

ELECTROPHYSIOLOGICAL CORRELATES OF THE INFLUENCES OF
PAST EXPERIENCE ON CONSCIOUS AND UNCONSCIOUS FIGURE-GROUND
PERCEPTION

by

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ABSTRACT

Figure-ground perception can be modeled as a competitive process with mutual inhibition between shape properties on opposite sides of an edge. This dissertation reports brain-based evidence that such competitive inhibition can be induced by access to preexisting object memory representations during figure assignment. Silhouette stimuli were used in which the balance of properties along an edge biased the inner, bounded, region to be seen as a novel figure. Experimental silhouettes (EXP) suggested familiar objects on their outside edges, which nonetheless appeared as shapeless grounds. Control silhouettes (CON) suggested novel shapes on the outside.

In an initial task, human observers categorized masked EXP and CON silhouettes (175 ms exposure) as “novel” versus a third group of silhouettes depicting “familiar” objects on the inside. Signal detection measures verified that observers were unconscious of the familiar shapes within the EXP stimuli. Across three experiments, novel categorizations were highly accurate with shorter RTs for EXP than CON. Event-related potential (ERP) indices of observers’ brain activity (Experiments 2 and 3) revealed a Late Potential (~300 ms) to be less positive for EXP than CON, a reduction in neural activity consistent with the presence of greater competitive inhibition for EXP stimuli. After controlling for stimulus confounds (Experiment 3), the P1 ERP (~100 ms) was larger for EXP than CON conditions, perhaps reflecting unconscious access to object memories.

In a second task, observers were informed about familiar shapes suggested on the outsides of the EXP silhouettes before viewing masked (Experiments 1 and 2) or unmasked (Experiment 3) EXP and CON silhouettes to report whether they saw familiar

shapes on the outside. Experiment 3 observers were more accurate to categorize CON vs. EXP stimuli as novel vs. familiar, with shorter RTs for EXP than CON. Task 2 N170 ERPs (~170 ms) were larger for EXP than CON in Experiments 2 and 3, reflecting the conscious perception of familiar shape in the outsides of EXP silhouettes. LP magnitudes were greater for CON than EXP, although their polarity was dependent on the presence/absence of a mask. Task 2 LPs may reflect competitive inhibition or longer processing times for CON stimuli.

1. INTRODUCTION

1.1 Figures and Grounds

The visual world we experience consists of a rich and varied collection of shapes presented against often formless backgrounds. The process by which the visual system separates regions of our visual field that are perceived as having shape (“figures”) from those that do not (“grounds”) is called *figure-ground segregation*.¹ Figure-ground segregation has been generally understood as taking place along a contour extracted by the visual system that is shared by two bordering regions in visual space (Rubin, 1915/1958). Typically the contour is allocated to one region or the other by the visual system, and the resulting perception of the region is of a shaped figure that occludes the remaining background. The ground region is perceived to be shapeless near the border shared with the figure and appears to continue behind it. In this manner, figure-ground segregation also encompasses assignment of depth as well as shape (Rubin, 1915/1958).

The allocation of a contour to a particular region is determined by the *configural properties* of the regions bordering the contour (Figure 1); the term “configural” was introduced by the Gestalt psychologists to refer to the fact that such properties lead to the perception of a figure. These properties “cue”, or signal, figure-ground relationships, and are thus called *configural cues* (Peterson, 2003). Several low-level configural cues have been identified so far (see Figure 1A, B; for review, see Hochberg, 1971; Pomerantz and Kubovy, 1986), including relative area (the relative sizes of different visual regions),

¹ Figure-ground segregation is one of several visual processes involved in visual object perception, which also include contour extraction from the retinal image, grouping of related visual elements, and surface completion.

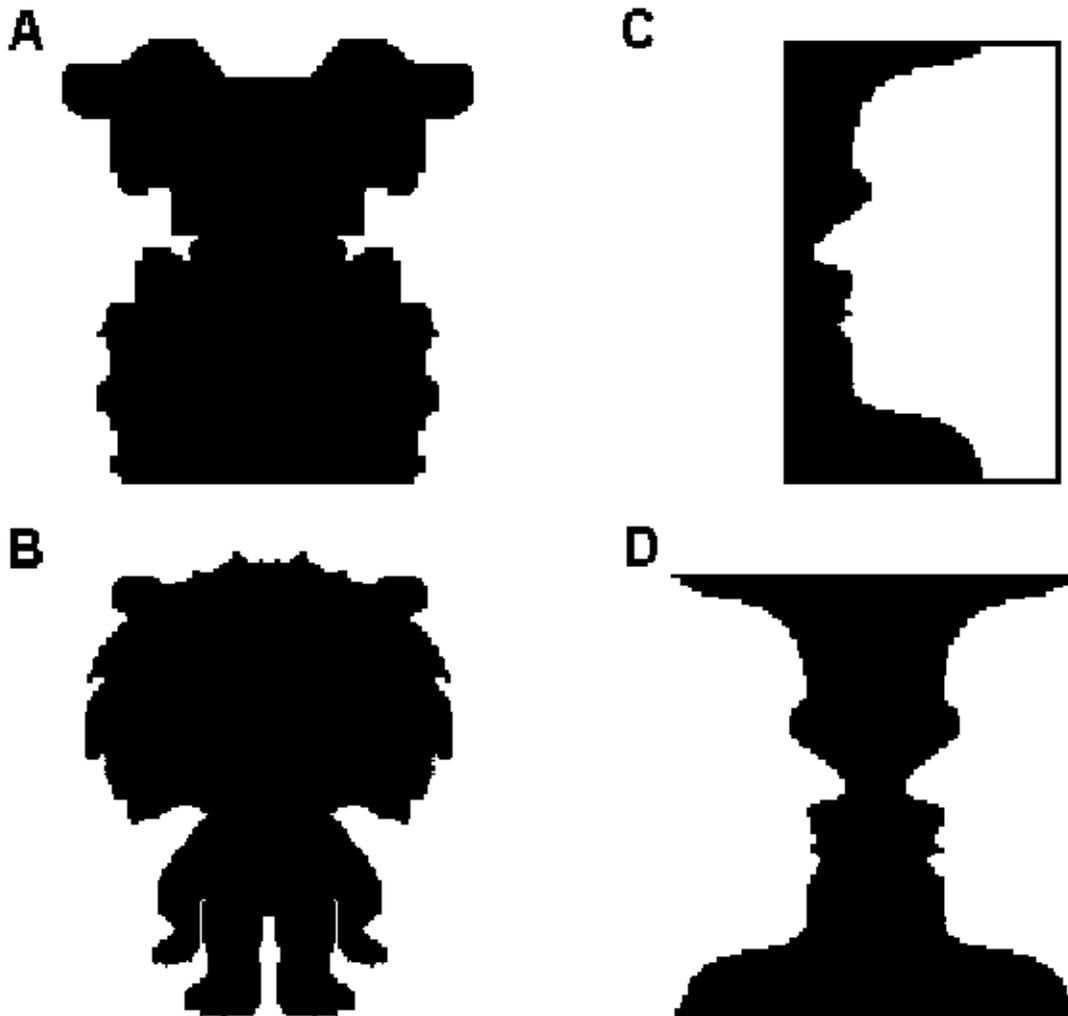


Figure 1. Configural cues to figure-ground segregation. The black regions of A), B), and D) are small in area, enclosed, symmetric about a vertical axis drawn through their centers, and contain convex regions that protrude into the surrounding white regions. A) A novel shape. B) A silhouette of a lion facing the viewer; the meaningfully shaped contour instantiates a cue of past of experience that favors the black region to be seen as a meaningfully shaped entity. C) An asymmetric bipartite stimulus in which two regions (black and white) share a border, with the white region portraying a known shape (a face). D) Rubin's face-vases stimulus which illustrates that both sides of a shared border may contain past experience cues. Rubin's stimulus also illustrates the coupling between figural status and conscious recognition, as the faces and vase are only consciously seen when seen as figure (see Section 1.3.2).

enclosure (whether the bounding contours of the regions are enclosed or open-ended),

symmetry (whether a given region is symmetric in shape), and *convexity* (whether the

region is convex or concave).

More recently it has been discovered that the high-level cue of *past experience* with the shape of a bounding contour - that is, the familiarity or meaningfulness of a contour in terms of resemblance to previously encountered shapes/objects - can also influence figure-ground segregation (Figure 1B, C, D). Past experience may favor only one side of a contour as figure (Figure 1B, C) or both (Figure 1D). Although initially contentious, substantial behavioral evidence supporting a role of past experience in figure assignment has accumulated over recent years (see Sections 1.3 and 1.4, below). The present study contributes to this literature by examining the neural correlates (as measured via human electrophysiology) of the influence of past experience as it interacts with other configural cues during figure-ground perception.

1.2 Competitive Models of Figure-Ground Segregation

Contemporary computational accounts of figure-ground segregation conceptualize figure assignment as arising from cross-edge competition between the configural cues of the regions bordering each side of a shared contour. Early models of figure-ground segregation, however, implemented cross-edge competition among low-level features such as color, texture, or luminance. For example, Kienker, Sejnowski, Hinton, & Schumacher, (1986) proposed a model consisting of two layers, an edge layer and a figure layer. Each point of the edge layer contained pairs of adjacent edge units pointing in opposite directions that inhibited each other, while neighboring figure units excited each other. Furthermore, edge units mutually excited adjacent figure units located in the

preferred direction of the edge units, and inhibited figure units in the opposite direction. The stimulus values input into the network, representing a variety of simple low-level visual features, filled adjacent regions to activate the edge and figure units on the two sides of a contour. These models also included a top-down effect of attention, which was simulated as an intrinsic bias in the figure units centered at a particular point; the strength of this bias dropped off with a Gaussian distribution over nearby units. When this attention bias was focused on a point in one region, activity increased in nearby figure units. As the edge and figure units interacted with each other over successive iterations of the network, activity of the figure units filling the attended region (and the edge units surrounding them) was enhanced relative to that of the complementary figure and edge units. This relative enhancement of figure unit activity was taken to instantiate figure assignment.

Consistent with this computational model, Lamme and his colleagues (e.g., Lamme, et al., 1999; Zipser, et al., 1996) found that the responses of low-level V1 neurons are enhanced when a figure rather than a ground lies within their receptive fields. These results were modeled by Roelfsema, Lamme, Spekreijse, and Bosch (2002) using feedback from units lying at higher levels to achieve an enhanced figural response. The higher level units had large receptive fields due to the fact that each unit pooled together inputs from topographically neighboring units at lower levels with smaller receptive fields. In turn, the high level units fed back activity to lower level units, releasing these units from lateral inhibition. As in the Kienker et al. (1987) model, this setup resulted in relatively enhanced figure responses in the low-level units responding to the simple

features filling the figure and ground regions. Neither Roelfsema et al. (2002) nor Kienker et al. (1987) directly incorporated the effects of past experience into their models, however.

In order to account for past experience, Vecera and O'Reilly (1998; 2000) proposed an interactive hierarchical model that implemented a similar architecture as the Kienker et al. (1987) model, with the addition of a third layer of units coding for orientation dependent object memories. Units in this object layer represent one entire bounded region lying on a given side of the shared contour depicted by an input figure-ground stimulus. This representation includes all of the edges and points contained within the region, and thus may be considered as a pointillistic object memory template. For any given stimulus, only one of the two potential figural regions would obtain a good match to a given template represented in the object layer, and thus would cause the corresponding object unit to become activated. This activation would then be fed back to the lower level figural level over successive iterations to cause the network to settle on the single figure interpretation that best matched the corresponding shape representation. One limitation of the Vecera and O'Reilly (1998; 2000) model is that competition only takes place among low-level features that fill the regions subsequently cued to be figure or ground; there is no competition among object units. Such low-level "fill features" are not the same as configural cues because the latter are defined in terms of the spatial relationships among these features including parts of the bounding contour.² Thus

² One exception to this may be the cue of relative area, which appears to rely more upon the quantity or strength of features present within a region.

PIMOCA (Parallel Interactive Model of Configural Analysis)

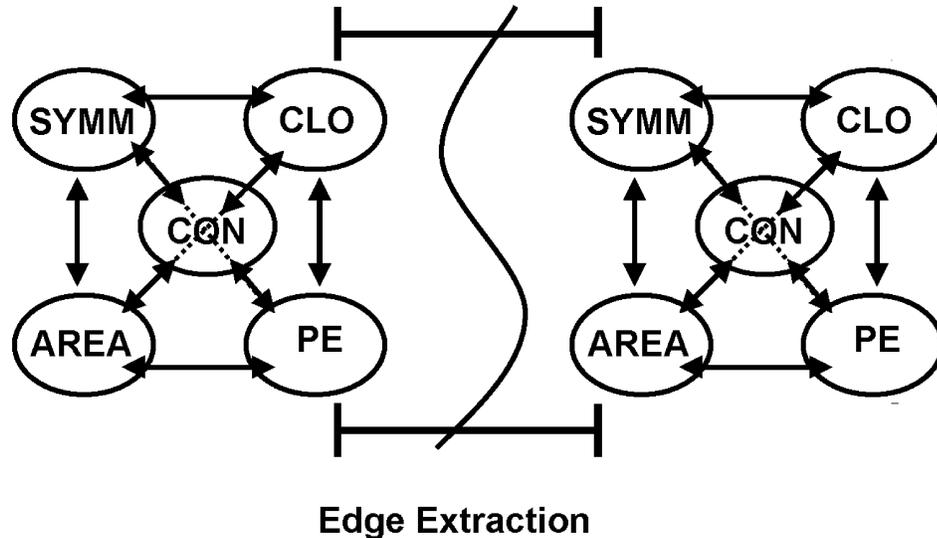


Figure 2. Parallel Interactive Model of Configural Analysis (PIMOCA). Figure-ground segregation occurs after an edge is extracted by the visual system. Cues on the same side of an edge cooperate and facilitate each other (represented by double arrows). Cues on opposite sides of an edge compete and inhibit each other (represented by T-shaped terminations). SYMM = symmetry, CLO = closure, AREA = relative area, CON = convexity, PE = past experience. Figure adapted from Vision Research, Vol. 40, Peterson, M. A., de Gelder, B., Rapcsak, S. Z., Gerhardstein, P. C., and Bachoud-Lévi A.C., "Object memory effects on figure assignment: Conscious object recognition is not necessary or sufficient", pp. 1549-1567, Copyright (2000), with permission from Elsevier.

the Vecera and O'Reilly model, as well as the models of Kienker et al. and Roelfsema et al., does not fully realize for the idea of competition among configural cues, especially the cue of past experience.

Peterson (1999a) and Peterson, de Gelder, Rapcsak, Gerhardstein, and Bachoud-Lévi (2000) proposed a competitive model of figure-ground segregation in which competition takes place among all configural cues present in a stimulus. In this model, called the Parallel Interactive Model of Configural Analysis (PIMOCA), edge-based

access to object memory representations occurs in parallel³ with the processing of depth and configural cues early on in the process of figure-ground segregation (see Figure 2). The configural cues (including past experience) on the same side of an edge cooperate and those on opposite sides compete. The balance of low- and high-level cues across the edge ultimately determines the final figure-ground segregation, with each set of cues mutually inhibiting each other until one set wins the competition to promote that region as figure while inhibiting the set of losing cues. Importantly, inhibition from the more strongly cued to the more weakly cued side of an edge explains the fact that grounds are perceived as shapeless.

