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# An attention account of neural priming

Preston P. Thakral[a], Chelsea M. Jacobs[b] and Scott D. Slotnick[b]

[a]Department of Psychology, Harvard University, Cambridge, MA, USA; [b]Department of Psychology, Boston College, Chestnut Hill, MA, USA

**ABSTRACT**
Repetition priming of familiar stimuli (e.g., objects) produces a decrease in visual cortical activity for repeated versus novel items, which has been attributed to more fluent processing for repeated items. By contrast, priming of unfamiliar stimuli (e.g., abstract shapes) produces an increase in visual cortical activity. The mechanism for priming-related increases in activity for repeated unfamiliar stimuli is unknown. We hypothesised that such increases in activity may reflect attentional allocation to these items. We tested this hypothesis using a priming-spatial attention paradigm. During Phase 1 of Experiment 1, participants viewed unfamiliar abstract shapes and familiar objects. During Phase 2, participants identified target letters (S or H). Each target letter was preceded by a non-informative shape or object cue that was repeated (from Phase 1) or novel in the same (valid) or opposite (invalid) hemifield. In Experiment 2, we manipulated shape familiarity by presenting shapes once or six times during Phase 1. For both experiments, at valid locations, target identification accuracy was higher following repeated versus novel unfamiliar item cues and lower following repeated versus novel familiar item cues. These findings support our hypothesis that priming-related increases in visual cortical activity for repeated unfamiliar items may, in part, reflect attentional allocation.

Repetition priming is a nonconscious form of memory that refers to facilitated or biased processing of a stimulus due to prior exposure (e.g., faster reaction time or increased accuracy for repeated than nonrepeated/novel stimuli; for a review, see Schacter, 1987). Repetition priming effects are measured using indirect memory tasks (for reviews, see Henson, 2003; Schacter, 1987). During indirect memory tasks, participant's judge repeated and novel stimuli based on a non-memorial feature (e.g., pleasant/unpleasant, large/small, abstract/concrete, or living/nonliving). Performance on such indirect tasks does not require conscious retrieval and therefore are typically assumed to largely reflect nonconscious/implicit memory.

Behavioural priming effects are associated with neural priming effects that are classically manifested by a reduction in neural activity for repeated relative to novel stimuli (for reviews, see Gotts, Chow, & Martin, 2012; Grill-Spector, Henson, & Martin, 2006; Henson, 2003; Schacter & Buckner, 1998; Schacter, Dobbins, & Schnyer, 2004). For instance, in one study (Buckner et al., 1998), repeated objects relative to novel objects were associated with a reduction in reaction time (i.e., behavioural priming) and a reduction in visual cortical activity (i.e., neural priming). Many models have been proposed to explain how neural priming effects support behavioural priming (for reviews, see Gotts et al., 2012; Grill-Spector et al., 2006). For example, according to the *sharpening model* of priming, the magnitude of activity is sustained in neurons that

were most active during the initial presentation but is reduced in neurons that were less active during the initial presentation. In this model, behavioural priming is a consequence of the increase in signal-to-noise ratio for repeated relative to novel stimuli. Of importance, all models assume that priming reflects reduced and thus more fluent processing for repeated stimuli.

The behavioural and neural priming effects described above are typically identified using familiar stimuli such as pictures of common objects and words (for reviews, see Henson, 2003; Schacter & Buckner, 1998). However, priming effects have also been identified using stimuli such as unfamiliar faces and symbols (Henson, Shallice, & Dolan, 2000), novel 3-D objects (Schacter et al., 1995; Uecker et al., 1997), pseudowords (Fiebach, Gruber, & Supp, 2005), and abstract shapes (Slotnick & Schacter, 2006; see also, Slotnick & Schacter, 2004; Thakral & Slotnick, 2015; Thakral, Slotnick, & Schacter, 2013). Neural priming effects dissociate as a function of stimulus familiarity. Specifically, repeated familiar stimuli have been associated with a decrease in neural activity (as described above), whereas repeated unfamiliar stimuli have been associated with an increase in neural activity.

To our knowledge, it has yet to be determined why neural priming effects for unfamiliar items are manifested by an increase in neural activity. We hypothesised that the increase in visual cortical activity during unfamiliar item priming may reflect the allocation of attention to

repeated unfamiliar items. This hypothesis was motivated by the classic sensory effects of attention in visual cortical regions that are believed to reflect the amplification of processing within these regions (e.g., Kelley, Serences, Giesbrecht, & Yantis, 2008; Slotnick, Schwarzbach, & Yantis, 2003; Slotnick & Yantis, 2005; Thakral & Slotnick, 2009; Yantis et al., 2002; for reviews, see Reynolds & Chelazzi, 2004; Yantis & Serences, 2003). For example, attention to a stimulus in the right visual field versus attention to the analogous stimulus location in the left visual field (while a stimulus is presented in the right visual field) produces an attention-related increase in the magnitude of activity within the left/contralateral early and late visual regions (e.g., Kelley et al., 2008; Slotnick et al., 2003). We reasoned that the greater visual cortical activity observed for repeated unfamiliar stimuli in priming studies may reflect greater attentional allocation.

