related to residual priming in healthy participants.

2.3.2. Computational experiment II: Repetition priming with common objects

DL was modeled based on the results from second behavioral experiment (see Section 2.2) as well as previously observed neural and behavioral signatures seen in experiments of repetition priming (Dobbins et al., 2004; Schnyer et al., 2006). After a single repetition, an object is associated with the previous decision, and this association gets stronger with multiple repetitions, until it finally saturates (Buckner et al., 1998). Further, DL depends on well-established representations. To model these characteristics, the convergence zone episodic memory architecture (Moll and Miikkulainen, 1997) was used. That is, a randomly sparse-encoded binding layer, acting as a convergence zone, was introduced between an object representation and a decision layer. Thus, when the object is encountered for the first time, the active decision unit

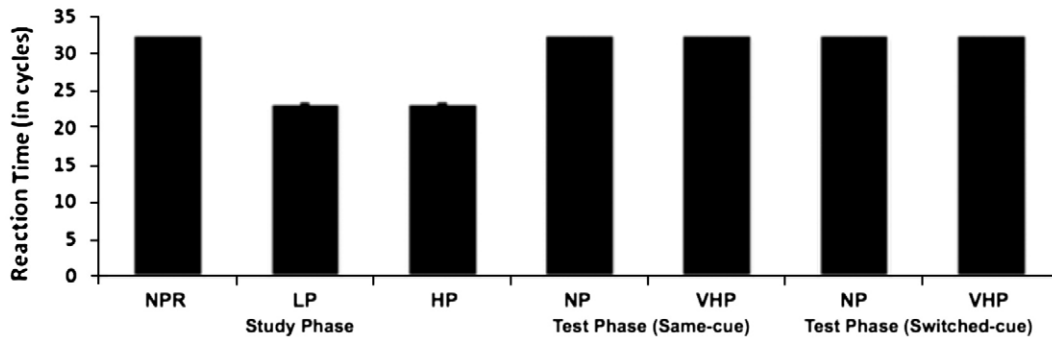
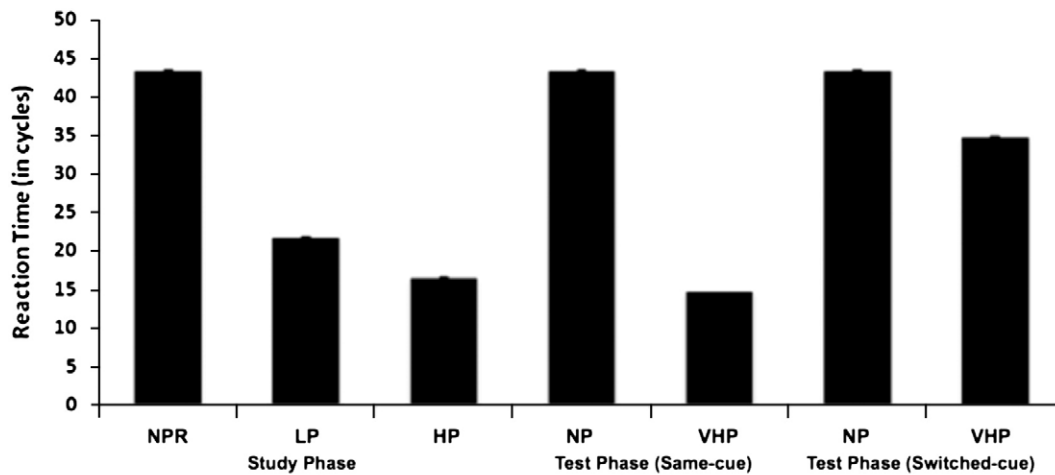
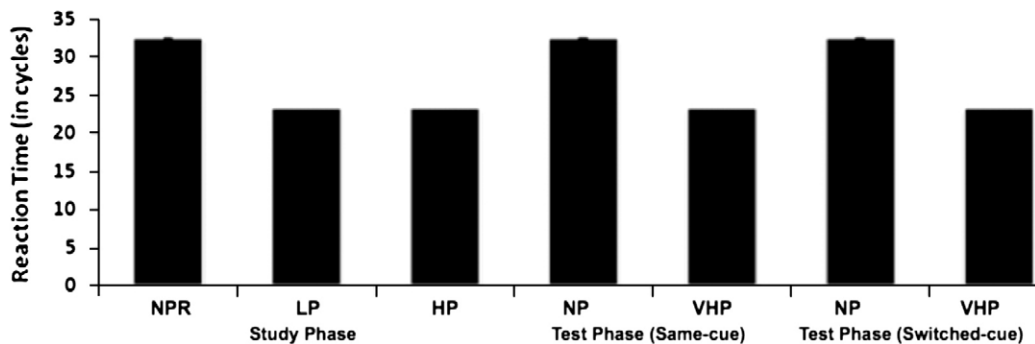
(a) Experiment I: RP using novel objects.**(b) Experiment II: RP using common objects.****(c) Experiment III: RP using common objects in amnesic population.**