A key prediction of this model is that the more competition present across an edge, the greater the cross-edge competition and mutual inhibition, at least in the initial stages of competition before one set of cues begins to dominate. This notion is illustrated in Figure 3. Figure 3A shows a representative figure-ground stimulus. The configural cues of closure, relative area, symmetry, and convexity favor the central black region of the stimulus to be seen as figure against the cue of convexity operating in the outside white region along the lateral border of the silhouette. In this case there is weak competition across the edge because only one cue favors the white region as figure. Since the amount of mutual inhibition assumed by the model is proportional to the degree of competition across the edge, it follows that there is weak mutual inhibition across the edge as well. The mutual inhibition is weak in the sense that the total inhibition

³ The initial activation of object memories by low-level edge detectors could be mediated by neuronal projections between lower and higher visual areas that bypass intermediate regions. Crude projections from V1 to V4 and V2 to TEO have been reported in macaque visual cortex (Nakamura et al., 1993).

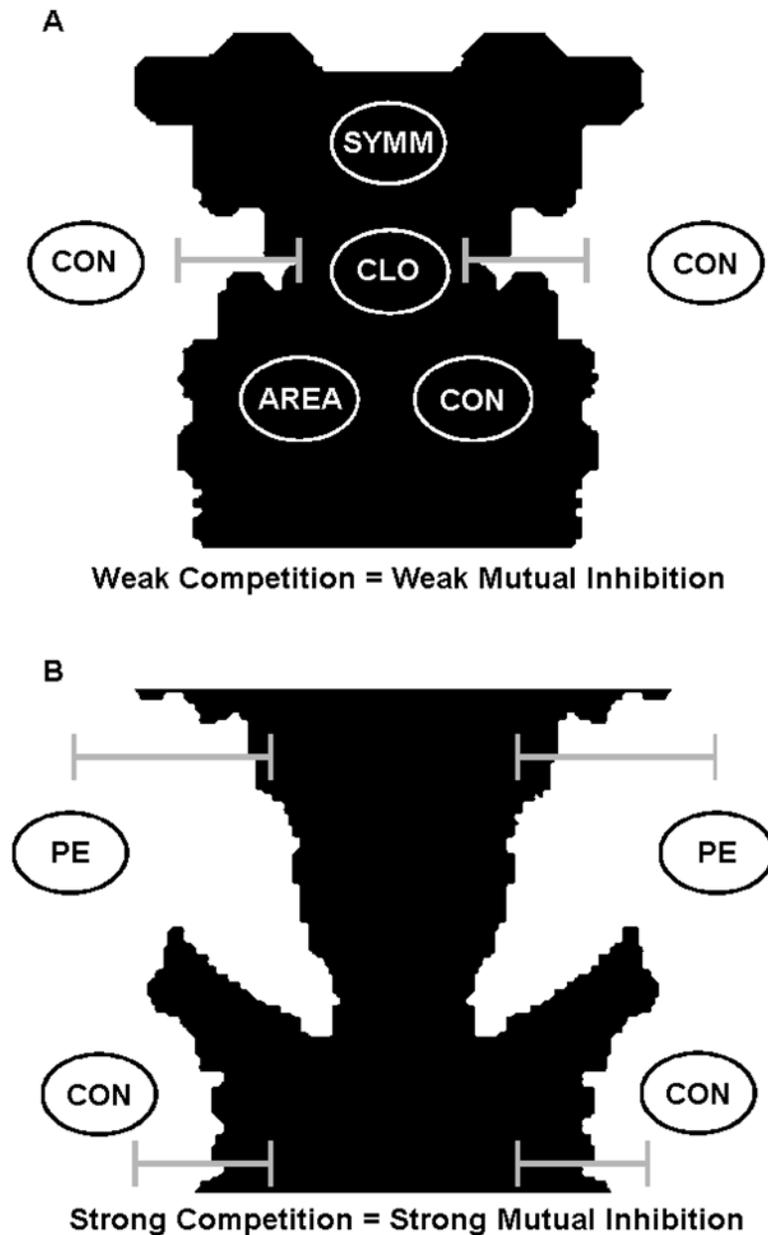


Figure 3. A) Weak competition equals weak mutual inhibition. The cues of symmetry (SYMM), closure (CLO), relative area (AREA), and convexity (CON) operate within the central black region and compete with the single cue of convexity operating along the outer white regions lateral to the silhouette edge. The cross-edge competition is weak, and thus the mutual inhibition (represented by the grey t-junction line) is also weak. B) Strong competition equals strong mutual inhibition. The cue of past experience (PE) operates in conjunction with convexity along the outer edges of the stimuli in competition with the same central cues as in A (not depicted). The more cues competing across the edge leads to greater mutual inhibition (represented by multiple grey t-junction lines).

occurring across the edge in both directions is asymmetrical, i.e. there is strong inhibition of cues within the white region by cues within the black region, but little-to-no inhibition of cues within the black region by cues within the white region.

Figure 3B shows another figure-ground stimulus that again has the same cues biasing the black region to be seen as figure. Along with convexity, however, cues to past experience are also operating along the outside edges of the silhouette. In this case there is stronger competition across the edge than for the stimulus depicted in Figure 3A because there are now two cues favoring the white region as figure. Since the cross-edge inhibition is now more symmetrical (although not completely so), the mutual inhibition of cues across the edge is stronger for this stimulus than for that of Figure 3A.

To summarize: the three main features of the PIMOCA framework are 1) cross-edge competition among configural cues, 2) mutual inhibition of cues on opposite sides of an edge, and 3) suppression of the cues on the losing side of the contour. To date, behavioral evidence has been found for cross-edge competition and suppression of cues of the ground side of a contour (Peterson and Kim, 2001; Peterson and Lampignano, 2003; Peterson and Enns, 2005; Peterson and Skow, submitted; see Section 1.4 for review), but not for mutual inhibition. A central purpose of the present study was to investigate if any evidence for mutual inhibition could be obtained during figure-ground perception.

In order to accomplish this goal, the present study (as in earlier tests of the PIMOCA model; see Section 1.4) used stimuli in which cues to past experience were placed in direct competition with other configural cues in order to induce competition and

mutual inhibition. As mentioned in Section 1.1, however, the status of past experience as a configural cue has been contentious. In order to provide the proper background for the experiments reported in this paper, the next section (Section 1.3) briefly discusses the historical controversy and early experimental evidence for a role of past experience in figure assignment. The subsequent section (Section 1.4) briefly reviews some evidence for competition and suppression among past experience and other configural cues as described by the PIMOCA framework. A final section (Section 1.5) outlines the rationale for, and basic design, of the experiments reported in the rest of this paper.

1.3 The Controversy Over a Role for Past Experience in Figure Assignment

It has long been thought that figure-ground segregation is an “early” process that occurs before, and is thus uninfluenced by, access to pre-existing object memories established through past experience. This *figure-ground-segregation-first* assumption (Peterson, 1999b) originated with the twentieth century Gestalt psychologists who held that imposition of shape upon unorganized visual input was necessary before the shape could be matched to pre-existing shape or object memories. This view arose in response to the earlier Structuralist viewpoint that past experience (memory) imposes shape directly upon unorganized visual input (Peterson, 1999b). The Gestaltists considered the Structuralist viewpoint problematic because of the large number of memories stored at any given time within the visual system; how is the proper memory chosen (out of all possible memories) to impose shape upon unorganized visual input in the rapid and efficient manner characteristic of the visual system? Instead, the Gestaltists reasoned that

it was necessary for visual input to be organized before making a match in memory; such organization would then constrain the shape memory matching process.

1.3.1 Does Past Experience Facilitate Figure Assignment?

The initial evidence taken in support of the figure-ground-segregation-first assumption is the fact that unfamiliar shapes are easily perceived as figures, thus precluding any influence of past experience (Peterson, 1999a; Peterson and Skow-Grant, 2003). This assumption was supported by the identification of the several low-level configural cues described in Section 1.1, above. Although these cues can form the basis of figure-ground segregation, it does not follow that figure-ground segregation is therefore uninfluenced by past experience (Peterson, 1999b). Confirming the figure-ground-segregation-first assumption requires the demonstration that systematic manipulation of familiarity does not affect figure-ground segregation while holding other configural cues constant. Although Rubin (1915/1958) found some evidence that past experience with a figure-ground display influences later viewings of the same display, as observers were more likely to perceive the same region as figure over repeated viewings, in general the Gestalt psychologists did not study the role of familiarity in a stringent and systematic manner.

Systematic examination of the influence of high-level shape cues on figure assignment began with the work of Peterson, Harvey, and Weidenbacher (1991) that used direct reports of first-perceived figure-ground organization in black and white figure-ground displays. These displays consisted of a black region enclosed by a white region,

with the regions sharing lateral contours (see Figure 4). These stimuli were designed using the Gestalt configural cues of symmetry, relative area, enclosure, and convexity such the central black region was perceived as figure. The shared contours were shaped in a manner such that the surrounding regions of the silhouette were interpreted by 97% of observers as depicting one of two familiar shapes when presented upright, a standing woman (Figure 4A) and a hooked-nose face in profile (Figure 4B) when presented upright. Thus the surrounding regions of the upright stimuli were highly denotative of a familiar shape. When these stimuli were inverted, however, only 16% agreed on a single interpretation of the surrounding regions; thus the inverted surrounds were lower in denotating a familiar shape than in the upright case. The stimuli were presented to experimental participants for 30-second intervals; their task was to hold either the black or white region as figure for as long as possible, and report via button press when a figure-ground reversal occurred. For each trial, the mean time intervals of intended and unintended figure perceptions were determined.

The study found that participants were able to maintain the surround as figure for longer intervals when it was upright than when inverted, while the center was maintained as figure for shorter times in the upright than inverted orientation. The latter results indicate that participants were more likely to reverse into seeing the high denotative region as figure in upright than inverted orientations. Thus these results suggest that high-level shape recognition procedures can influence both the temporal length of figural maintenance and the probability that figural status will reverse into the surround as figure

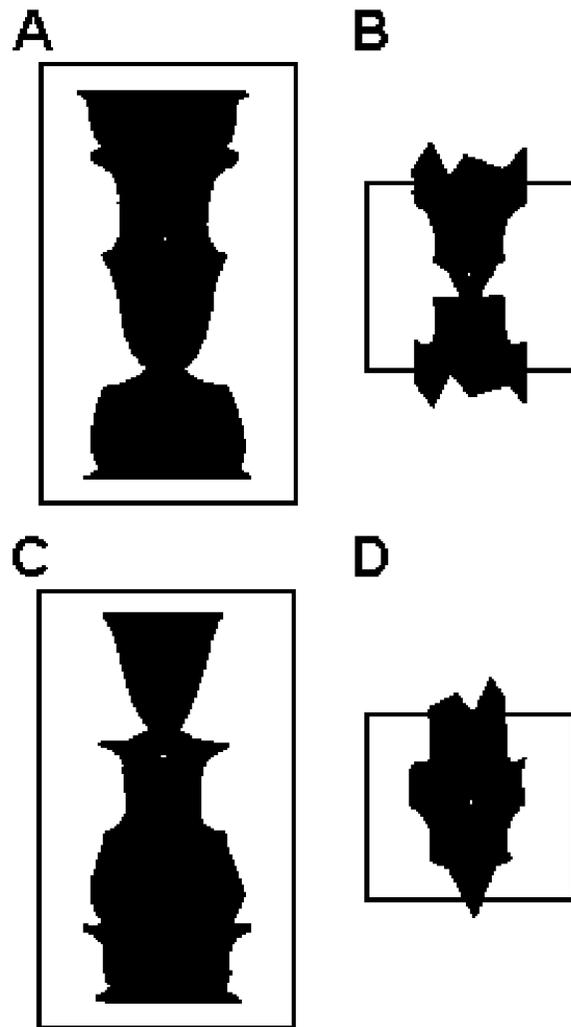


Figure 4. Upright versions of figure-ground stimuli used by Peterson et al. (1991). Silhouettes outer regions in A) and B) respectively denote a standing women and hooked-nose faces in profile. C) and D) show scrambled versions of stimuli in A and B. Reprinted with permission from *Journal of Experimental Psychology: Human Perception and Performance*, Vol. 17, M.A. Peterson, E.M. Harvey, and H.J. Weidenbacher, “Shape recognition contributions to figure-ground reversal: which route counts?”, pp. 1075-1089, Copyright (1991).

interpretation. An additional experiment used scrambled versions of the original stimuli (Figure 4C, D) created by partitioning the contours at minima of curvature defined with respect to the inside of the surround and rearranging them so that no two contour partitions that were connected in the original stimuli remained connected in the

scrambled versions. This was to investigate whether these shape recognition procedures operated on local contour features, or were dependent upon the relative location of the feature parts. This experiment found no differences for upright vs. inverted conditions for the scrambled stimuli, suggesting that relative location of features is relevant to shape recognition procedures. Further manipulations ruled out the possibility that knowledge-dependent strategies influenced figural maintenance times.

This same basic paradigm was extended by Peterson and Gibson (1994) to include masked stimuli. In this experiment the stimuli again consisted of black and white regions that shared an edge (Figure 5). Again the contours were either high-denotative or low denotative, and past experience effects were manipulated by presenting the stimuli in either upright or inverted orientations. An additional variable that was manipulated was symmetry of the two regions sharing the edge. For symmetric stimuli, the two edges of a given region were identical over a vertical reflection (see Figure 5, right column); for asymmetric stimuli the two edges of a region were not identical (see Figure 5, left column). The stimuli were presented to subjects for 14, 28, 57, 86, or 100 ms, followed immediately by a mask. Subjects responded by button press to indicate which region of the stimulus appeared as figure at the central edge. As before, participants saw the high-denotative regions as figure more often when they viewed upright stimuli than inverted stimuli, with effects observed first in the 28 ms condition. Furthermore, symmetric regions were more likely to be seen as figure than asymmetric regions. In addition, high-denotative regions were more likely to be seen as figure when they were upright and

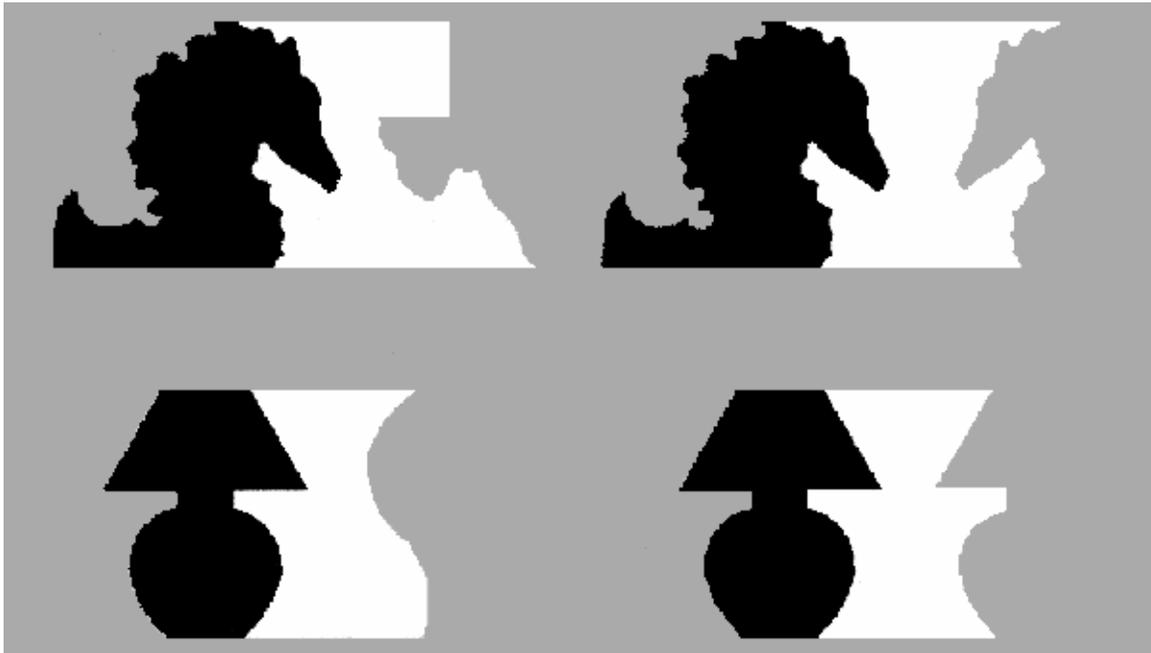


Figure 5. Upright versions of stimuli used by Peterson and Gibson (1994). Stimuli with asymmetric high denotative regions are shown in the top row; symmetric high denotative regions are shown in the bottom row. Stimuli with asymmetric low denotative regions are shown in the left column; symmetric low denotative regions are shown in the right column. In these example stimuli, the high denotative contours depict a seahorse (top row) and a table lamp (bottom row). Figure adapted and reprinted with permission from *Psychological Science*, Vol. 5, M.A. Peterson and B.S. Gibson, "Must shape recognition follow figure-ground organization? An assumption in peril", pp. 253-259, Copyright (1994), Blackwell Publishing.

symmetric as compared to upright and asymmetric, and less likely to be seen as figure when the low-denotative regions were symmetric rather than asymmetric. Further, analyses indicated that for inverted stimuli, where high-level shape cues were reduced, symmetry cues dominated; however, for upright stimuli when both shape and symmetry cues were present, they competed for influence of segregation. This study shows that object memories and lower level cues such as symmetry can facilitate or compete for segregation influence. This counters arguments suggesting that top-down effects would

always dominate segregation processes. Another study found a similar competition between object memory influences and disparity (Peterson and Gibson, 1993), using three-dimensional displays.