In the present paper, we tested our novel hypothesis in two behavioural experiments by employing a priming-spatial attention paradigm. In Phase 1 of Experiment 1, participants viewed unfamiliar abstract shapes and familiar objects and made a speeded judgment as to whether each shape or object was relatively "pleasant" or "unpleasant" (Figure 1(A)). In Phase 2, participants identified target letters (S or H). Each target letter was preceded by a non-informative shape or object cue that was repeated (from Phase 1) or novel (Figure 1(B)). In the current study, the term novel refers to shapes and objects that were presented for the first time. Cues were either valid (in the same hemifield as the target) or invalid (in the opposite hemifield as the target). Based on our hypothesis that the increase in visual cortical activity during unfamiliar item priming is due, in part, to attentional allocation, we predicted that target identification accuracy would be greater for repeated versus novel shape cues. We also predicted this would occur at valid locations, as each cue was expected to increase target identification accuracy at the same spatial location (relative to fixation). In Experiment 2, we manipulated shape familiarity by presenting shapes once or six times in Phase 1. The results in both experiments were in line with our prediction that there was greater attentional allocation to repeated unfamiliar items. These findings support our hypothesis that the priming-related increase in visual cortical activity reflects attentional allocation.

## Experiment 1

### Method

#### Participants

Twenty Boston College undergraduates with normal or corrected-to-normal vision received credit for a general psychology course or $10 for participation. The experimental protocol was approved by the Institutional Review Board of Boston College and informed consent was obtained prior to participation. The sample size was selected to be consistent with prior studies examining repetition

priming using abstract shapes (Slotnick & Schacter, 2006) and objects (Buckner et al., 1998).

### Stimuli and task

Each participant completed two experimental phases. In Phase 1, participants viewed 100 unfamiliar items and 100 familiar items. The unfamiliar items were abstract shapes that were constructed by connecting four Bézier curves and each shape had internal lines with a unique colour and orientation (for details on shape construction, see Slotnick & Schacter, 2004). Familiar stimuli consisted of line drawings drawn from a pool of 520 objects (International Picture Naming Project at the University of California, San Diego, Center for Research in Language; minimum valid response rate = 96%, minimum name agreement = 90%, and names had 1–2 syllables; http://crl.ucsd.edu/experiments/ipnp/). Pictures of objects primarily consisted of those from Snodgrass and Vanderwart (1980). Shapes subtended 4.9° of visual angle and objects subtended 2.0°–7.2° of visual angle.

During Phase 1, each item was presented 6.9° of visual angle to the left or right of central fixation for 100 ms with an inter-stimulus interval of 1800 ms (Figure 1(A)). Participants were asked to maintain fixation and make a pleasantness judgment for each item by pressing one of the two buttons. Participants were instructed that pleasantness referred to the degree to which they thought the shape was aesthetically appealing, as if they were viewing a piece of visual art. They were also told that the pleasantness judgment was relative, where approximately half of the time they should respond "pleasant" and the other half of the time they should respond "unpleasant" (see Thakral, Kensinger, & Slotnick, 2016). Participants were instructed to respond as quickly as possible without sacrificing accuracy. Trials were randomised with the constraint that no more than three stimuli of the same type or spatial location were consecutively presented.

In Phase 2, participants performed a target identification task (Figure 1(B)). On each trial, a non-informative shape or object cue was presented for 100 ms to the left or right of fixation followed by a fixation cross that was presented for 100 ms. Cues were repeated shapes and objects from Phase 1 or novel shapes and objects. A target letter, an S or H that subtended 4.2° × 3.9° of visual angle, was then presented for 200 ms on either the same side of the preceding cue (i.e., valid trials) or on the opposite side of the preceding cue (i.e., invalid trials). Targets were presented at the same spatial location as the cues. After the target, the trial concluded with a fixation cross for 1800 ms. Cue and target timing was adapted from Gibson and Kelsey (1998). Participants were told that a shape or object might be presented before each target but the shape or object location would not predict the location of the target. Participants were instructed to identify the target by pressing one of the two buttons as quickly as possible without sacrificing accuracy.