Fig. 10 – Simulation results. The horizontal axis identifies the condition or phase, while the vertical axis displays the reaction time, measured in processing cycles. The model was simulated under three different scenarios, for 1000 iterations in each scenario. The inputs to the model were black and white images of different shapes of size 20×20 pixels. The output of the model was a binary value, depicting decision “yes” or “no”. (a) In a novel-object priming simulation in healthy participants, significant priming was observed only in the study phase ($p < 0.05$, using two-tailed, pairwise t-tests). Priming gains did not transfer from the study to the test phase. (b) In common object priming in healthy participants, significant priming took place both in the study and the test phase ($p < 0.05$, using two-tailed, pairwise t-tests). Further, cue inversion disrupted the DL, i.e., episodic memory-based associations, but the PCS provided some level of intact priming. (c) The simulation of repetition priming in amnesic patients using common objects yielded threshold-type priming gains in both study and test phase. Further, these gains were not affected by cue inversion. Thus, the simulation results successfully replicate the behavioral priming results obtained in current and previous studies with common and novel objects. The model also predicts that for amnesic patients single stepwise reduction in response time would be found in repetition priming experiments using novel objects, similar to what is found in healthy population.

becomes associated with the active object representation unit, utilizing this binding layer. Further, the episodic memory-based architecture was modified to include associative learning with repetitions. With each repetition, the synaptic strength between the binding layer, object unit, and decision unit grows stronger. Thus, successive encounters with an item produce higher activation in the binding layer units and the associating decision unit. This increase in activation in turn leads to faster response selection and hence reductions in response time with repetitions (Fig. 10b). The ability to strengthen associations with multiple repetitions allows for added facilitation. This result mirrors the behavioral results of several multiple-repetition priming studies (Dobbins et al., 2004; Buckner et al., 1998).

Further, the PCS and DL systems were integrated to see if the repetition priming results could now be fully explained. During the first encounter with an item, in addition to developing an episodic memory-based association between the previous decision unit and the object representation unit, PCS was implemented to cache the object representation units. Thus on second encounter with an item, PCS helps bypass the object identification/retrieval step and episodic memory-based DL helps bypass the higher-order semantic information extraction and comparison steps. The episodic memory-based DL provides increasing facilitation in response times associated with multiple repetitions. However, upon inverting the decision cue, the object–decision associations of episodic memory are rendered useless and a significant portion of priming gains are lost. Nonetheless, the preserved PCS between visual and object representation layers gives rise to some remaining residual priming advantage, as has been observed in human subjects (Fig. 10b).

Integrating PCS and DL thus appears to fully explain the repetition priming results as observed in healthy population with common objects. However, amnesic patients with damaged MTL structures lack episodic memory. The next experiment shows how PCS alone can explain the repetition priming results in amnesic patients.

2.3.3. Computational experiment III: Repetition priming in amnesic patients using common objects

The results from the repetition priming experiment using common objects, showed intact priming gains in amnesic patients (Schnyer et al., 2006). Due to damaged MTL structures, the episodic memory-based DL cannot contribute to this priming, and the results confirmed this prediction. The current model proposes to formalize the underlying mechanism using PCS alone. Thus on second encounter with the same item, PCS would facilitate the object identification process and thereby help produce a faster response. However, because there is no associative learning in the PCS and there is a limited capacity, a single stepwise reduction in response time with repetitions results, similar to the results of the current fMRI experiment with novel objects. Further, since no association is formed between previous decision and any other layer of processing, cue inversion should not affect the priming gains. The simulation results, as shown in Fig. 10c, are similar to the behavioral results observed in case of amnesic patients (Schnyer et al., 2006).