One question is whether the effects of past experience involve the access of memories for object structure along an entire edge or along a part of an edge (Peterson, 2003). Peterson and Hector (1996) addressed this question by using rectangular displays of a central articulated contour that denoted two objects, one above the other. In half of the displays the objects were the same; in the other half they were different. Also, objects could appear on the same side of the display or on different sides. The right and left sides of each display were matched on several additional cues to figure assignment. Peterson and Hector (1996) found that the percentage of trials in which figure assignment was perceived to cross over from one side to the other side along the contour was greater for different-side stimuli than same-side stimuli. This result indicates that object memories may be accessed along a portion of an edge rather than a whole edge, and further suggests that such memories may involve sub-configurations of objects rather than whole objects per se (Peterson, 2003; see also Section 6, General Discussion).

1.3.2 Does Figure Assignment Occur in a Serial Hierarchical Manner?

Another line of evidence previously taken in support of the figure-ground-segregation-first assumption is a study (Warrington and Taylor, 1973) of a visual agnostic who could perform figure-ground segregation well, while being poor at object recognition and shape identification. This finding has been interpreted within a serial

hierarchical view of vision in which the results of each visual processing stage are completed before being outputted to the next stage, with figure-ground segregation an intermediate stage in the process (e.g. Marr, 1982). On this view, figure-ground segregation occurs before achieving a match in object memory; thus the lesion of Warrington and Taylor's patient must be located higher than brain regions devoted to figure assignment, while lower than regions in which object memories are stored (Marr, 1982). This serial hierarchical view is concordant with the feedforward architecture of the visual cortex where lower cortical regions (V1/V2) relay primitive stimulus information to higher areas (V4/IT) that mediate componential to holistic object memories (Tanaka, 1996).

The reasoning applied to this evidence in support of the figure-ground-segregation-first hypothesis is problematic for two reasons. First, the existence of feedback connections from high-level visual regions to low-level regions (Salin and Bullier, 1995) suggest that visual object perception and recognition do not necessarily emerge from rigid serial hierarchical processing. This opens the possibility that object memory access can influence low- and intermediate-level processes involved in the determination of figure and ground. Second, the patient's naming responses gathered in the Warrington and Taylor (1973) study only indexed conscious recognition and identification. Such responses cannot unequivocally indicate whether or not access to object memories occurred at all during the course of figure assignment; access may have occurred in an unconscious, albeit impaired manner. To determine if access to object memories can occur during figure assignment, one must compare figure assignment for

regions matched in Gestalt cues, but mismatched in terms of cues to past experience. Indeed, using stimuli similar to those shown in Figure 4, Peterson et al. (2000) showed evidence for object memory influences on the shape assignment performance of a visual agnostic patient despite the fact that the patient was severely impaired in conscious object recognition.

A third line of evidence taken to support the figure-ground-first assumption is the fact that shaped regions are consciously seen as such only when they attain figural status. For example, in the famous Rubin face-vase stimulus (Figure 1D), the vase can be recognized only when it is seen as figure at the border with the surrounding white region, but not when it is seen as ground. A similar situation holds for the face regions of the stimulus. This coupling of figural status and conscious perception has also been taken to suggest a serial processing sequence, but in fact only suggests that consciously seen shapes must have figural status. This finding says nothing about whether or not object memories can be accessed unconsciously during figure assignment before the onset of conscious figure perception (Peterson and Skow-Grant, 2003). The performance of Peterson et al.'s agnostic patient discussed above indicates that such shape memories can be accessed unconsciously. Furthermore, Peterson et al. (2000) tested another neurologically damaged patient with preserved recognition abilities who failed to show influences of object memories on figure assignment. Thus the findings of Peterson et al. indicate that consciousness is neither necessary nor sufficient for effects of past experience on figure assignment, and thus has no bearing on the figure-ground-segregation-first hypothesis.

The experiments reviewed in this section show that past experience can influence conscious judgments of a stimulus region as figure. Since these cues depicted familiar objects previously encountered outside the laboratory, the results of these studies suggest that access to object memories and/or memories for object parts (e.g. Peterson, 2003) occurs during the course of figure-ground segregation. The next question to consider is whether such past experience cues compete with other configural cues in the manner described by the PIMOCA model. This is the subject of the next section.

1.4 Behavioral Evidence for the PIMOCA Framework

1.4.1 Cross-Edge Cue Competition

Peterson and Lampignano (2003) provided the first evidence for cross-edge competition of configural cues by reinterpreting the findings of a previous priming study (Treisman and DeSchepper, 1996) and then adapting the basic paradigm in order to test this reinterpretation. Treisman and DeSchepper (1996) presented participants with figure-ground stimulus displays (primes) consisting of an articulated curved edge shared by two complementary black and white regions (Figure 6A). Participants matched the black region to a black comparison shape shown below a central fixation point. On the next (probe) trial, two separated shapes, one black and one white, were shown above the fixation point (Figure 6B). The shapes were spaced a small distance apart so that they no longer shared an edge. In addition, the regions were no longer complements of one another and had the same left–right arrangement as that of the black and white regions in the prime display.

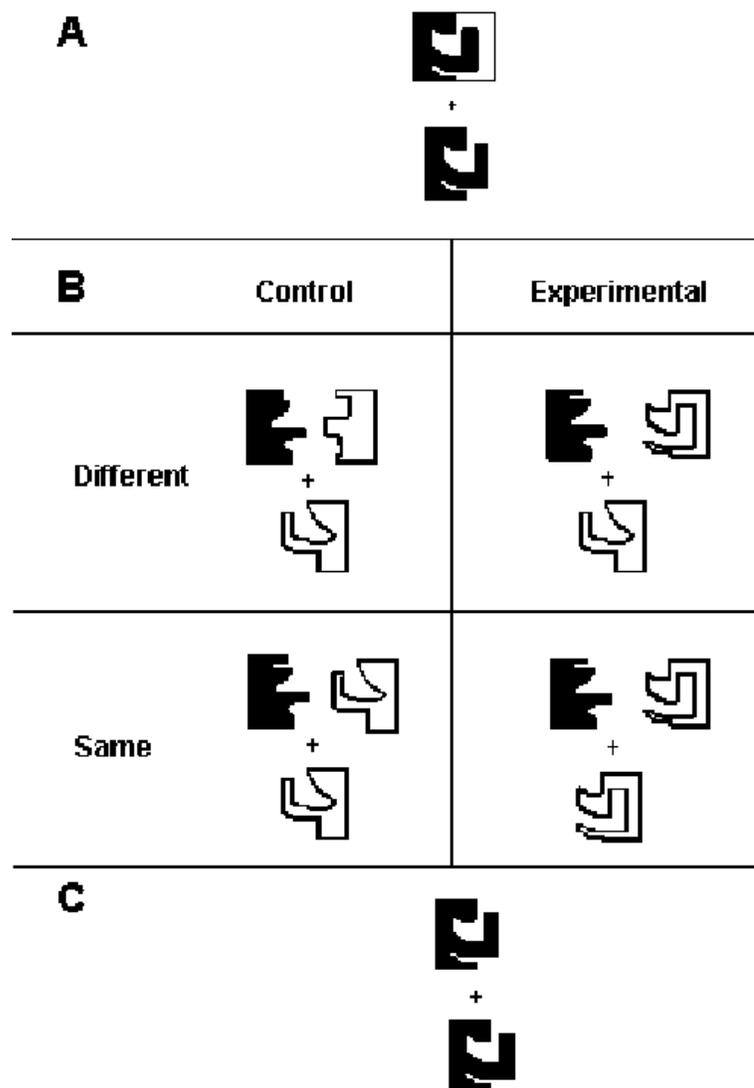


Figure 6. Stimuli used to index cross-edge competition by Treisman and DeSchepper (1996) and Peterson and Lampignano (2003). A: The prime display used by Treisman and DeSchepper (1996); Reprinted with permission from A. Treisman and B. DeSchepper, "Object tokens, attention, and visual memory". In T. Inui & J. L. McClelland (Eds.), *Attention and performance XVI: Information integration in perception and communication*, pp. 15-46, Copyright (1996), MIT Press. B: Sample probe trials used by Treisman and Decshepper (1996) and Peterson and Lampignano (2003). In both studies the prime and probe displays were shown on a gray background, with neither the white region of the prime nor the white probe shapes outlined in black. The white regions are outlined in black in the present figure to distinguish them from white background. C: The prime display used by Peterson and Lampignano (2003). Figure 7 is adapted with permission from *Journal of Experimental Psychology: Human Perception and Performance*, Vol. 29, M. A. Peterson and D.W. Lampignano, "Implicit memory for novel figure-ground displays includes a history of cross-border competition", pp. 808-822, Copyright (2003).

Black shapes shown above fixation on probe trials were unique distractors with novel articulated borders (Figure 6B). White shapes shown above fixation during probe trials were the standards which were compared to a second white shape located below fixation and facing in the same direction as the standard shape. The task of the observers was to determine whether the standard and comparison shapes were the same or different on probe trials. On experimental trials, the standard shape was the white region isolated from the prime figure-ground displays. Control standard probe shapes had novel edges that had not been seen before.

Treisman and DeSchepper (1996) observed their participant's response times to be longer on experimental probe trials than on control probe trials. It was concluded that the two bounded regions lying on opposite sides of a border were ascribed shape before figure and ground were determined, and thus equivalent memories were formed for both figure and ground, despite the fact that the ground was ultimately perceived as shapeless. Treisman and DeSchepper interpreted the longer latencies they obtained on experimental versus control probe trials as reflecting an "ignore" tag attached to the episodic memory of the shape of the ground.

Although Treisman and DeSchepper's interpretation is an alternative to the figure-ground segregation-first assumption, it is also very different from the PIMOCA framework put forward by Peterson and colleagues. Peterson and Lampignano (2003) reinterpreted Treisman and DeSchepper's findings in terms of the PIMOCA framework by arguing that the repeated articulated edge on probe trials was associated with a memory of where the figure was the first time it was encountered on the prime trial. This

memory would favor assigning the articulated edge on probe trials to what is now its unbounded side, while the configural cues of closure and relative area would favor assigning the articulated edge to the opposite (bound) side. Cross-edge competition of these cues would be expected to slow figure assignment on experimental probe trials compared with that on control probe trials because in the latter case the borders of the white probe shapes have not previously been encountered, and thus past experience does not favor assigning the articulated edge to the unbounded side. It follows that the longer reaction times observed by Treisman and DeSchepper (1996) on experimental versus control probe trials may reflect such competition-induced delay in figure assignment rather than the consequences of attaching an ignore tag to a memory for the whole shape of the ground.

To test this idea, Peterson and Lampignano (2003) decreased the similarity between the white probe shape and the global ground region in the prime by eliminating the white bounded region from the prime (Figure 6C); they presented the black prime shapes alone on a larger gray background. Thus the white probes were substantially different in shape from the gray ground on the prime trials, except for the repeated articulated edge. If Treisman and DeSchepper's (1996) findings were due to an ignore tag attached to the memory for the shape of the ground, priming effects should be substantially reduced (or even eliminated) by reducing the similarity between the prime and the probe shape (e.g. Jacoby, 1983; Scarborough, Gerard, & Cortese, 1979). Alternatively, if the latency differences reported by Treisman and DeSchepper reflect competition from past experience for ownership of the repeated articulated border,

repeating the border under conditions favoring assigning it to the opposite side should still lead to longer reaction times for experimental versus control conditions with no diminution of the effect. This is exactly what Peterson and Lampignano (2003) found, in support of the cross-edge competition hypothesis.

Peterson and Enns (2005) provided further evidence for cross-edge competition by extending the experimental paradigm of Driver and Baylis (1996), a study that incorrectly concluded that past experience does not influence figure-ground segregation. Driver and Baylis presented observers with stair-stepped figure-ground stimuli (primes; for an example of similar stimuli, see Figure 7A) followed by either two figure probes (i.e. shapes that faced in the same direction as the figures in the primes, see Figure 7B, left), or two ground probes (shapes that faced in the same direction as the grounds of the prime trials, see Figure 7B, right). One of the two probes always had the same edge (experimental condition), the other did not (control condition). Observers were instructed to remember the shape of the contour separating the figure region from the ground region of the prime stimulus, and then to report which of the two probe shapes had the same edge. Driver and Baylis (1996) found that observers were faster to identify previously seen contours present within figure probes than when the same contour was present within ground probes. It was concluded that the grounds were not processed in the prime stimuli because if they were, then responses to ground probes should have been just as fast as to figure probes due to the facilitating effect of past experience with the primes.