Phase 2 consisted of 400 trials subdivided into those that were cued by shapes (80 repeated shapes and 80
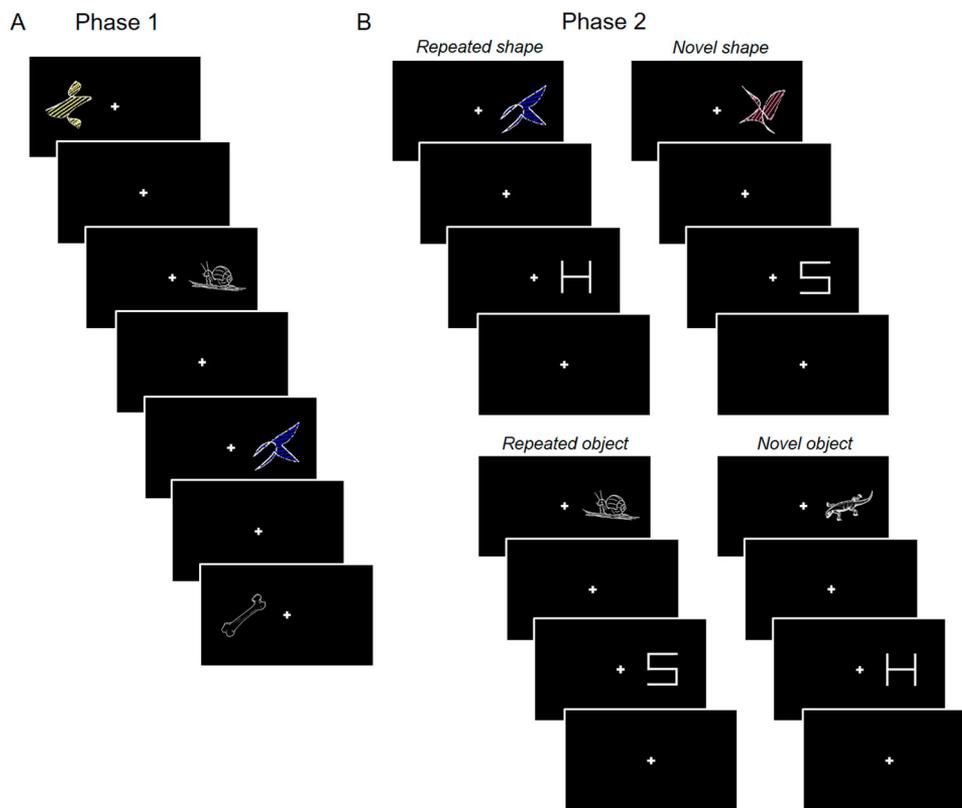
**Figure 1.** (A) Phase 1 of the priming-spatial attention task. Shapes and objects were shown to the left or right of fixation for 100 ms followed by a central fixation cross for 1800 ms. Participants classified each item as relatively "pleasant" or "unpleasant". (B) Phase 2 of the task. Participants identified target letters (S or H) presented for 200 ms in the left or right visual field. Each target letter was preceded by a non-informative shape or object cue (presented for 100 ms) that was repeated or novel in the same/valid hemifield or the opposite/invalid hemifield (only valid trial types are shown).

novel shapes) and those that were cued by objects (80 repeated objects and 80 novel objects). Each of these trials was further equally subdivided into valid and invalid cues. There were an additional 80 trials during which a fixation cross was presented instead of the shape/object cue (i.e., no cue trials), which served as a baseline condition. Repetition (repeated and novel) and validity (valid and invalid) were counterbalanced across participants. Trials were randomised with the constraint that no more than three cue types or spatial locations were consecutively presented.

A final phase (Phase 3) was also conducted for the purposes of acquiring a measure of behavioural priming. In this phase, 20 of the shapes and 20 of the objects that were only presented in Phase 1 were presented intermixed with a set of 20 novel shapes and 20 novel objects. The task was identical to Phase 1 (i.e., participants made a speeded pleasantness response to each item). Data from Phases 1 and 3 were corrupted and could not be analysed. As cue-target response compatibility was not a factor and behavioural priming effects were observed in Experiment 2, this was not of concern.

Phase 2 analyses were conducted on target identification accuracy as well as reaction time for valid trials. Given the specificity of our hypothesis that priming-related increases in activity reflect greater attentional

allocation, we focused on data from valid trials for two reasons. First, valid trials are associated with greater attentional allocation than invalid trials (Posner, 1980). Second, analogous to the valid cues currently employed, it has previously been shown that abrupt onsets occurring at target locations capture attention in a spatially specific manner (Jonides & Yantis, 1988; Mounts, 2000; Remington, Johnston, & Yantis, 1992; for a review, see Yantis, 1993). For completeness, we also provide results pertaining to the invalid trials.