The modeling results in computational experiment I suggest that the learning associated with the PCS do not transfer from

study to test phase, in case of novel objects. However, in case of common objects (in computational experiments II and III), the model suggests that it does. Since common objects have more robust visual and object representations than novel objects, the PCS appears to be less affected by interference between items. It is interesting to note that the observed priming gains in amnesic patients were significant only for the first test phase and were not significant for later test phases (Schnyer et al., 2006). In addition, the model predicts that, for amnesic patients, the response time would be reduced in a single stepwise fashion in repetition priming experiments using novel objects, similar to what is found in healthy population.

3. Discussion

To test how DL depends on well-established object representations and to determine whether it is possible to associate visual representations and previous decisions directly, to attain even higher degrees of automaticity, a new repetition priming experiment using 2-D novel objects was conducted. Both behavioral and neuroimaging results indicate that novel objects result in relatively short-term priming, and response time decreases in a single stepwise fashion with repetition. This pattern does not fit previous formulations of DL, thereby suggesting that well-established representations are required for DL. This finding can be explained by the fact that the episodic memory-based system is not well designed to deal with similarity-based interference (Thorndyke and Hayes-Roth, 1979), caused from less robust representations of similar-looking novel object stimuli. The presented model for episodic memory-based DL also supports this argument. The model implements a binding layer (or a convergence zone) between the visual representation and the previous decision made for an item. By architecture, this association works best only if robust localized activity is formed in the visual representation layer. However, the visual representation for novel objects is not sufficiently robust, which leads to catastrophic interference in the binding layer and eventually in the decision layer and hence renders the association useless.

Interestingly, neuroimaging results indicated reduced cortical activity during the study phase in right inferior prefrontal cortex (RIPC) for novel items that were presented three times as compared to those that were shown only once. This reduction suggests that weak DL was starting to be established after two repetitions but was not strong enough to transfer to the test phase. This finding is different from what has been previously observed in RP experiments using common objects, where the cortical activity is found to be reduced primarily in the left inferior prefrontal cortex (LIPC) with repetition and the reductions appear temporally robust. The difference in location is consistent with the idea that the right hemisphere processes more specific information, as required in identifying novel items, and the left hemisphere processes more abstract, easily namable representations like those that exist for common objects (Marsolek, 1999).

Other evidence for weak DL for novel shapes was found in the error rate analysis conducted on the test phase. With a liberal statistical threshold, there was some indication of a significant increase of number of errors associated with the switched-cue condition relative to the same-cue condition for

repeated items. No such increase between cues was found for nonrepeated items in the test phase. This finding of greater errors for very high primed (VHP) items after switching the cue suggests that some degree of decision learning was established for such items. However, this effect is evident only with liberal statistical thresholds and hence unreliable and weak.

If the priming gains observed in the current experiment are inconsistent with DL, could they be due to a neural tuning mechanism? The early formulation of tuning theory (Wiggs and Martin, 1998) postulates that the efficient object processing, with repetition, results from pruning of neural activations that are not essential for the task. Thus, in the current experiment, the tuning perspective would predict increasing decrease in response time with multiple repetitions, instead of a one-time stepwise reduction in response time (Buckner et al., 1998).

Although there were robust neuroimaging effects of repetition in the study phase, the test phase exhibited effects only with a more liberal statistical threshold. Nevertheless, results from the test phase were suggestive of possible frontal/posterior dissociation during same- and switched-cue conditions. For instance, regions of PFC, namely left and right middle frontal gyrus demonstrated repetition suppression in the same cue condition, consistent with a DL component. In contrast, repetition suppression was evident in posterior regions during both same- and switched-cue conditions in the test phase. Furthermore, significant correlations between repetition-induced cortical activity reductions in occipitotemporal gyrus and behavioral response time reductions during the study phase strongly suggest that some form of perceptual memory is also involved in RP using novel objects. Based on these results, the posterior component is formulated as a perceptual memory-based caching system (PCS) in this paper. By definition, caching is a method for storing frequently accessed information temporarily to speed up the processing. This one-time storage provides instant priming gains but without associative learning, i.e., multiple repetitions will not further strengthen it.