Peterson and Enns (2005) correctly pointed out that Driver and Baylis' position assumed that both sides of the contour are processed equally during the presentation of

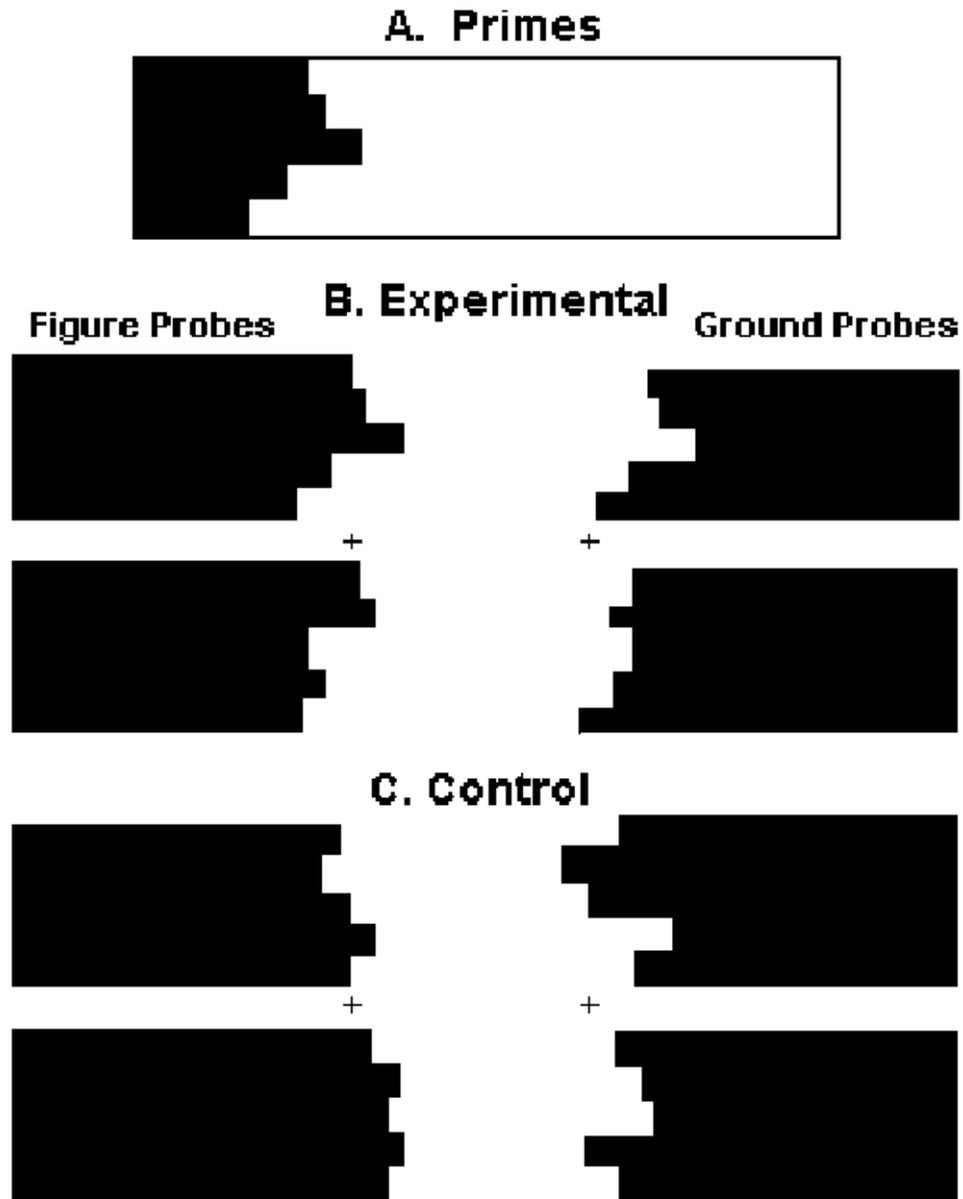


Figure 7. Prime and probe displays used by Peterson and Enns (2005). In panel A, the smaller region in the prime is black, and the larger area is white; in the experiments, these colors were bright yellow and dark red, respectively. The black outline of the larger area, shown in white here, serves to illustrate the boundary of the ground region; the original displays did not contain outlines. (B and C) Experimental probes and control probes, respectively. Left: figure probes. Right: ground probes. In this illustration, the stepped edge of experimental probes in the top probe matches the stepped edge in the prime. This figure is adapted with permission from *Perception & Psychophysics*, Vol. 67, M.A. Peterson and J.T. Enns, “The edge complex: Implicit memory for figure assignment in shape perception”, pp. 808-822, Copyright 2005.

the prime stimulus. If instead they were processed unequally with the separating contour assigned to the prime figural region and not the ground region, then a memory could be established of where the figure was the first time it was encountered on the prime trial (c.f. Peterson and Lampignano, 2003). It follows that on ground probe trials there would be cross-edge competition between the shape memory cue favoring the assignment of the repeated edge of the experimental stimuli to what is now its unbounded side and the configural cues favoring the other (formerly ground) side of the contour. In contrast, figure probe trials should see no such competition because nearly all the cues favor one side as figure. Thus the increased competition present for the ground probe trials should lead to longer times to determine figure-ground segregation, and responses to figure probes should be faster than for ground probes, as observed by Driver and Baylis (1996).

In order to determine which framework (PIMOCA or figure-ground-segregation-first) best describes the findings of Driver and Baylis (1996), Peterson and Enns (2005) used stair-step stimuli as primes similar (Figure 7A) to those of Driver and Baylis (1996), but also introduced additional ground probe stimuli that contained novel contours not previously presented. In addition, participants were no longer instructed to remember the edges of the prime stimuli. The critical comparison was to compare responses to ground probes containing a contour that was presented previously (*experimental ground probes*, see Figure 7B) with ground probes in which the contour is novel (*control ground probes*, see Figure 7C). If the figure-ground segregation-first hypothesis is correct, then reaction times should be equivalent between the two types of probes, as there is no competition present in either case. In contrast, if the PIMOCA framework is correct, then

there should be competition present for experimental ground probes that is not present for control ground probe trials. Peterson and Enns (2005) found faster responses for control versus experimental ground probe stimuli, even given a single prior exposure to a repeated contour. This finding suggests that cross-edge competition was indeed present for the experimental ground probe trials. This finding, taken together with the results of Peterson and Lampignano (2003), supports the PIMOCA framework while providing further evidence that past experience can act as a configural cue.

1.4.2 Suppression of Cues Losing Cross-Edge Competition

According to the PIMOCA framework, configural cues that lose the cross-edge competition during figure assignment are inhibited, thus accounting for the shapelessness of grounds. One way to index this inhibition would be to investigate whether the losing cues continue to be suppressed after cross-edge competition has been resolved. Peterson and Kim (2001) used such a strategy in a priming study where participants were presented with figure-ground displays (primes) followed by familiar and novel line drawings (probes); see Figure 8 for examples of the black and white line drawings. The figure-ground displays consisted of small black novel-shaped silhouettes against a white background (see Figure 9 in Section 1.2.2, top and middle rows). The overall constellation of Gestalt cues (symmetry, enclosure, relative area, convexity) in these stimuli promoted figure assignment to the black regions. Two types of silhouettes were created. *Control silhouettes* (Figure 9, top row) possessed contours that sketched novel shapes on their ground sides (the white regions laterally adjacent to the black figural

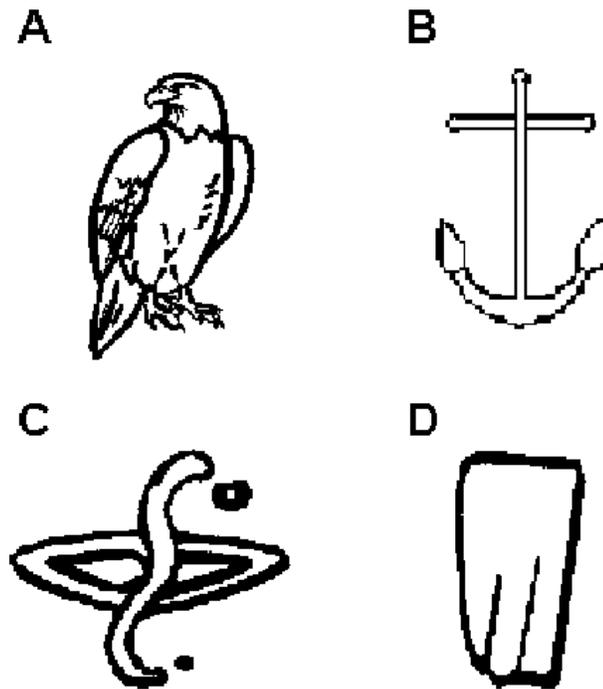


Figure 8. Stimuli used by Peterson and Kim (2001). Example line drawings of real objects (an eagle in A and an anchor in B) and novel objects (C and D).

regions of the silhouette). The contours of *experimental silhouettes* (Figure 9, middle row) sketched portions of single basic-level objects along their ground sides.

The silhouettes were presented for 50 ms, removed from the screen, and then followed by a black line drawing. The participants' task was to determine whether the line drawing portrayed a familiar, real world object, or novel object, as quickly as possible.

Participants were instructed to attend to the silhouettes, and not respond to them. On control trials the silhouettes preceding familiar line drawings were novel silhouettes; on experimental trials, the silhouettes preceding familiar line drawings were experimental silhouettes with grounds portraying objects from the same basic level category as the line drawing. Importantly, the ground side of the experimental silhouettes appeared to be

shapeless (as assessed by post-experiment questionnaire); the known object was not perceived consciously. All novel line drawings were preceded by control silhouettes.

Under an 83 ms SOA condition (with a prime exposure duration of 50 ms and ISI of 33ms), Peterson and Kim (2001) found that response latencies were *longer* in the experimental condition than in the control condition, but only in those participants with short latency responses. These results are consistent with the occurrence of access to memories of object structure during the experimental condition that was not present in the novel condition. The slower reaction times suggest that, in the experimental condition, the object memories initially accessed along the more weakly cued side of the silhouette edges were inhibited at the time of secondary access during recognition of the line drawing. The effect observed by Peterson and Kim (2001) cannot be explained in terms of memory for the specific border of the silhouettes because the line drawings and silhouettes had completely different contours. One possibility, however, is that the observed reaction time differences could be due to differences in figural resolution time for experimental and control silhouettes from competition of cues across the contours of the experimental silhouettes.

This possibility was eliminated by a later study (Peterson and Skow, submitted) that compared responses to line drawings preceded by silhouettes with grounds suggesting known objects from the same basic level category as the paired line drawing (termed *same basic level category- grounds*, or *same BLC-grounds*) with responses to line drawings preceded by silhouettes with grounds suggesting known objects from a different superordinate level category as the paired line drawing (termed *different*

superordinate level category-grounds, or different SLC-grounds). Peterson and Skow (submitted) found that reaction times were longer in the same BLC-ground condition relative to the different SLC-ground condition in fast responding participants (i.e. those participants with reaction times in the 1st quartile of RTs across participants).

In a second experiment, Peterson and Skow (submitted) added additional control silhouettes that did not depict familiar shapes in their grounds. These control silhouettes were paired with the line drawings of the same BLC-ground condition and the different SLC-ground condition to yield a *control BLC-ground* condition and a *control SLC-ground* condition. In addition, the numbers of trials per condition were increased in order to enhance the sensitivity of the experimental design. Evidence of suppression was found in the fastest three quartiles of participants rather than in just the first quartile participants; responses were faster in the experimental different SLC-ground condition than in the experimental same BLC-ground condition. A similar finding was found when examining the fastest (1st half) responses of all participants. Furthermore, in the quartile analysis, the comparison of experimental and control reaction times in the different SLC-ground condition showed no evidence that competition slowed responses to the line drawings, indicating that the observed RT differences between experimental BLC-ground and experimental SLC-ground conditions were due to suppression rather than cross-edge competition.

In a third experiment, Peterson and Skow-Grant (submitted) replaced the original Peterson and Kim (2001) silhouettes with a set of silhouette primes altered such that the regions seen as grounds were now seen as figures. Participants again categorized line

drawings of familiar and novel objects. Silhouettes and line drawings were paired into two conditions: a same BLC-figure condition and a different SLC-figure condition; each of the line drawings also appeared after a control figure silhouette that always portrayed an object from a different superordinate category from the line drawing. If the pattern of results obtained in this experiment was the same as that found in Experiments 1 and 2 of Peterson and Skow (submitted), that it would suggest that the results are not due to competition-induced-suppression, but instead reflect some other process that occurs for figures as well as for grounds, such as participants ignoring the silhouettes because they were irrelevant to their object decision task. In contrast, if the pattern of results found in Experiments 1 and 2 reflects suppression of the familiar configurations suggested on the groundside of the silhouettes, then a different pattern of results should be observed when the familiar shape is perceived as the shaped figure in the silhouette than when the familiar shape was suggested but not perceived on the groundside of the silhouettes in Experiment 2.

Peterson and Skow (submitted) found a different pattern of differences in the results of Experiment 3, in that differences between RTs to line drawings following experimental versus control figure silhouettes tended to be smaller in the same BLC-condition than in the different SLC-figure condition. Furthermore, the patterns of results obtained in Experiments 2 and 3 differed statistically, as shown by an interaction among Experiment (2 vs. 3), silhouette type (experimental versus control) and condition. This indicates that the findings of Experiments 1 and 2 represent the effects of suppression rather than inattention.

The experiments reviewed in this section and Section 1.4.1 provide evidence for cross-edge competition and suppression of cues that lose that competition, thus supporting the PIMOCA framework. In addition, these experiments provide further evidence that object memories are accessed during the course of figure assignment because cues to past experience were utilized to induce the cross-edge competition. Furthermore, none of these studies involved conscious judgments of figural status, instead relying on same-different or object decision tasks. This removes a lingering criticism raised against the earlier evidence for past experience effects based on direct reports of figural status (reviewed in Section 1.3) that such judgments could have been biased by conscious recognition strategies on the part of the subjects (Driver and Baylis, 1995b).

What these experiments do not do is provide direct evidence of mutual inhibition. At best, these experiments provide indirect evidence of mutual inhibition because (according to the PIMOCA model) the latter occurs simultaneously with competition, the outcome of which leads in turn to the behavioral responses measured in the studies reviewed in Sections 1.4.1 and 1.4.2. Nonetheless, mutual inhibition might be directly indexed by measuring the neural activity associated with behavioral indices of competition. According to a cognitive neuroscience perspective, perceptual representations are biophysically instantiated by neural networks within the brain.⁴

⁴ Although the discussion presented in this paper will take place within the cognitive neuroscience perspective, it should be noted that the assumption of mind-brain identity is controversial, and is one of many different approaches to the so-called “mind-body problem”. Other major approaches to this issue include dualism, idealism, and emergentism (see Chalmers, 1997 for review).

Therefore mutual inhibition among competing figure-ground representations should then be reflected within inhibition among the neural networks mediating those representations. Such a possibility was a central motivation for the study reported in this paper, which is outlined next in the final introductory section.

1.5 The Present Study: Overview

The study reported here investigated the neural consequences of placing past experience cues in competition with other configural cues during a basic shape recognition task (see Sections 1.5.1, 1.5.2 below, and Section 2.1.3) to see if such neural responses are consistent with the presence of mutual inhibition and cross-edge competition, as predicted by the PIMOCA model presented in Section 1.2. Furthermore, if such neural responses are differentially selective for conditions in which past experience cues are present versus absent, then this would constitute the first brain-based evidence for an influence of past experience on figure assignment. Human neural activity was indexed via an event related potential (ERP) brain imaging technique in which scalp electroencephalographic (EEG) signals evoked in response to visual stimuli were averaged over trials (see Methods, Section 3.1.5). The resulting ERPs reflect the average stimulus-locked bioelectric brain activity with a high degree of temporal precision. Thus the ERPs should be sensitive to neural responses both early and late in visual processing of the stimuli.