## Results

Figure 2 shows target identification accuracy for valid cue trials as a function of cue type (shape and object) and repetition (novel and repeated). Target detection accuracy was greater than chance in all conditions ($ts(19) > 5.06$, $ps < .001$) except for repeated object cues ($t(19) < 1$, $p > .20$). A two-way repeated measures ANOVA revealed a significant cue type × repetition interaction ($F(1, 19) = 12.77$, $p < .01$; these and all the following degrees of freedom are corrected for nonsphericity using the Greenhouse–Geisser procedure). Follow-up comparisons revealed that accuracy was significantly higher for targets preceded by repeated shapes than novel shapes ($t(19) = 4.79$, $p < .0001$; unless otherwise noted, pairwise $t$-tests are two-
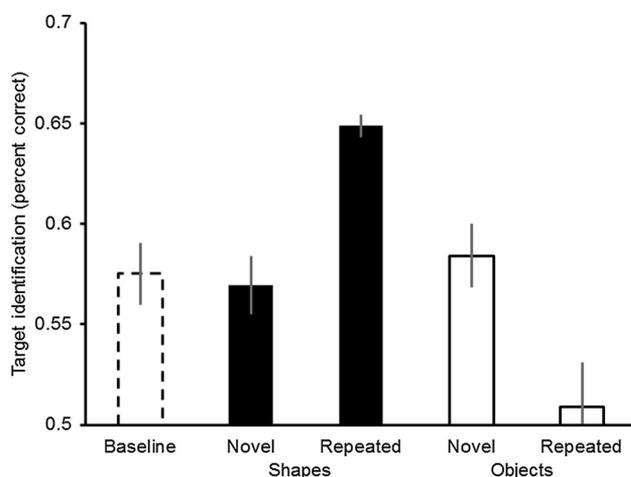
**Figure 2.** Results from Experiment 1. Mean target letter identification accuracy for valid cue trials plotted as a function of cue type (baseline, shape, or object) and repetition (novel or repeated). Baseline refers to target accuracy for no cue trials. Error bars denote ±1 standard error of the mean.

tailed). The opposite pattern was revealed for object cues in that accuracy was significantly lower for targets preceded by repeated than novel objects ($t(19) = 2.28$, $p < .05$).

To further investigate the factors driving the crossover interaction, we conducted a follow-up one-way ANOVA on target accuracy following novel shape cues, novel object cues, and no cue trials (i.e., baseline). Accuracy following these three cue types did not significantly differ ($F < 1$), which suggests the cue type × repetition interaction was due to higher accuracy following repeated shape cues and lower accuracy following repeated object cues. In further support of this, a one-way ANOVA on target accuracy following repeated shape cues, repeated object cues, and no cue trials was significant ($F(1.61, 30.52) = 21.59$, $p < .001$). Follow-up comparisons revealed that accuracy was significantly higher for targets preceded by repeated shapes than repeated objects and no cue trials ($t$s$(19) > 3.30$, $p$s $< .01$). Accuracy following repeated objects was significantly lower than no cue trials ($t(19) = 3.77$, $p < .001$). The difference in target discrimination accuracy did not significantly differ between novel shape cues and novel object cues ($t(19) < 1$, $p > .20$).

Table 1 lists the reaction times for valid cue trials as a function of cue type (shape and object) and repetition (novel and repeated). The cue type × repetition interaction was significant ($F(1, 19) = 12.90$, $p < .001$). Follow-up comparisons revealed that reaction times were significantly slower for targets preceded by novel shape cues than

repeated shape cues ($t(19) = 2.23$, $p < .05$). The opposite was observed for targets preceding objects; reaction times were faster for novel objects than repeated objects ($t(19) = 2.66$, $p < .05$).

Table 2 lists the target identification accuracy for invalid cue trials as a function of cue type (shape and object) and repetition (novel and repeated). The cue type (shape and object) × repetition (novel and repeated) interaction was significant ($F(1, 19) = 16.12$, $p < .001$). Follow-up comparisons revealed that accuracy did not significantly differ for targets preceded by repeated shapes and novel shapes ($t(19) < 1$, $p > .20$), which suggests that repeated shape cues did not affect attentional allocation to the non-cued location. Accuracy was significantly greater for targets preceded by repeated objects than novel objects ($t(19) = 4.44$, $p < .001$), which suggests that repeated object cues increased attentional allocation to the non-cued location. An analogous analysis performed on the reaction times (Table 3) for the same trials types failed to reveal any significant effects ($F$s $< 1$).

## Experiment 2

The previous results suggest that only repeated shapes (i.e., unfamiliar items) increase attentional allocation and boost subsequent target identification accuracy. We conducted a second experiment with two aims. First, we aimed to replicate the previous crossover interaction of cue type and repetition. Second, we aimed to experimentally manipulate familiarity of the abstract shapes to assess whether less familiar shapes, but not more familiar shapes, increase attentional allocation. To manipulate familiarity, we presented shapes and objects once or six times during Phase 1.