Although multiple components contributed to it (such as PCS and weak DL), priming gains were not transferred from the study phase to the test phase. This observation can be explained either by limited capacity of PCS (due to interference between similar looking novel objects) or temporal decay of activation in storage areas. The current fMRI study utilized 60 unique novel items per study–test run and such a high number would quickly overwhelm the lower-level PCS. However, this reason suggests that an experiment that uses fewer novel items, repeated multiple times, might be able to utilize this system to implement longer-term priming gains. The possibility of a rapid temporal decay effect was tested by examining reduction in RT with repetition and distance from the first presentation. Significant log relation was found in the study phase (between LP and NPR), indicating a rapid decay of priming gains as the distance between presentations was increased. This finding suggests that since the test phase items are at the maximal experimental distance from their first presentations in the study phase, the lack of priming was due to this relatively rapid decay of activation. An experiment aimed at finding the capacity and decay curve for the perceptual memory is left as an open question for future research.

This paper proposes that one potential component in understanding repetition priming is the PCS. A system of this type has not been previously formulated in contrast to a DL or

response learning system because the gains achieved from bypassing higher-level cognitive processes overshadowed the gains achieved from bypassing lower-level processes. However, the experiment using novel objects revealed this phenomenon. In addition, modeling PCS alone, and with the DL component, explained previously found intact priming in amnesic patients, and residual priming in healthy population, respectively.

In summary, behavioral, neuroimaging, and computational modeling results suggest that repetition priming involves multiple components, and a tight interaction between experiments and computational theory is necessary to disentangle their contributions.

4. Experimental procedures

4.1. Subjects

4.1.1. Experiment I

Twenty-two young native speakers of English, with normal or corrected to normal vision, took part in the fMRI experiment. The subjects (14 males and 8 females, mean age of 23.68 years with range from 20 to 28 years) were recruited through flyers and advertisements at local colleges and universities and received \$50 for their participation. The subjects were screened for current psychiatric and neurological disorder, history of brain injury, or excessive drug or alcohol use. They were also screened to make sure they were free from any risks of magnetic resonance imaging. Written informed consent was obtained from each subject prior to experimental session. The Institutional Review Board (IRB) of the University of Texas at Austin approved all procedures.

4.1.2. Experiment II

Twelve young native speakers of English, with normal or corrected to normal vision, took part in the behavioral experiment. The subjects (6 males and 6 females, mean age of 18.5 years with range from 18 to 20 years) were recruited from the PSY301 pool of research subjects and received an hour of credit for their participation. The subjects were screened for current psychiatric and neurological disorder, history of brain injury, or excessive drug or alcohol use. Written informed consent was obtained from each subject prior to the experimental session. The Institutional Review Board (IRB) of the University of Texas at Austin approved all procedures.

4.2. Materials

4.2.1. Experiment I

Two hundred fifty novel object images (from Slotnick and Schacter, 2004) were used in the experiment. The stimuli were presented using a PC notebook computer running DMDX (software developed at Monash University and at the University of Arizona by K.I. Forster and J.C. Forster) and an LCD projection system. The responses were collected using the participants' right-hand and an MR-compatible two-button response box.

4.2.2. Experiment II

Two hundred fifty common object images (from Schnyer et al., 2006) were used in the experiment. The stimuli were presented

using a PC computer running DMDX (software developed at Monash University and at the University of Arizona by K.I. Forster and J.C. Forster) on a monitor. The responses were collected using the participants' right-hand and a two-button mouse.