The basic experimental paradigm used in this study was divided into two separate behavioral tasks. These two tasks were distinguished by whether or not the cues to past

experience were unconscious (Task 1) or conscious (Task 2) to the human participants. These two behavioral tasks are outlined in the next two sections.

1.5.1 Figure Assignment During Unconscious Access to Memory Representations of an Object

In Task 1, human participants categorized vertically-symmetric silhouettes as depicting either familiar and novel shapes. The *familiar silhouettes* (Figure 9, bottom row) depicted shapes of familiar objects and symbols previously encountered by experimental participants outside of the laboratory. The *novel silhouettes* (Figure 9, top and middle rows) depicted shapes not previously encountered before by our participants. The novel silhouettes were slightly modified versions of the silhouettes used by the studies of Peterson and Kim (2001) and Peterson and Skow (submitted), as described in Section 1.4.2. As in those previous experiments, the novel silhouettes were divided into *control silhouettes* (where the edges sketched a novel shape along the outer/ground regions) and *experimental silhouettes* (where the edges sketched a portion of a basic-level object along the outer/ground regions). Importantly, the unbounded sides of the experimental stimuli appeared to be shapeless grounds; the known shapes were not perceived consciously. Since participants responded about their immediate perception of the silhouettes, Task 1 may be considered a direct behavioral index of the processes leading to the perception of the silhouettes as shaped figures. This task also provides online evidence of whether participants are seeing familiar or novel shapes, unlike previous work.

1.5.2 Figure Assignment During Conscious Perception of Familiar Shape on the Outside of Experimental Silhouettes

In Task 2, participants were made aware of the known shapes depicted by the unbounded sides of the experimental silhouettes they had seen in Task 1. They then were shown only experimental and control silhouettes that were different from the stimuli seen in Task 1. Participants were instructed to categorize the outer regions as depicting either familiar or novel shapes. This task therefore allowed examination of the neural responses under conditions of *conscious* awareness of the known shapes suggested by the outer regions of the experimental silhouettes. In addition, if in Task 2 participants saw the unbounded regions of experimental stimuli as familiar more often than for control stimuli, then it can be assumed that they were able to see the outside regions as figures; recognition of the object portrayed by a region can only be achieved when that region is seen as figure. Thus, comparison of the ERP responses across Tasks 1 and 2 allows examination of the neural differences when 1) the side of an edge suggesting a known object is seen as ground versus figure, and 2) when memories for known shapes (or parts thereof) are accessed unconsciously vs. consciously. Such manipulations have not yet been performed in a clear manner by studies of the PIMOCA framework. Peterson and Skow (submitted) did compare the difference in short-term suppression of past experience cues that lost the cross-edge competition during processing of a prime stimulus when those cues were located on the figure side of the bonding contour (and thus more likely to be seen consciously) versus when the cues were located on the ground side (and thus more likely to be processed unconsciously). However, that study did not

compare behavioral responses to the prime stimuli themselves, nor was an effort made to assess on an individual stimulus level if participants consciously saw the familiar shapes when depicted as figures by the primes.

Comparison of neural responses to conscious versus unconscious perception of the known shapes in the experimental silhouettes will contribute further information regarding the neural correlates of conscious visual perception. The neural correlates of consciousness (NCC) may be generally divided into two categories (Chalmers, 2000), a neural correlate of creature consciousness (i.e. conscious awareness *per se*), and a neural correlate for the contents of consciousness (i.e. consciousness within some specific sensory and/or cognitive modality). A neural correlate of creature consciousness may be defined as “a minimal neural system N such that there is a mapping from states N to states of consciousness, where a given state of N is sufficient, under conditions C, for the corresponding state of consciousness” (Chalmers, 2000; p. 31).

This definition entails two main consequences. First, the definition requires that a given system is minimally sufficient; i.e. that the states of N must be sufficient for the corresponding states of consciousness, yet there is no subset of N which by itself suffices for consciousness. This ensures that only “core” (i.e. minimally sufficient) processes play a role in the production of conscious states. Second, the clause “under conditions C” ensures that a particular neural state instantiates a NCC only under the proper environmental and internal conditions necessary for that neural state to properly function as a NCC, as discussed above. This has the effect of implicating only core processes.

A NCC for content is then defined as “a minimal neural representational system N such that representation of a content in N is sufficient, under conditions C, for representation of that content in consciousness” (Chalmers, 2000; p. 31). Most studies of the neural correlates of conscious visual perception involve investigation of a NCC for content. The present study also investigated a NCC for content because participants were consciously aware of both experimental and novel stimuli as figures across Tasks 1 and 2, while being differentially aware of the “content” contained within the experimental stimuli (i.e. the shape on the unbounded side of the edge) across both tasks. It should be noted that this approach to studying consciousness is that of “contrastive analysis” (Baars, 1997) in which states of consciousness are directly contrasted with states of unconsciousness. In so far as other relevant variables are approximately equal across the comparisons performed in the present study, then any differentially active brain responses to experimental and control stimuli of Task 2 should correspond to activity reflective (at least in part) of the NCC for conscious perception of object shape.

1.5.3 Outline

Section 2 describes the initial experimental piloting of the basic silhouette categorization task (Experiment 1). This behavioral experiment establishes that the task used here leads to processing differences between experimental and control stimuli. Section 3 describes the results of ERP measurements gathered while participants performed the silhouette categorization task (Experiment 2). The behavioral results of

Experiment 2 replicate those of Experiment 1, and also reveal differences in the neural processing of the experimental and control stimuli.

Section 4 then addresses concerns that the stimuli used in these initial experiments may have been imbalanced across conditions in terms of physical stimulus characteristics. Early ERP components are well-known to be sensitive to differences in these low-level attributes (Van Rullen and Thorpe, 2001), and such differences among stimulus types could affect behavior as well (Section 3.2). These concerns led to the creation of new stimuli well-matched along several key stimulus characteristics (Section 4.3). These improved stimuli were then used in a third experiment (Experiment 3, Section 5) which established definitive early ERP correlates of the object recognition task and replicated the behavioral and late ERP findings of Experiments 1 and 2.

Finally, in the General Discussion (Section 6) it is argued that 1) the results of all three experiments are consistent with the hypothesis that past experience influences figure-ground segregation under conditions of conscious and unconscious awareness of the familiar shape portrayed along one side of an edge; and 2) these results are consistent with the PIMOCA competitive model under the assumptions that 2i) the cognitive process of mutual inhibition among configural cues is biophysically instantiated within the inhibitory interactions among the competing cell assemblies that form the neural representations of the different cues; and 2ii) differences in mutual inhibition between conditions arising from differential access to object memories results in unequal neural feedback across conditions, where such feedback relays signals from high-level visual

areas representing familiar objects (or portions thereof) to lower visual areas mediating neural representations of contour and surface shape.

2. EXPERIMENT 1 - OVERVIEW

2.1 Methods

2.1.1 Participants

Thirty undergraduate participants (22 female, 8 male; 6 left-handed, 24 right-handed; mean age = 19.13 ± 0.31 years) were recruited from the University of Arizona's undergraduate subject pool. During the experiment, 7 participants became conscious of the objects hidden within the high-denotative silhouettes during the course of the experiment ("Seers"; 5 females, 2 males; 1 left-handed, 6 right-handed; mean age = 18.86 ± 0.26), while 23 participants did not ("Non-Seers"; 17 females, 6 males; 5 left-handed, 18 right-handed; mean age = 19.22 ± 0.39). Only the Non-Seers' data were retained; the Seers' data were not analyzed further. All participants were screened to ensure normal visual acuity, and were fully informed of the experimental methods and proceedings before their consent to participate was obtained. The experimental protocol was reviewed and approved by the Institutional Review Board for Human Studies at the University of Arizona.

2.1.2 Stimuli

The stimuli consisted of vertically-symmetric enclosed silhouettes depicting familiar and novel shapes (see Figure 9). Eighty-four novel shaped silhouettes were taken from the set created specifically for the experiment of Peterson and Kim (2001). The enclosed central regions of the novel silhouettes depicted shapes not previously encountered before by our participants. There were two types of novel silhouettes. The

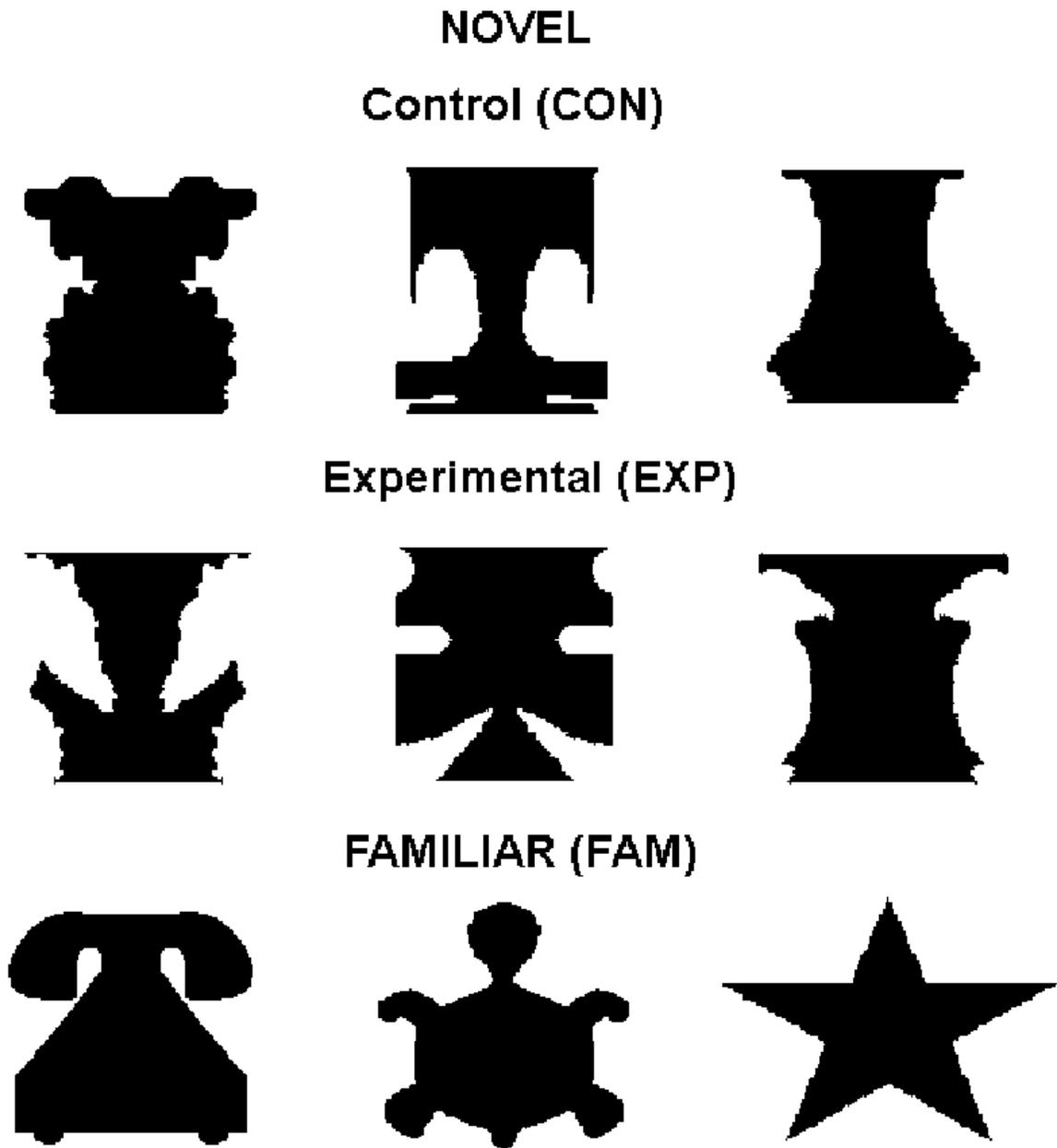


Figure 9. Example control (CON, top row), experimental (EXP, middle row), and familiar (FAM, bottom row) silhouettes. Objects depicted by the ground (white) side of the example EXP silhouettes include a seahorse in profile (middle left), anchor (middle center) and eagle in profile (middle right). Objects depicted by the figure (black) side of the FAM silhouettes include a telephone (bottom left), turtle (middle center) and five-pointed star (bottom right).

edges of half of the novel silhouettes sketched a novel shape along the ground side; these were *control silhouettes* (CON; Figure 9, top row). The edges of the other half of the silhouettes sketched a portion of a basic-level object along the ground side; these were *experimental silhouettes* (EXP; Figure 9 middle row; see Appendix A for a listing of objects portrayed by the unbounded regions of the EXP silhouettes). Importantly, the ground sides of the EXP stimuli appeared to be shapeless; the object shape was not perceived consciously by Non-Seers whose data were analyzed in the experiment (see Participants, Section 2.2.2, Procedure, Section 2.1.3, and Section 2.2, Results).

Novel EXP and CON stimuli were further divided into two sub-sets A and B (see Appendix A), with the object categories portrayed by EXP stimuli roughly equated for the number of animate and inanimate objects. Forty-two familiar shaped silhouettes (FAM; Figure 9, bottom row; see Appendix B for a listing of the objects depicted by the FAM stimuli) were created from photos and artwork depicting animate and inanimate objects, animals, plants, and symbols previously encountered by experimental participants outside of the laboratory. The FAM silhouettes were scanned into the Adobe Photoshop software package (Adobe Systems Inc., San Jose, CA, USA) and digitally manipulated into silhouette form. The enclosed regions of all of the silhouettes were black in color and were displayed against a white background.

All silhouettes subtended an approximate visual angle of 4.71° in height, while ranging from approximately 1.77° to 9.42° in width. All stimuli were pattern masked during presentation (see Section 2.1.3 Procedure, below); the pattern masks subtended approximate visual angles of 4.71° in height and 9.42° in width (for a sample mask, see

Figure 10). Seven different masks were used, with each mask following each silhouette equally often; the same set of masks was used in all experimental conditions. All silhouettes and masks were black in color and were displayed against a white background. Participants viewed the stimuli from a distance of 96 cm while seated in a comfortable chair; head motion was stabilized via a chin rest. Stimulus materials were presented to the participants on a 20" computer CRT screen using the DMDX stimulus presentation software (Forster and Forster, 2003).

2.1.3 Procedure

After consent and demographic information were obtained, the participants were brought into the experimental chamber and instructed in the experiment task. This experiment consisted of two portions (Tasks 1 and 2; see Figure 10).

2.1.3.1 Procedure - Task 1

The participant's task was to categorize the silhouettes as depicting either familiar or novel shapes, as quickly and as accurately as possible (see Figure 10A). Participants responded using two response buttons mounted in a button box placed on table located between the participant and computer screen. Participants were instructed to press the appropriate response buttons when they saw the enclosed black region of the silhouettes as depicting a familiar or novel shape. To preclude any potential confound of handedness, assignment of left and right response buttons to familiar and novel silhouettes was counterbalanced across subjects.