### Participants

Twenty Boston College undergraduates with normal or corrected-to-normal vision received credit for a general psychology course or $10 for participation. Data from four

**Table 2.** Accuracy results for invalid cue trials in Experiment 1.

|  | Novel | Repeated |
|---|---|---|
| Shapes | 0.60 (0.01) | 0.59 (0.02) |
| Objects | 0.52 (0.01) | 0.61 (0.02) |
| No cue | 0.59 (0.02) | |

Notes: Mean target letter (S or H) identification accuracy (±1 standard error of the mean) as a function of cue type (shape, object, or no cue) and repetition (novel or repeated).

**Table 1.** Reaction times for valid cue trials in Experiment 1.

|  | Novel | Repeated |
|---|---|---|
| Shapes | 439.09 (14.96) | 420.01 (14.13) |
| Objects | 397.69 (17.46) | 431.48 (14.71) |
| No cue | 455.57 (13.89) | |

Notes: Mean target letter (S or H) identification reaction time (±1 standard error of the mean) as a function of cue type (shape, object, or no cue) and repetition (novel or repeated).

**Table 3.** Reaction times for invalid cue trials in Experiment 1.

|  | Novel | Repeated |
|---|---|---|
| Shapes | 390.46 (15.84) | 403.60 (17.05) |
| Objects | 406.60 (17.82) | 406.88 (16.07) |
| No cue | 455.57 (13.89) | |

Notes: Mean target letter (S or H) identification reaction time (±1 standard error of the mean) as a function of cue type (shape, object, or no cue) and repetition (novel or repeated).

participants were corrupted and thus discarded before the analysis was conducted. One additional participant was excluded from the reaction time analysis because they had no responses to one item type.

## Method

Unless otherwise stated, the experimental procedure was identical to Experiment 1. In this experiment, we manipulated the familiarity of the cue stimuli (shapes or objects). During Phase 1, 40 shapes and 40 objects were shown once and a separate set of 40 objects and 40 shapes were each shown six times (item repetition was counterbalanced across participants). Participants made the same pleasantness judgement as in Experiment 1 (as expected, the mean percent pleasantness ± 1 standard error was 0.52 ± 0.02 for shapes and 0.51 ± 0.02 for objects). During Phase 2, cues consisted of 80 novel shapes, 80 novel objects, 40 shapes previously shown once, 40 objects previously shown once, 40 shapes previously shown six times, 40 objects previously shown six times, and 80 no cue trials. As in Experiment 1, the analysis focused on valid cue trials, but for completeness, results pertaining to invalid trials are also reported.

## Results

Figure 3(A) shows target identification accuracy for validly cued trials as a function of cue type (shape and object) and repetition (novel, repeated once, and repeated six times). Target detection accuracy was greater than chance in all conditions ($ts(15) > 3.75$, $ps < .01$) except for object cues repeated once ($t(15) = 1.60$, $p = .13$). A two-way repeated measures ANOVA revealed a significant cue type (shape and object) × repetition (novel, repeated once, and repeated six times) interaction ($F(1.85, 27.71) = 11.73$, $p < .001$).

First, we assessed whether we replicated our previous findings. A two-way repeated measures ANOVA revealed a significant cue type (shape and object) × repetition (novel and repeated once) interaction ($F(1, 15) = 28.47$, $p < .001$; see bars 2, 3, 5, and 6 in Figure 3(A)). Follow-up comparisons revealed the identical pattern as the previous experiment. That is, accuracy was significantly higher for targets preceded by repeated shapes than novel shapes ($t(15) = 7.33$, $p < .0001$) and accuracy was significantly lower for targets preceded by repeated objects than novel objects ($t(15) = 2.46$, $p < .05$).