4.3. Procedure

4.3.1. Experiment I

Before going into the scanner, subjects took part in a brief practice session, where five examples of each category (fat or slim) were shown to them. They were told that the task requires them to visually measure area occupied by each stimuli and answer <yes/no> to the shown decision cue. Further, they were told there was no wrong answer in this task and they should try to remain consistent in their criteria. Once settled in the scanner, a brief task instruction screen was shown followed by four alternating "study–test" cycles. During the study phase of each cycle, 20 pictures were presented once (NPNR) and 20 different pictures were presented three times (NPR, LP, and HP), for a total of 80 presentations. In addition, null trials were added to the sequence to increase the efficiency of the design (20 in study phase and 10 in test phase). The sequence of these presentations was generated in a pseudo-random order using optseq2 program (Dale et al., 1999; Dale, 1999). Participants were asked to make relative size judgments by deciding whether the stimulus was "fat" or "slim." They indicated their decision by pushing a "yes" or a "no" key with the index and middle fingers, respectively, of their right hand. Following the study phase and a short pause, participants took part in the test phase consisting of one of two test blocks. Each test block consisted of 20 pictures presented three times during the study (i.e., presented for the fourth time; VHP), along with 20 pictures never shown before (NP). None of these pictures were repeated within or between test blocks. The test blocks differed only on the basis of decision cue. In one test block, participants responded to the decision cue "is the stimulus fat?"; in the other test block, they were asked to respond to "is the stimulus slim?". Thus, in the first and third study–test cycles, the participants were asked "is the stimulus fat?" in both study and test phase. However, in the second and fourth test phases, the participants were asked "is the stimulus slim?". Pictures were randomly assigned to one of the four study–test cycles. Within each cycle, pictures in the test phase were rotated between the two possible conditions (shown-once (NP) and shown-fourth time (VHP)). In addition, the order of switching was counterbalanced across subjects. Thus, in total, there were four versions of the experiment. Pictures were presented at the rate of one every 3 seconds and were accompanied at the bottom of the screen by the decision cue to be used on that trial. In addition, the duration for null trials was randomly distributed across the sequence using the optseq2 tool. Each study phase lasted for about 300 seconds, and each test phase lasted for about 150 seconds.

4.3.2. Experiment II

The procedure in this experiment was kept exactly similar to the experiment I, except for the stimulus material and decision cue. Instead of using novel objects, the common object images were used (from Schnyer et al., 2006). The subjects were told that the task requires them to compare the

"real-world" size of the shown stimulus from a "shoebox" and answer <yes/no> to the shown decision cue.

4.4. fMRI data acquisition

Scanning was performed on a 3-T GE scanner using standard 8-channel head coil. A multiecho GRAPPA parallel imaging EPI sequence developed at Stanford was used that optimizes BOLD signal in regions that are typically vulnerable to susceptibility artifact. Functional EPI images were collected utilizing whole-head coverage with slice orientation to reduced artifacts (approximately 20° off the AC–PC plane, TR=2 seconds, three-shot, TE=30 ms, 35 axial slices oriented for best whole head coverage, acquisition voxel size=3.125×3.125×3 mm with a 0.3-mm interslice gap). The first four EPI volumes were discarded to allow scans to reach equilibrium. In all cases, stimuli were viewed utilizing a back-projection screen and a mirror mounted on the top of the head coil. Responses were collected with MR-compatible buttons that were held in the right hand. In addition to EPI images during the task, two high-resolution T1 SPGR scans that had been empirically optimized for high contrast between GM and WM and between GM and cerebrospinal fluid (CSF) were acquired. These images were acquired in the sagittal plane using a 1.3-mm slice thickness with 1.0-mm³ in-plane resolution.

4.5. Statistical analysis of neuroimaging data

Data were processed using FSL (Smith et al., 2004, and <http://www.fmrib.ox.ac.uk/fsl/>). For fMRI analysis, images were motion-corrected, smoothed with an 8-mm Gaussian filter, high-pass-filtered and prewhitened before event-related responses were estimated using event-related convolution with an ideal hemodynamic response represented by a gamma function and its temporal derivative. Explanatory variables were modeled for each of the three conditions (NPR, LP, and HP) in the study phase and two conditions (NP and VHP) in the test phase. A second-level analysis was conducted on each individual subject by registering each subject to the standard MNI152 template and combining the critical contrasts from the four runs. Group-level maps of these contrasts were calculated with a higher-order statistical parametric map utilizing the FLAME (FMRIB's Local Analysis of Mixed Effects) technique implemented through FSL and threshold at $p < 0.05$, cluster-corrected. Two subjects were excluded from group-level analysis due to high motion artifacts. The following contrasts were calculated in the study phase: (1) NPR>all prime, (2) NPR>HP, and (3) NPR>LP; and in the test phase: (1) NP>VHP.

4.6. Computational model architecture

Three different pathways of processing were included in the model: (1) the sequential series of cognitive processes, (2) the episodic memory-based decision learning, and (3) the perceptual memory-based caching in a <yes/no> type classification task such as used in the fMRI experiment. Each of these is described below.