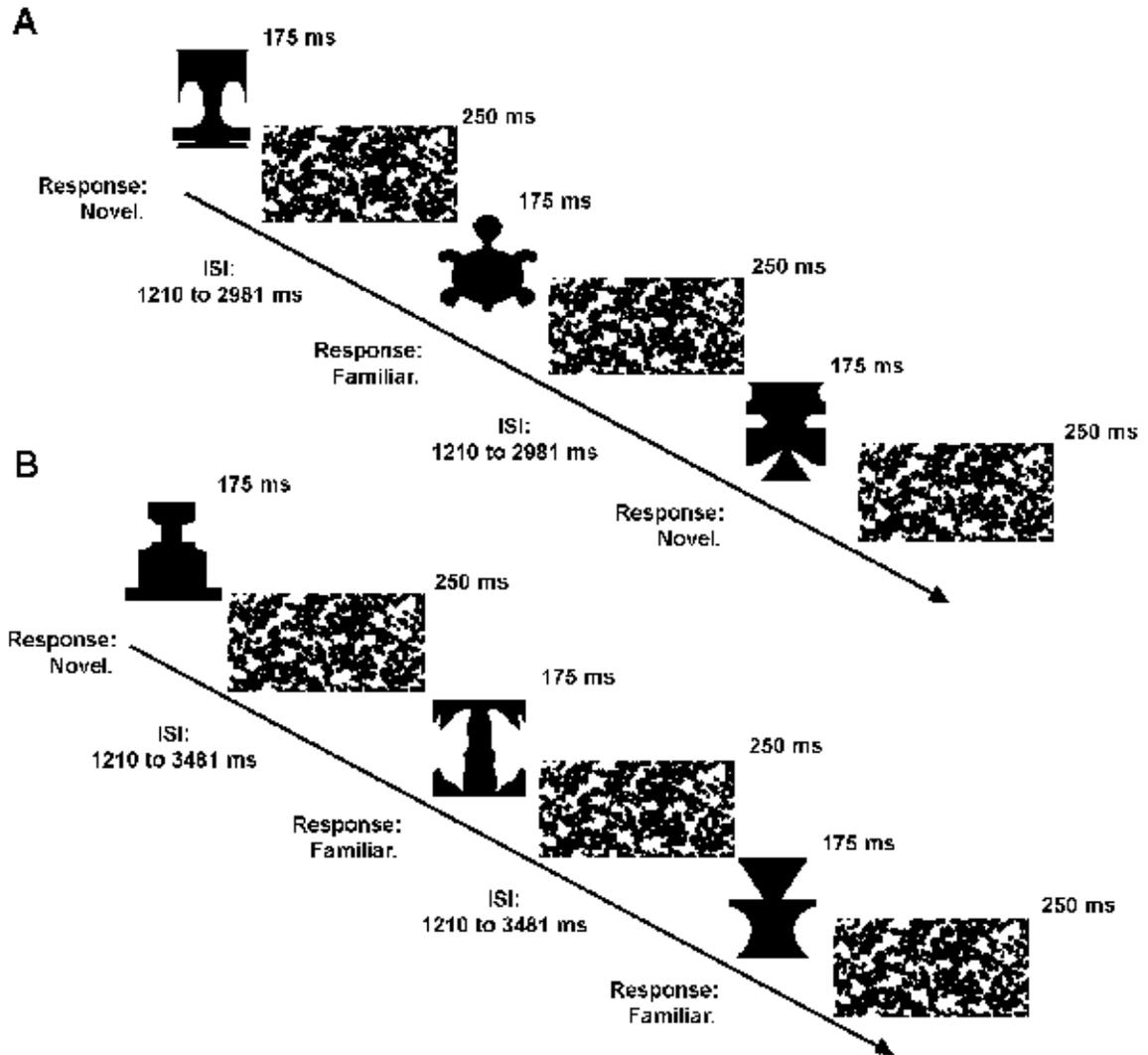


Figure 10. Basic experimental design for A) Task 1 and B) Task 2 of the shape categorization task. See text for details. Response text in figure indicates the correct response for that stimulus.

Before beginning the experiment, participants underwent a training block of 11 trials using CON silhouettes not included in the experiment CON sets; during training participant's were automatically given feedback after incorrect performance on a given

trial. Participants received four blocks of 84 trials (42 FAM, 21 CON, and 21 EXP silhouettes), with short breaks between each block. Each silhouette was presented for 175 ms, immediately followed by a 250 ms mask. In between trials, a small cross was presented in the center of the screen on which participants were instructed to fixate their eyes; all silhouettes and masks were presented at fixation.

All silhouettes were repeated across the four blocks, with the ordering of individual trials randomized for each block. Inter-trial intervals varied from 1210 to 2981 ms. Participants had 1500 ms to respond before the stimulus presentation software automatically advanced to the next trial. Accuracy and reaction time to categorize the silhouettes were recorded by an IBM-compatible PC with a Pentium microprocessor and were analyzed offline.

After completing Task 1, participants were queried regarding whether or not they saw any known objects or shapes in the surrounds of the silhouettes, and they were asked to recall any objects or shapes they might have seen (see Appendix C for a sample of the Task 1 post-experiment questionnaire). Participants who reported seeing familiar shapes in the grounds of the EXP silhouettes (“Seers”) were excluded from further analysis (see Participants Section 2.1.1); participants who did not report seeing familiar shapes in the grounds of the EXP silhouettes (“Non Seers”) were retained. In order to corroborate their reports, Seers and Non Seers alike were given lists of objects and asked to identify which objects (if any) they saw depicted by the *bounded* regions of the silhouettes during the

course of Task 1 (see Appendix C)⁵. Although none of the listed objects had been depicted by the FAM stimuli, half of the objects had been depicted by the unbounded regions of the EXP silhouettes. The remaining listed objects were not depicted by either the EXP or FAM silhouettes. Sensitivity to the familiar shapes depicted by the unbounded regions of the silhouettes was assessed by a non-parametric estimate of the proportion of the area under the receiver operating characteristic (ROC) curve, $P(A)$, for this identification task. Following McNicol (1972) for the case where only a single pair of hit and false alarm rates are available, this area was estimated for each participant as

$$P(A) = \frac{1}{2} + \frac{(H - FA)(1 + H - FA)}{4H(1 - FA)} \quad \text{for } H \geq FA \quad (1)$$

$$P(A) = \frac{1}{2} - \frac{(H - FA)(1 + H - FA)}{4H(1 - FA)} \quad \text{for } H < FA \quad (2)$$

where H = Hits, FA = False Alarms, and $P()$ denotes proportion. The $P(A)$ estimate ranges from 0 to 1, where $P(A) \rightarrow 0$ when $H \ll FA$, $P(A) \rightarrow 1$ when $H \gg FA$, and $P(A) = 0.5$ when $H = FA$. The average Task 1 $P(A)$ measure for the 23 Non-Seers retained in this experiment was $P(A)_{\text{avg}} = 0.57 \pm 0.04$. This finding of a $P(A)$ value close to 0.5 indicates that participants did not see the familiar shapes depicted by the unbounded regions of the silhouettes, nor biased towards a high FA rate.

⁵ Post-experiment questioning revealed that most Seer participants did not see meaningful shapes in the EXP grounds on every trial. However, most of the objects and shapes indicated by the Seers during recall were among those actually depicted by the unbounded regions of the silhouettes, as often indicated by the Seers when given the item recognition lists. In such cases, Seers asked if they could also identify listed shapes that were seen in the unbounded regions of the silhouettes, and were allowed to do so. Thus, the Seers were excluded in order to avoid the possibility of including trials into the analysis in which participants were consciously aware of the hidden objects.

2.1.3.2 Procedure - Task 2

Before beginning Task 2 (see Figure 10B), participants were shown several examples of the EXP stimuli they had seen during Task 1, and were made aware of the presence of the hidden objects contained in their grounds. Participants were then presented with a new set of novel EXP and CON silhouettes and were instructed to categorize the unbounded outer regions as depicting either familiar or novel shapes as quickly and as accurately as possible by pressing the appropriate response buttons.

Following a training block of 10 trials (5 EXP and 5 CON stimuli previously presented during Part1), eight blocks of 21 CON and 21 EXP silhouettes were presented to participants in a randomly intermixed manner; there was a short break between each block. Each stimulus was presented for 175 ms and was immediately followed by a 250 ms mask. The EXP and CON silhouettes presented during Task 2 were a different subset of the stimuli than presented during Task 1 (see Stimuli Section 2.1.2). The order of presentation of these subsets was counter-balanced across participants and Parts 1 and 2; half of the participants were presented with subset A during Task 1 and subset B during Task 2, and vice-versa for the other half of subjects. As in Task 1, a small central fixation cross was presented in between trials, and all silhouettes and masks were presented at fixation. Assignment of left and right response buttons to familiar and novel silhouettes was the same as in Task 1.

EXP and CON silhouettes were repeated across the eight blocks, with the ordering of individual trials randomized for each block. Inter-trial intervals varied from 1210 to 3481 ms. Participants had 2000 ms to respond before the stimulus presentation software

automatically advanced to the next trial. Accuracy and reaction time to categorize the silhouettes were recorded by an IBM-compatible PC with a Pentium microprocessor and were analyzed offline.

After participating in Task 2, participants were queried regarding whether or not they saw any known objects in the surrounds of the silhouettes (see Appendix C for a sample of the Task 2 post-experiment questionnaire). To corroborate these reports, participants were given lists of objects and asked to identify which objects (if any) they saw depicted by the silhouettes during the course of the experiment (see Appendix C). Half of the listed objects were depicted in the grounds of the EXP silhouettes; the remaining listed objects were not depicted by either the EXP or FAM silhouettes. Participants remembered seeing specific familiar shapes depicted in the unbounded regions of the EXP silhouettes to a fairly large degree, as indicated by a relatively high sensitivity measure ($P(A)_{\text{avg}} = 0.79 \pm 0.01$). The $P(A)$ measure for Task 2 was greater than in Task 1 ($P(A)_{\text{Task 2}} - P(A)_{\text{Task 1}} = 0.22 \pm 0.04$; paired $t(22) = 5.37$, $p < 0.01$), further supporting the claim that participants actually saw familiar shapes in the unbounded regions of the EXP stimuli during Task 2, but did not see such shapes during Task 1.

2.1.4 Behavioral Data Analysis

For both Task 1 and Task 2 data, the proportions of correct categorization (% correct) of the familiar and novel silhouettes and corresponding reaction times (RTs) were calculated. For Task 1, trials with reaction times ≥ 1500 ms or < 200 ms were not included in the analysis; for Task 2 this range was extended to reaction times ≥ 2000 ms

or < 200 ms. Between-condition differences were statistically assessed via paired t-tests, for both Tasks 1 and 2. These tests were performed between the EXP and CON trials and, for Task 1, FAM vs. novel trials (NOVEL) after collapsing novel responses across EXP and CON conditions. No tests were made between FAM and EXP or CON conditions individually because the latter two conditions did not contain an equivalent number of trials as the FAM condition, and thus the two conditions would be mismatched in statistical power.

2.2 Experiment 1- Results

In Task 1, participants were faster at categorizing FAM stimuli than NOVEL stimuli (FAM – NOVEL difference = -27.52 ms, $p < 0.01$, two-tailed; see Figure 11A), replicating a well-established finding in the object recognition literature (e.g. Smith 1967; Bülthoff and Bülthoff, 2003). There were no significant accuracy differences to categorize FAM and NOVEL stimuli ($p > 0.1$; see Table 1). Comparison between EXP and CON trials showed that participants were faster to categorize EXP stimuli as novel than CON stimuli as novel (EXP – CON difference = -24.34 ms, $p < 0.01$, two-tailed; see Figure 11B). Furthermore, participants categorized EXP trials more accurately than CON trials ($p < 0.01$, two-tailed; see Table 1). This accuracy difference was not significantly reduced after a secondary analysis in which participants exhibiting high error rates ($> 20\%$ across EXP, CON, and FAM conditions) were removed (EXP: $94 \pm 1\%$ vs. CON: $90 \pm 2\%$, $p < 0.01$, two-tailed).

During Task 2, participants were not significantly faster to categorize the unbounded regions of EXP stimuli as familiar than they were to categorize the

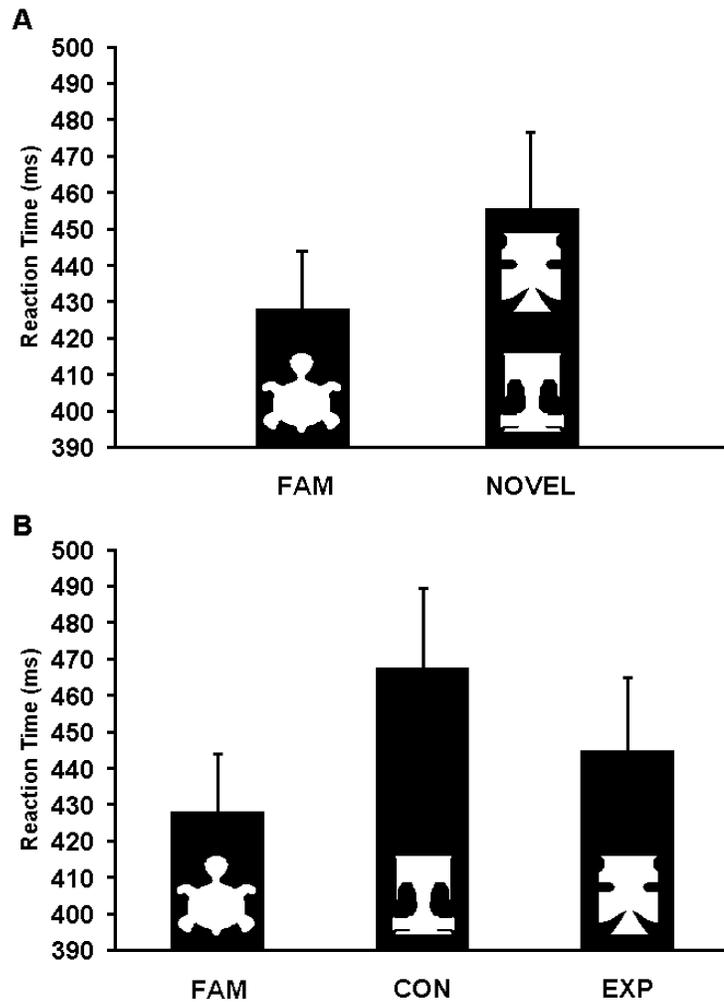


Figure 11. A) Reaction times (in ms) to categorize FAM stimuli as “familiar” and NOVEL (EXP & CON) stimuli as “novel” during Task 1, Experiment 1. B) RTs after separating responses to EXP and CON stimuli.

Response	“Familiar”		“Novel”	
	FAM	CON	EXP	EXP & CON
% Correct	82% ± 3%	83% ± 3%	89% ± 2%	86% ± 2%

Table 1. Accuracy rates for Experiment 1, Task 1.

Response	<i>“Familiar”</i>	<i>“Novel”</i>
	EXP	CON
% Correct	57 ± 3%	63 ± 5%

Table 2. Accuracy rates for Experiment 1, Task 2.

unbounded regions of CON stimuli as novel (486 ± 37 ms vs. 478 ± 30 ms, respectively; $p > 0.3$). This lack of significance may be mitigated, in part, by the generally poor accuracy rates observed for this task (see Table 2), although the latter were significantly greater than chance performance (EXP: $p < 0.05$, two-tailed; CON: $p < 0.01$, two-tailed). Also, there was no response bias in Task 2; participants were approximately equally likely to respond “familiar” (52%) or “novel” (53%) overall. Finally, there were no significant between-condition differences in accuracy to categorize the unbounded regions of the EXP stimuli as “familiar” versus the same regions of the CON stimuli as “novel” ($p > 0.1$).