Second, we assessed whether increasing shape familiarity by repeating them six times during Phase 1 reduced attentional allocation. A two-way ANOVA on target accuracy did not reveal a significant cue type (shape and object) × repetition (novel and repeated six times) interaction ($F < 1$; see bars 2, 4, 5, and 7 in Figure 3(A)). Even when directly comparing accuracy for the two pairs (i.e., bar 2 versus bar 4 and bar 5 versus bar 7), no significant differences were observed ($ts(15) < 1.06$, $ps > .20$). These
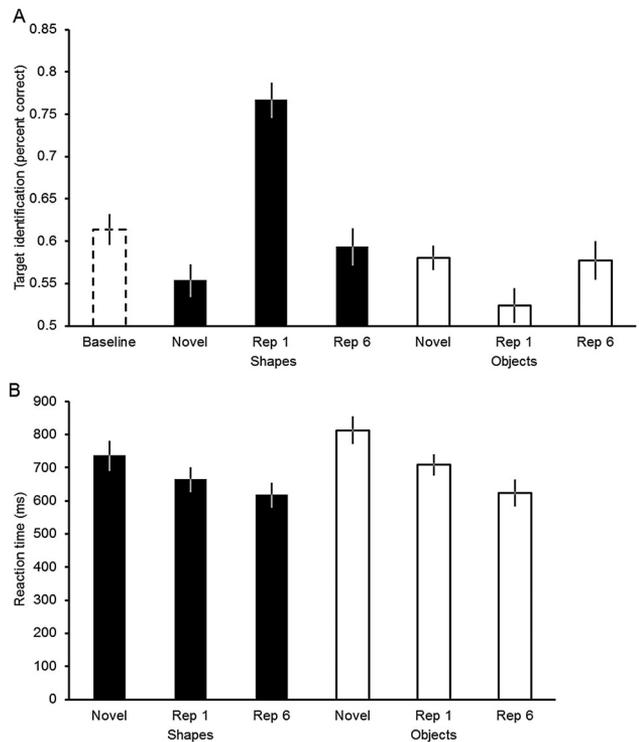


**Figure 3.** Results from Experiment 2. (A) Mean target letter identification accuracy for valid cue trials plotted as a function of cue type (baseline, shape, or object) and repetition (novel, repeated once, or repeated six times). Baseline refers to target accuracy for no cue trials. (B) Mean Phase 1 pleasantness judgment reaction time (in milliseconds) for shapes and objects as a function of repetition (novel, repeated once, and repeated six times). Error bars denote ±1 standard error of the mean.

results indicate that with sufficient exposure, shapes are no longer associated with increased attentional allocation.

Table 4 lists the reaction times for valid cue trials as a function of cue type (shape and object) and repetition (novel, repeated once, and repeated six times). Analyses of the reaction time data failed to reveal any significant effects ($Fs < 4.25$, $ps > .05$).

Table 5 lists the target identification accuracy for invalid cue trials as a function of cue type (shape and object) and repetition (novel, repeated once, and repeated six times). An ANOVA with factors cue type (shape and object) and repetition (novel and repeated once) revealed a significant interaction ($F(1, 15) = 16.60$, $p < .001$). Follow-up comparisons did not reveal any significant differences between targets preceded by novel shapes or shapes repeated once ($t(15) = 1.00$, $p > .20$), which replicates Experiment 1 and suggests that repeated shape cues did not affect

**Table 4.** Reaction times for valid cue trials in Experiment 2.

|  | Novel | Repeated once | Repeated six times |
| --- | --- | --- | --- |
| Shapes | 451.22 (19.18) | 478.89 (23.67) | 448.41 (14.19) |
| Objects | 450.46 (17.67) | 440.22 (16.42) | 470.19 (20.23) |
| No cue | 443.82 (14.02) | | |

Notes: Mean target letter (S or H) identification reaction time (±1 standard error of the mean) as a function of cue type (shape, object, or no cue) and repetition (novel, repeated once, or repeated six times).

**Table 5.** Accuracy results for invalid cue trials in Experiment 2.

|  | Novel | Repeated once | Repeated six times |
|---|---|---|---|
| Shapes | 0.63 (0.02) | 0.58 (0.04) | 0.61 (0.03) |
| Objects | 0.55 (0.02) | 0.61 (0.02) | 0.61 (0.03) |
| No cue | 0.61 (0.02) | | |

Notes: Mean target letter (S or H) identification accuracy (±1 standard error of the mean) as a function of cue type (shape, object, or no cue) and repetition (novel, repeated once, or repeated six times).

attentional allocation to the non-cued locations, or between novel objects and objects repeated once ($t(15) = 1.41$, $p > .10$). Another ANOVA with factors cue type (shape and object) and repetition (novel and repeated six times) did not reveal any significant effects ($Fs < 3.09$, $ps > .05$). Analogous analyses performed on the reaction times (Table 6) did not reveal any significant effects ($Fs < 3.73$, $ps > .05$).

We also confirmed that our stimuli were associated with standard behavioural priming effects of faster reaction times with increasing repetition. Figure 3(B) shows reaction times as a function of shape and object repetition in Phase 1, during which pleasantness judgments were made. A two-way repeated measures ANOVA revealed a significant stimulus type (shape and object) × repetition (novel, repeated once, and repeated six times) interaction ($F(1.47, 20.56) = 4.85$, $p < .05$). The interaction was driven by a significantly greater difference in reaction time for objects repeated six times versus novel objects than the difference in reaction time for shapes repeated six times versus novel shapes ($t(14) = 2.10$, $p < .05$; compare bar 1 versus bar 3 and bar 4 versus bar 6). Follow-up comparisons revealed a monotonic decrease in reaction time as a function of repetition (novel > repeated once > repeated six times) for each stimulus type ($ts(14) > 2.04$, $ps < .05$, one-tailed; see Henson, 2003). These behavioural priming effects replicate those observed in prior studies (e.g., Buckner et al., 1998).