4.6.1. The sequential series of cognitive processing

It was modeled using recurrent artificial neural networks. Total number of processing cycles taken by the model from

input to decision making was summed over each stage. Below is a brief description of how activation in the model operates; for more details, see [Cohen et al. \(1990\)](#). The units update their activations by calculating a weighted sum of the inputs they receive from the previous level in the network. The net input S_j at time t for unit U_j (at layer L_n) is given by:

$$S_j(t) = \sum_i a_i(t) * w_{ij}(t) \quad (1)$$

where $a_i(t)$ is the activation of U_i at L_{n-1} , and w_{ij} is the strength of the connection weight between units i and j . The activation of a unit is the weighted average of its current net input and its previous net input:

$$a_j(t) = \sigma * (\tau * S_j(t) - (1 - \tau) * S_j(t - 1)), \quad (2)$$

where τ is the cascade rate. For all simulations in this paper, 0.8 was used as the value of τ . Here, the sigmoid function, σ , was used to keep the activation a_j between 0 and 1.

Back-propagation was used to implement learning ([Rumelhart et al., 1986](#)). Learning occurs by adjusting the connection strengths to reduce the difference between the output pattern produced by the network and the one desired in response to the current input. Each processing stage (object recognition, visual processing, decision making) was trained separately and the output from each previous stage was fed to the next one as input. Each stage in the network was trained to about 96% accuracy to avoid overfitting.

To match experimental RT behavior, variability was incorporated into the model by selecting responses based on a random walk and a diffusion process ([Link, 1975](#); [Ratcliff, 1978](#)). Each potential response is paired with an evidence accumulator that takes input from the output units of the network. At the beginning of each trial, all the evidence accumulators are set to 0, and at each time-step of processing (a cycle), evidence accumulates as a function of the activation in the relevant output unit. The amount of evidence, e_i , accumulated for response i is given by the following equation:

$$e_i = N(x[x_i - \max(a_j \neq i)], \sigma), \quad (3)$$

where $N(\cdot)$ is a random value sampled from a normal distribution with mean μ and standard deviation σ . A response was generated when one of the accumulators crosses the threshold. (For all the simulations in this paper, following values were used, $\mu=0.1$, $\sigma=0.1$, and threshold=1).

4.6.2. Episodic memory-based decision learning

Convergence zone episodic memory architecture ([Moll and Miikkulainen, 1997](#)) was used to implement the episodic memory-based decision learning between object representations and previous classification decisions. Convergence zone memory model consists of two layers of real-valued units; the feature layer and the binding layer. In the current model, the feature layer consists of two vectors, one representing the object and the other the decision. Each unit in these vectors specifies a different object or a decision. The feature units are connected to the binding layer with bidirectional-weighted connections. Activation in the feature layer causes a number of units to become active in the binding layer, and vice versa. In effect, the binding layer activation is a compressed, distributed encoding of the feature representation.

Initially, all connections are inactive at 0. An association between the object representation and decision in the episodic memory is build up in three steps. First, those units that represent the appropriate feature values are activated at 1. Second, a subset of m binding units are randomly selected in the binding layer as the compressed encoding for the pattern, and activated at 1. Third, the weights of all connections between active units in the feature maps and the active units in the binding layer are activated, i.e., set to 1. Thus, only one presentation is necessary to store an association. An association is retrieved in four steps. First, all binding units are set to 0. A partially specified association (i.e., the object representation feature vector) is propagated to the binding layer. The activation is thresholded to obtain the most active units, reducing noise. It is then propagated back to the decision feature layer, thereby retrieving the decision. It has been shown that the convergence zone memory has a very large capacity ([Moll and Miikkulainen, 1997](#)).

The repetition-related facilitation effect was modeled by modifying the convergence zone architecture, by updating the connection weights gradually (instead of 0/1 as in the original convergence zone model). Thus after each repetition of an item the weight between the object representation and decision vector was increased, which in turn gave rise to faster responses in the decision layer.

4.6.3. Perceptual memory-based caching system

This process is used to model lower-level memory-based binding, using caching. In case of novel objects, it caches the task-related perceptual information, so that during successive encounters with the same item, the cached information can be used and hence speed up the processing. In case of known objects, it caches the appropriate object unit during first encounter, by doing so it helps facilitate the object identification/retrieval process during further encounters with the same item. This process is a direct storage of information and involves no learning in terms of weight change. The cache has a limited capacity, resulting in short-term storage only. In the presented model, the connections were manually configured to store the bindings.

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