2.3 Experiment 1- Discussion

Task 1 reaction time and accuracy differences indicate that EXP and CON stimuli were processed differently, as RTs to categorize EXP stimuli as novel were shorter than to similarly categorize CON stimuli. Accuracy rates were higher for EXP than CON stimuli as well. These findings were obtained when participants consciously saw the center silhouette regions as novel shaped figures, while blind to the familiar shapes depicted by the grounds of the EXP silhouettes. Thus the Task 1 behavioral results most likely reflect unconscious processing differences of EXP and CON stimuli.

It should be noted that the greater competition in the EXP silhouettes did not increase RTs here as they did in the studies of Peterson and Lampignano (2003) and Peterson and Enns (2005); indeed, RTs were faster for EXP relative to CON stimuli. Although this result is unexpected, a possible explanation for this discrepancy may lie in the fact that the greater mutual inhibition among configural cues for EXP relative to CON stimuli could lead to a reduction in the salience of the perceptual representation of the former relative to both CON and FAM stimuli. If participants based their judgments on the overall salience of the silhouette shape representations, then this might lead to a different pattern of RTs than observed in the previous studies of Peterson and Lampignano (2003) and Peterson and Enns (2005). Such a possibility will be discussed in more detail in Section 6.

No RT and accuracy differences were observed during Task 2 when participants consciously sought to see the outside regions of the silhouettes as figure, while categorizing those regions as “familiar” (EXP) or “novel” (CON). Of course, the two responses required in this task (familiar vs. novel) are different, therefore making the interpretation of RT comparisons difficult. This pattern of behavior did occur within the context of generally poor behavioral performance close to (but still significantly above) chance levels, however. This poor performance, though unbiased towards “familiar” or “novel” responses overall, may be responsible for the lack of significance of the EXP vs. CON RT differences. This poor performance may arise from the inherent difficulty in reversing the figural status of these stimuli so that that the outside regions are seen as figure. This difficulty in figure reversal was likely further compounded by the subsequent

presentation of the masks, which may have reduced the time to accomplish figure reversal before the iconic memory of the silhouettes was disrupted by the processing of the masks. In such a situation, task set must work against the configural cues that are biased to assign figural status to the center bounded regions of the silhouettes. This difficulty in reversing figural status was also likely influenced by the masking of the stimuli, which impaired the viewing of the outside regions of the EXP and CON silhouettes.

3. EXPERIMENT 2 - OVERVIEW

The purpose of Experiment 2 was to replicate the behavioral findings of Experiment 1 while simultaneously investigating task-related neural responses in the form of event-related potentials (ERPs).

3.1 Methods

3.1.1 Participants

Thirty-six undergraduate participants (15 female, 21 male; 5 left-handed, 31 right-handed; mean age = 22.78 ± 1.15 years) were recruited from the University of Arizona's undergraduate subject pool. Eight participants were removed from further analysis due to technical difficulties with their EEG recordings. Of the remaining 28 participants, there were 4 Seers (1 female, 3 males; 4 right-handed; mean age = 22.75 ± 2.29) and 24 Non-Seers (11 females, 13 males; 3 left-handed, 21 right-handed; mean age = 20.88 ± 0.73); only the Non-Seers' data were analyzed. All participants were screened to ensure normal visual acuity, and were fully informed of the experimental methods and proceedings before their consent to participate was obtained. The new experimental protocol was reviewed and approved by the Institutional Review Board for Human Studies at the University of Arizona.

3.1.2 Stimuli and Procedure

For Experiment 2, all silhouettes and masks were changed to white in color, displayed against a black background. This contrast reversal was motivated by the goal of

increasing the attentional impact of the stimulus presentation, as a bright stimulus against a dark background may be more salient than a dark stimulus against a light background.⁶

The silhouettes subtended an approximate visual angle of 4.00° in height, while ranging from approximately 1.50° to 7.98° in width. All stimuli were pattern masked after presentation; the pattern masks subtended approximate visual angles of 4.00° in height and 7.98° in width. Seven different masks were used, with each mask following each silhouette equally often; the same set of masks was used in all experimental conditions. Participants viewed the stimuli from a distance of 80 cm while seated in a comfortable chair; head motion was not stabilized via use of a chin rest; participants were instructed to keep their heads still and resting on the back of the chair. Stimulus materials were presented to the participants on an 18" computer CRT screen using the DMDX stimulus presentation software.

After consent and demographic information were obtained, the participants underwent EEG setup (see EEG Recordings Section 3.1.3, below). They then were brought into the experimental chamber and instructed in the experiment task. The remaining design, task, and procedures of Tasks 1 and 2 of Experiment 2 were nearly identical to Experiment 1. Silhouette and mask exposure durations were 167 ms and 250 ms, respectively. Participants categorized silhouettes using two joystick buttons held one in each hand. Inter-trial intervals varied from 1210 to 3481 ms.

⁶ It should be noted that this change in stimulus contrast polarity should negligibly impact the processing of the silhouette edges and the competition of configural cues across the edge. This is because light detectors in the retina essentially detect differences in contrast (Nolte, 2002), and such differences would only change in polarity, not magnitude, upon color reversal of the silhouette figure/background.

After participating in Tasks 1 and 2, participants were queried regarding whether or not they saw any known objects in the surrounds of the silhouettes (using the same questionnaire as in Experiment 1; see Appendix C for a sample of the post-experiment questions). Participants who recalled seeing any familiar shapes in the unbounded regions of the silhouettes during Task 1 (“Seers”) were excluded from further analysis (see Participants Section 2.1.1). To corroborate these reports, participants were again given lists of objects and asked to identify which objects (if any) they saw depicted by the unbounded regions of the silhouettes during the course of the experiment (see Appendix C). Half of the listed objects were depicted in the grounds of the EXP silhouettes; the remaining listed objects were not depicted by either the EXP or FAM silhouettes. P(A) measures of sensitivity revealed that during Task 1 the 24 Non-Seers retained in this experiment did not reliably remember seeing familiar shapes depicted by the unbounded regions of the EXP silhouettes ($P(A) = 0.56 \pm 0.03$). During Task 2, participants remembered seeing many familiar shapes depicted in the unbounded regions of the EXP silhouettes ($P(A) = 0.78 \pm 0.02$). As in Experiment 1, the Experiment 2 P(A) measure for Task 2 was greater than in Task 1 ($P(A)_{\text{Task 2}} - P(A)_{\text{Task 1}} = 0.22 \pm 0.04$; paired $t(23) = 4.97$, $p < 0.01$), again supporting the claim that participants actually saw familiar shapes in the unbounded regions of the EXP stimuli during Task 2, but did not see such shapes during Task 1.

3.1.3 EEG Recordings

Sixty four channels of scalp EEG were recorded during all portions of the experiment, using sintered Ag/AgCl electrodes mounted in an electrode cap (Neuroscan, Compumedics Ltd., El Paso TX, USA) with two additional bipolar electrode pairs outside the cap to monitor vertical and horizontal eye movements.

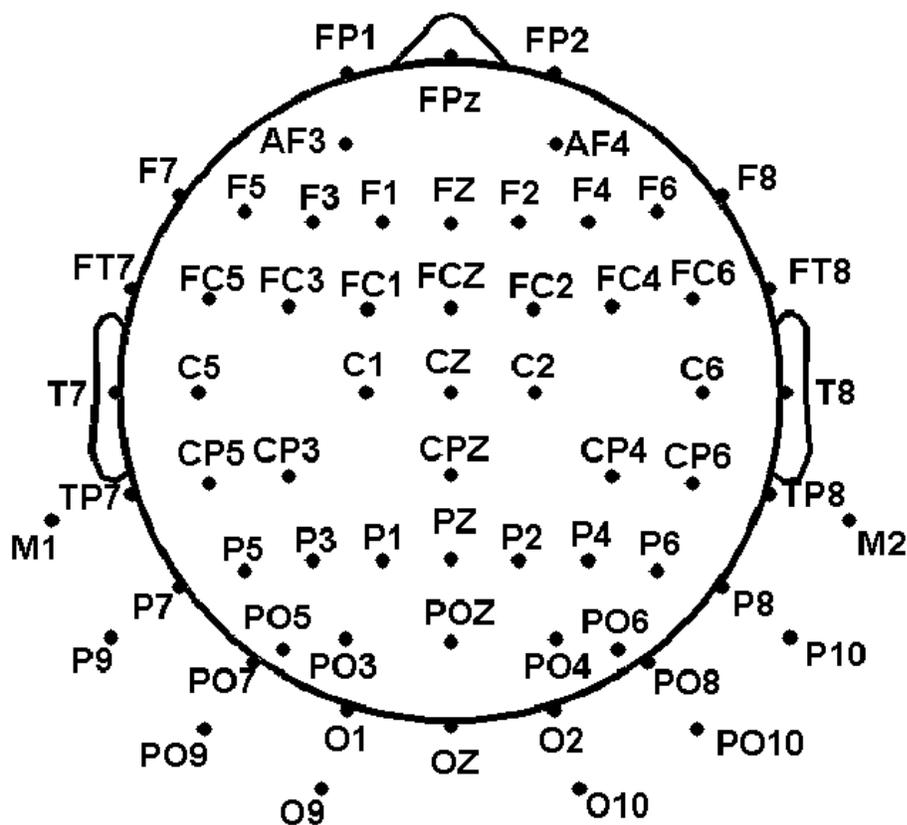


Figure 12. Extended 10-20 scalp locations of EEG recording electrodes. Note that sites outside the radius of the head represent locations that are below the equatorial plane (FPZ-T7-T8-OZ plane) of the (assumed spherical) head model.

Recording sites in the electrode cap included standard and extended 10-20 system locations (FP1, FPZ, FP2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, P9, C1, CZ, C2, P10, C6, T8, M1, TP7, CP5, CP3, O9, CPZ, O10, CP4, CP6, TP8, M2, P7, P5, P3, P1, PZ, P2, P4, P6, P8, PO7, PO5, PO3, POZ, PO4, PO6, PO8, PO9, O1, OZ, O2, PO10; see Figure 12), recorded with respect to a physically linked-ears reference. Two pairs of Ag/AgCl bipolar recording leads, affixed to the outer canthi of both eyes and also to the superior and inferior orbit of the left eye, recorded eye movements and blinks (EOG). All scalp/ear channels were amplified 20,000 times via a Neuroscan Synamps II amplifier system in DC mode at a sampling rate of 1000 Hz. Eye leads were amplified 5,000 times. Impedances were reduced below 5k ohms. All EEG muscle artifacts were removed from the raw EEG record by visual inspection. Portions of the EEG record containing EOG activity $>$ or $< \pm 75 \mu\text{V}$ were rejected from the analysis via an automatic algorithm available with the Neuroscan Edit 4.3 software.

3.1.4 Behavioral Data Analysis

The same behavioral measures (RT and % correct) and analyses used in Experiment 1 were used in Experiment 2.

3.1.5 ERP Data Analysis

Single 750 ms EEG trials were extracted from the continuous record for EXP and CON conditions. These trials ranged from -250 ms to 500 ms with respect to silhouette

onset. The single trials were then spline fit to a 1024 HZ sampling rate, transformed to an average reference, and then low-pass filtered (30 HZ cutoff; 96 db rolloff; zero phase shift). Stimulus-locked ERPs were computed by averaging trials separately for the EXP and CON conditions for each subject. ERPs were baseline corrected to the -100 ms to 0 ms pre-stimulus interval.

Following a priori hypotheses concerning the loci of neural activation (visual cortex), ERP analyses were restricted to posterior scalp sites including occipital (OZ, O1, O2, O9, O10), parietal (PZ, P1, P2, P3, P4, P5, P6), parietal-occipital (PO3, PO4, PO5, PO6, PO7, PO8) and temporo-parietal (P7, P8, P9, P10, P09, P010) regions. For each subject and condition, ERP component peak latencies and amplitudes were measured over these scalp sites for the P1 (80 – 140 ms post-stimulus interval), the N170 (140-200 ms), and a Late Potential (270 – 340 ms). The decision to restrict analyses to these posterior electrodes was motivated by the dipolar nature of the observed ERP scalp topographies (see Results), which indicates that portions of anterior ERP responses (i.e. the Vertex Positive Potential, or VPP) can arise through volume conduction of electric fields emanating from the same source(s) as the posterior responses (Rossion et al. 2003). Thus the anterior and posterior ERP components of interest are not spatially independent, and may be statistically indexed by the subset of electrodes located over visual brain regions.

Statistical analyses of ERP amplitudes and latencies were carried out using non-parametric permutation t-tests (Burgess and Gruzelier, 1999; Nichols and Holmes, 2001) corrected for multiple comparisons across electrodes. An empirical t-distribution was

estimated from the data by computing t-statistics from each of 5000 random within-subject permutations of data values across the EXP and CON conditions under the null hypothesis. Distributions were computed for each electrode site of interest. Type-1 error was controlled for multiple comparisons across electrodes by extracting the maximum t-statistic across all electrodes of interest and ERP component time interval at each permutation step (Burgess and Gruzelier, 1999; Nichols and Holmes, 2001). These values were collapsed together to form a single distribution of t-values used to test for the presence of between-condition differences at each electrode. P100, N170, and LP amplitudes and latencies were simultaneously tested across all relevant electrodes.

For graphical display, individual ERPs were averaged across participants within each condition, generating grand-average ERPs for EXP and CON conditions. ERP component scalp topographies were visualized by first extracting amplitude values for all electrodes at the peak latency for each condition and then displaying them as scalp topographies using algorithms from the EEGLAB toolbox (Delorme and Makeig, 2004) for the Matlab computing software (The Math Works, Inc., Natick, MA, USA).

3.2 Experiment 2 - Results

3.2.1 Behavior

In nearly all respects the behavior of Experiment 2 replicates the behavior of Experiment 1. During Task 1, participants were faster to categorize FAM stimuli as familiar than NOVEL stimuli (EXP and CON) as novel (FAM – NOVEL difference = -43.65 ms, $p < 0.01$, two-tailed; see Figure 13A). In addition, participants were more

accurate at categorizing NOVEL stimuli as novel than FAM stimuli as familiar ($p < 0.05$, two-tailed; see Table 3). Comparison between EXP and CON trials shows that participants were faster to categorize EXP than CON stimuli as novel (EXP – CON difference = -20.25 ms, $p < 0.01$, two-tailed; see Figure 13B). Furthermore, participants categorized EXP stimuli more accurately than CON stimuli ($p < 0.01$, two-tailed; see Table 3).

Experiment 2 Task 2 accuracy rates were generally higher than Experiment 1 Task 2 accuracy rates (see Table 4), and were significantly above chance (EXP: $p < 0.01$, two-tailed; CON: $p < 0.001$, two-tailed). There was a small overall bias to categorize the unbounded regions of the silhouettes as “novel” (“novel” = 57% of trials; “familiar” = 43% of trials). Participants were more accurate in categorizing the unbounded regions of the CON stimuli as depicting novel shapes than they were at categorizing the same regions of the EXP stimuli as depicting familiar shapes ($p < 0.05$, one-tailed). Although reaction times to accurately categorize the unbounded regions of EXP stimuli appeared to be faster than RTs to categorize the unbounded regions of CON stimuli (684 ± 39 ms vs. 714 ± 46 ms, respectively), this difference was not significant ($p > 0.1$).

Response	<i>“Familiar”</i>	<i>“Novel”</i>		
	FAM	CON	EXP	EXP & CON
% Correct	89% \pm 3%	94% \pm 1%	97% \pm 1%	95% \pm 1%

Table 3. Accuracy rates for Experiment 1, Task 1.