There was no correspondence between the mean of the pleasantness responses for each item in Phase 1 and the subsequent target response in Phase 2 for shapes (0.43 ± 0.02) or objects (0.46 ± 0.02; $t(15) < 1$, $p > .20$). This indicates that the preceding target identification results were not influenced by response compatibility.

## Discussion

Prior studies have demonstrated that unfamiliar item priming is associated with an increase in neural activity (Fiebach et al., 2005; Henson et al., 2000; Schacter et al.,

**Table 6.** Reaction times for invalid cue trials in Experiment 2.

|  | Novel | Repeated once | Repeated six times |
|---|---|---|---|
| Shapes | 453.29 (18.25) | 462.57 (17.56) | 449.95 (19.29) |
| Objects | 455.23 (14.64) | 437.17 (14.75) | 422.50 (15.32) |
| No Cue | 443.82 (14.02) | | |

Notes: Mean target letter (S or H) identification reaction time (±1 standard error of the mean) as a function of cue type (shape, object, or no cue) and repetition (novel, repeated once, or repeated six times).

1995; Slotnick & Schacter, 2006; Uecker et al., 1997). We hypothesised that these repetition-related increases in activity are mediated, in part, by attentional allocation to repeated unfamiliar items. The results across both experiments in the present study support our hypothesis that neural priming effects for unfamiliar items are mediated by increased attentional allocation. Specifically, target identification accuracy was greater following repeated unfamiliar shapes cues than novel unfamiliar shape cues. As we experimentally manipulated shape familiarity in Experiment 2, we also found evidence that sufficient exposure to unfamiliar items – such that they become familiar – reduced their ability to draw attention. In direct opposition to the results for unfamiliar shape cues, there was a decrease in target identification accuracy for repeated versus novel familiar object cues.

It is notable that the present error rates were relatively higher than the error rates of Gibson and Kelsey (1998), as both studies employed similar stimulus timing. There are two important differences between these studies. First, reaction times for our study were faster than Gibson and Kelsey. This can be attributed to our stressing that response speed was very important. Of particular relevance, the colour condition of Experiment 2 in Gibson and Kelsey is most parallel to our study, as the colour distractors did not share any features with the targets. Similarly, in our study, the shape distractors did not share any features with the targets. In Gibson and Kelsey, the reaction time for valid trials was approximately 540 ms, while in our study the reaction time for valid trials was approximately 420 ms. Thus, the relatively higher error rates in our study can be attributed to a speed-accuracy trade-off. Of additional relevance, Gibson and Kelsey did not observe any reaction time effects in this condition, which is consistent with our null cue type × repetition reaction time effects in Experiment 2. Second, the relationship between the cues and targets differed between our study and the Gibson and Kelsey study. In our study, the cue (object or shape) spanned the entire spatial location of the target (S or H); the targets were smaller than cues. However, in Gibson and Kelsey, the cue was a box outlined in yellow or red and the targets appeared within the box. Thus, the spatial location of the target in Gibson and Kelsey was not masked. As such, one possible explanation for why the current error rates are relatively higher is due to forward masking by the cue as it occupied the same spatial location as the target. Critically, we replicated the findings of Experiment 1 in Experiment 2, which demonstrates that our accuracy effects are reliable. Thus, the intermediate accuracy in the current study can be attributed to the unique task instructions and/or stimulus parameters we employed.

It is important to consider stimulus differences across the shapes and objects (e.g., colour) that may have affected the results. There are two reasons why stimulus differences cannot account for our results. First, there would have been differences in the target identification accuracy following

novel shape cues and novel object cues. This was not the case in either experiment. Second, we would not have been able to experimentally manipulate the familiarity of shapes and objects such that identification accuracy did not differ. That is, in Experiment 2 target detection accuracy following shapes repeated six times was statistically equivalent to target detection accuracy following objects repeated six times. Therefore, if our effects were due to stimulus differences, our manipulation of repetition would not have been effective (i.e., there would have been a residual difference in attention due to the stimulus differences, which was not observed).

The present study is unique with respect to its overall approach. Specifically, we conducted a behavioural study to uncover the cognitive processes associated with a neural finding. This stands in contrast to the vast majority of cognitive neuroscience experiments that have been conducted with the aim of uncovering the neural regions associated with a behavioural finding. As the present experiments provide evidence for the involvement of the cognitive process of attention during a priming task, future studies that identify neural activity during priming tasks should consider that such activity might reflect attention rather than simply assuming it reflects fluency (cf., Thakral et al., 2016).

It is important to point out that standard measures of priming are complex and should not be assumed to reflect a single process (e.g., fluency). The present behavioural findings suggest that attention may also influence priming effects. Of direct relevance to this point, a recent neuroimaging study examined unfamiliar shape priming (Thakral et al., 2016) and identified activity with the contrast of novel shapes > repeated shapes. Activity was identified in the superior parietal lobule, an area commonly attributed to attentional control processing (for a review, see Yantis & Serences, 2003). This finding strengthens the claim that attentional processing can occur during priming tasks. Of additional relevance, in Slotnick and Schacter (2006), participants made a speeded internal line orientation judgment to repeated old, repeated similar, and novel shapes. Reaction time did not differ between repeated old shapes and repeated perceptually similar shapes and was faster for both item types as compared to novel shapes. fMRI analyses revealed distinct visual regions associated with non-specific priming (i.e., (repeated old = repeated similar) > novel) and specific priming (i.e., repeated > (novel = related)). These findings support the idea that priming is an amalgam of many underlying neural and cognitive operations (see also, Dehaene et al., 2001).

We have attributed neural priming effects for unfamiliar items to magnification of sensory processing due to attention. However, this does not preclude the possibility that more fluent processing may also be occurring when unfamiliar items are repeated (i.e., the traditional explanation for neural priming effects; see Gotts et al., 2012;

Grill-Spector et al., 2006; Schacter, Wig, & Stevens, 2007). That is, the processes of fluency and attention are not mutually exclusive. It may be the case that with repetition, unfamiliar items are more fluently processed but the effects of attention (e.g., an increase in visual cortical activity) overshadow the effects of fluency (e.g., a decrease in visual cortical activity). We also note that the attentional account of priming effects for unfamiliar items may also extend to familiar items. As can be seen in Figure 2, accuracy following repeated object cues was significantly lower than accuracy following novel object cues (and novel object cue and no cue accuracy did not differ). These results suggest that attentional processing may be significantly reduced when familiar items are repeated (cf., Henson & Rugg, 2003). Interestingly, attentional processing did not appear to change when unfamiliar or familiar items were repeated six times (Figure 3(a)). This suggests that attentional processing of repeated items dissipates with increased item repetition, which is a topic of future research.

Although the current results support an attention account of neural priming, there is an alternative that deserves mention. According to prior proposals (e.g., Henson et al., 2000; Martens & Gruber, 2012), repetition-related increases in activity associated with unfamiliar stimuli reflect the formation of new cortical representations. This stands in contrast to neural priming for familiar stimuli that is associated with repetition-related decreases in neural activity and is assumed to reflect the sharpening of an already existing representation (see the "Introduction" section). This formation account of unfamiliar item priming may co-exist with our attentional account. For example, it may the case that attention fosters the formation of a new cortical representation by amplifying the processing of repeated unfamiliar item features.

One line of research has indicated that when a stimulus is of biological relevance (Brosch, Sander, Pourtois, & Scherer, 2008; Pool, Brosch, Delplanque, & Sander, 2014) or valued (Anderson, Laurent, & Yantis, 2011; Anderson & Yantis, 2012), it is more likely to capture attention. With regard to the present findings, it is unclear whether repeated shapes might be of greater biological relevance or value than novel shapes, or whether attention is allocated to repeated unfamiliar items for some other reason. This is a topic of future research.

In the present study, abstract shapes were classified as unfamiliar stimuli and objects were classified as familiar stimuli. In a prior study by Henson et al. (2000), face stimuli were employed. Familiar stimuli in that study were famous faces and unfamiliar stimuli were nonfamous faces. Although, faces in and of themselves are familiar, nonfamous faces produced a repetition-related increase in activity. Considered together, the present results and those of Henson et al. (2000) suggest that the extent to which a stimulus is familiar may depend on the particular

paradigm. This is an important and open question that deserves further investigation.

The current findings are the first to suggest that priming-related increases in visual cortical activity may be mediated by attention. As the accuracy effects directly paralleled the known neural priming effects for both unfamiliar and familiar stimuli, the current study provides a mechanism for neural priming. Specifically, unfamiliar item priming takes the form of an increase in activity for repeated items that is analogous to the increase in target accuracy following repeated shape cues (i.e., as there was greater attentional allocation when they were repeated). In contrast, familiar item priming takes the form of a reduction in activity that is analogous to the decrease in target accuracy following repeated object cues (i.e., as there was less attentional allocation when they were repeated). Future fMRI research should assess whether unfamiliar item repetition priming and attention produce activity in the same neural regions, which would bolster the present behavioural findings.

## Acknowledgements

## Disclosure statement

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