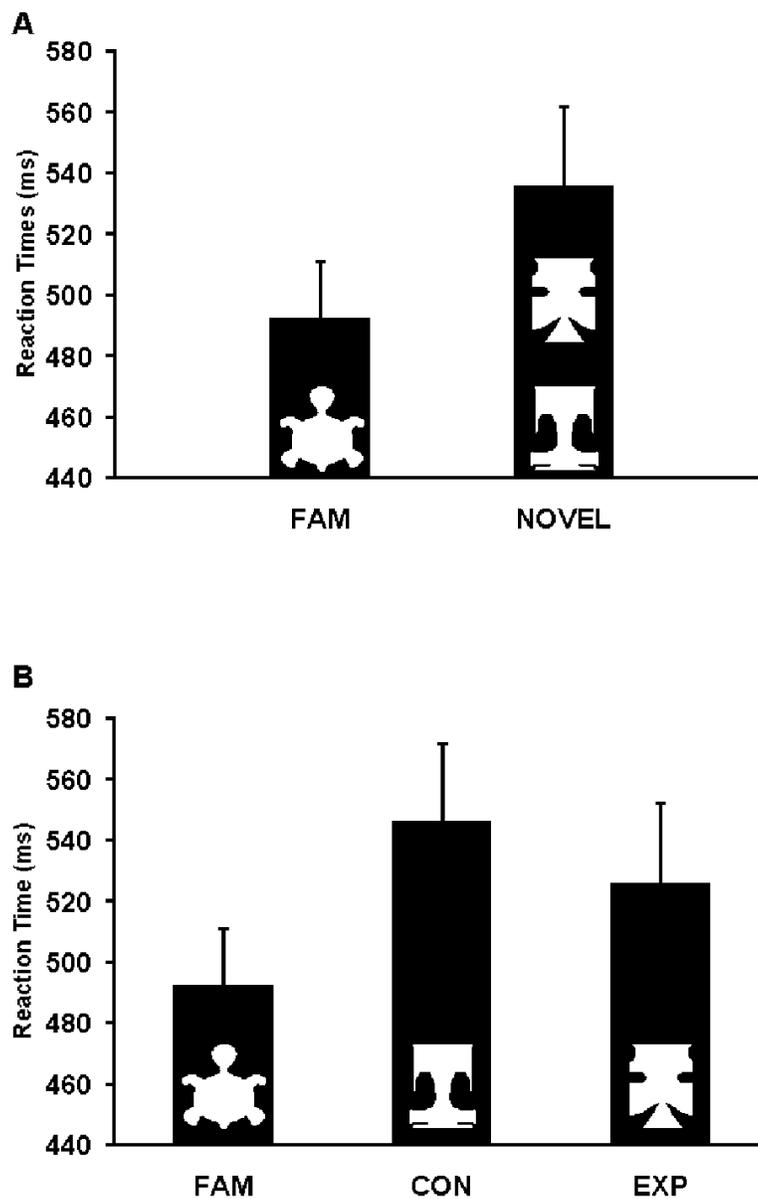


Figure 13. A) Reaction times (in ms) to categorize FAM stimuli as “familiar” and NOVEL (EXP & CON) stimuli as “novel” during Task 1, Experiment 2. B) RTs after separating responses to EXP and CON stimuli.

Response	<i>“Familiar”</i>	<i>“Novel”</i>
	EXP	CON
% Correct	62 ± 4 %	76 ± 4 %

Table 4. Accuracy rates for Experiment 1, Task 2.

3.2.2 ERP Analysis

The morphologies of the EXP and CON grand-average ERP waveforms observed across all scalp locations during Task 1 (see Figure 14) and Task 2 (see Figure 16) of Experiment 2 were typical of visual evoked potentials. These ERP responses consisted of three basic features: a positive response occurring at ~ 110 ms (P100); a negative response occurring at ~ 160 ms (N170); and a positive Late Potential (LP) emerging around 200 ms to a maximum peak at ~ 272 ms which was sustained for the rest of the epoch (See Table 5). Scalp topographies of each ERP component had maximum amplitudes at posterior scalp locations (Figures 14 and 16). The P100 was more distributed over central and lateral occipital scalp sites, the N170 was distributed over lateral temporo-parietal locations, and the positive LP was distributed over lateral occipital regions.

Figure 15 compares representative ERP responses to EXP and CON stimuli when the inner (white) regions were categorized as novel in Part1 of Experiment 2. There was a small, but reliable N170 between-condition amplitude difference at right hemisphere site PO6 (Figure 15A), where the EXP N170 response was greater than the CON N170 ($t(23) = -2.91$; $t_{critical} = 2.75$, $p < 0.05$, two-tailed). Other significant between-condition amplitude differences did not emerge until ~ 250 ms post-stimulus during the onset of the LP over right hemisphere scalp sites (Figure 15B). LP amplitudes in response to EXP stimuli were smaller than for CON stimuli from ~ 250 – 375 ms at PO6, PO10, O2, O10 (PO6: $t(23) = -3.06$, PO10: $t(23) = -3.29$, O2: $t(23) = -2.96$, O10: $t(23) = -2.77$; $t_{critical} = -2.75$, $ps < 0.05$, two-tailed). Thus the LP responses reflected the configural cue differences between EXP and CON silhouettes. No significant between-condition latency difference

	P1				N170				LP			
	Amplitude		Latency		Amplitude		Latency		Amplitude		Latency	
Task 1	PO5	PO6	PO5	PO6	PO5	PO6	PO5	PO6	PO5	PO6	PO5	PO6
FAM	4.44	6.54	110	109	-2.61	-0.77	160	164	10.88	13.74	287	355
CON	5.18	6.50	110	107	-1.71	-0.08	158	160	12.46	15.33	280	272
EXP	5.29	6.32	111	106	-1.81	-0.77	156	158	12.33	14.41	274	272
Task 2												
CON	5.22	6.33	112	108	-1.83	-1.52	163	166	8.89	11.87	375	359
EXP	4.77	6.21	109	106	-2.97	-3.19	162	165	7.92	10.37	375	364

Table 5. Representative peak amplitudes (μV) and associated latencies (ms) for P100, N170, and LP ERP components by condition.

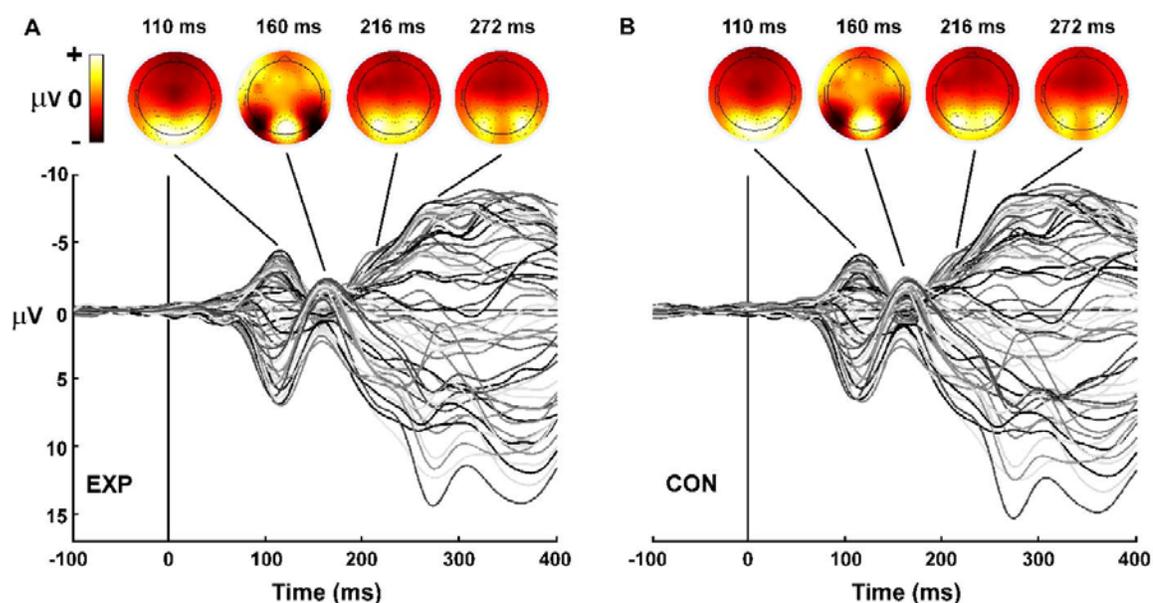


Figure 14. Grand-average ERP waveforms at all scalp locations to EXP (A) and CON (B) stimuli categorized as novel during Task 1 of Experiment 2. Head maps show ERP scalp topography at the indicated latencies. Scaling of head maps is separately set to the maximum/minimum of each response to better display the fine details of each component's scalp topography. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

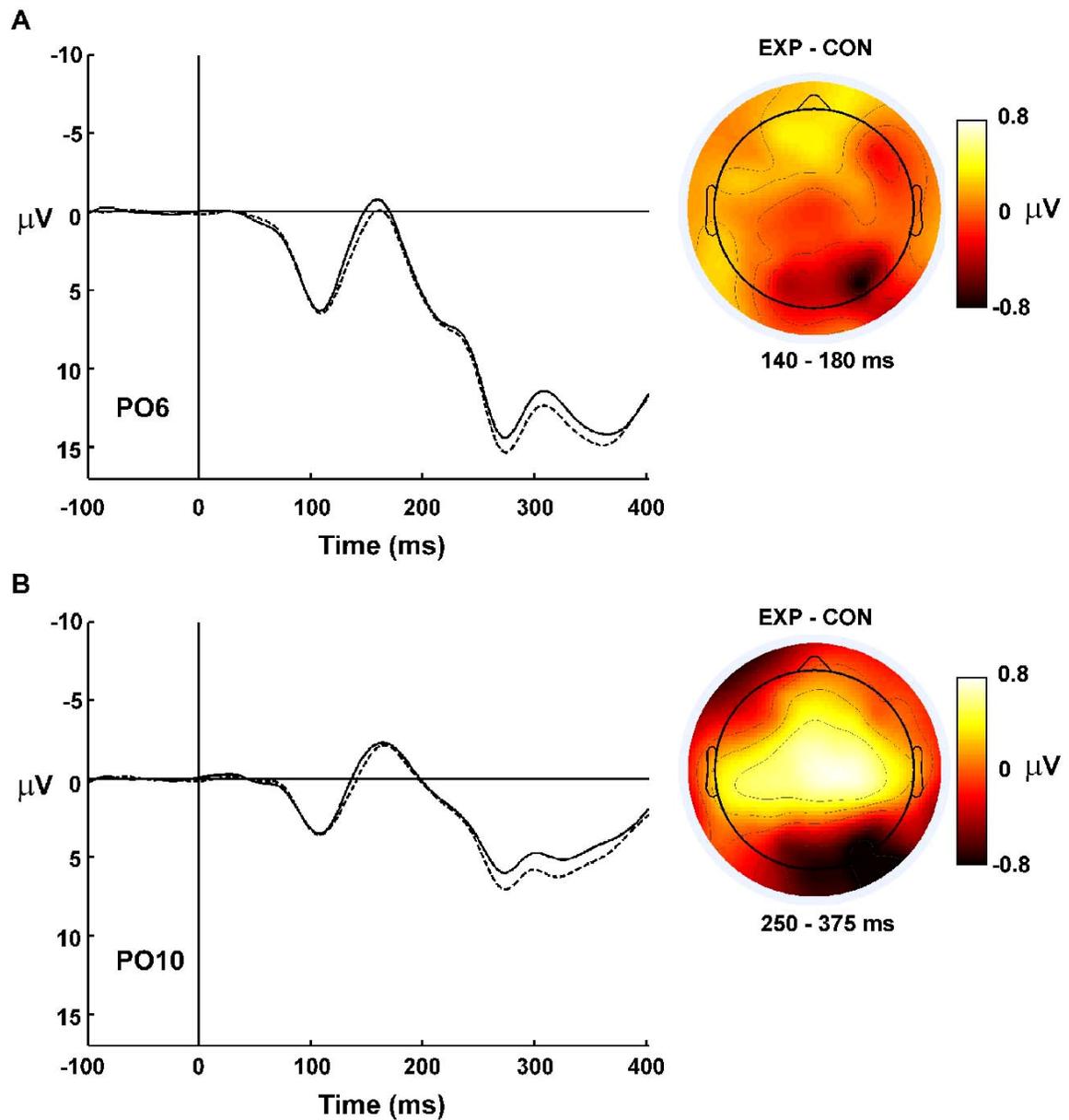


Figure 15. Comparison of Experiment 2, Task 1 ERP responses to EXP (solid black line) and CON (dashed black line) stimuli when the inner (bounded) regions were categorized as novel. A) ERP waveforms at site PO6. Inset: Scalp topography of EXP – CON difference waveform averaged over the indicated interval. B) ERP waveforms at site PO10. Inset: Scalp topography of EXP – CON difference waveform averaged over the indicated interval. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

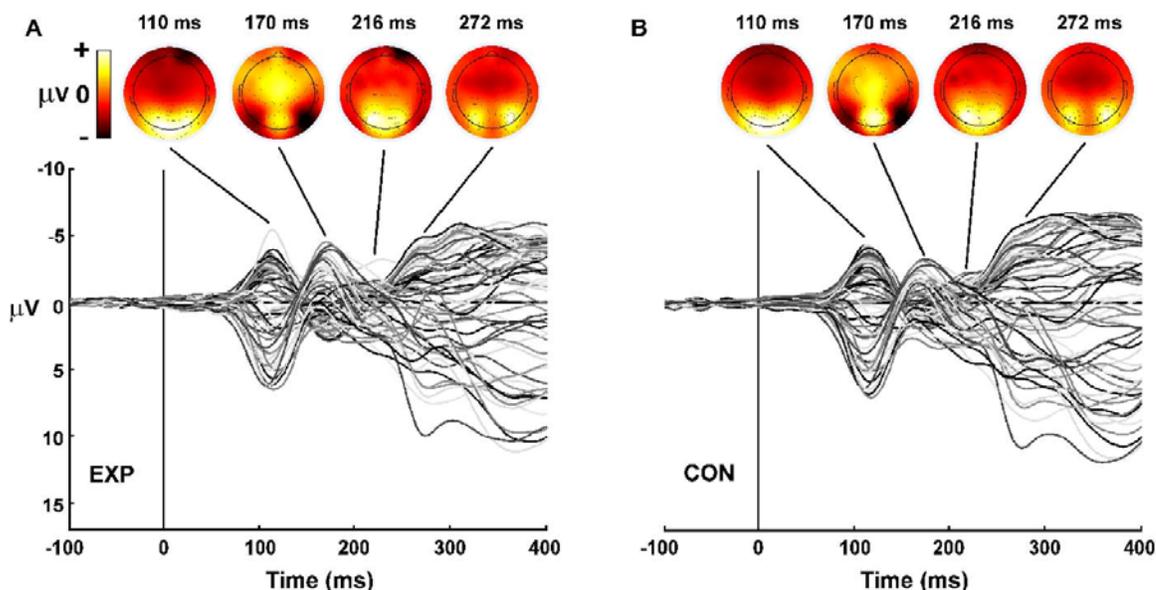


Figure 16. Grand-average ERP waveforms to EXP (A) and CON (B) stimuli when the outer (unbounded) regions were categorized as familiar and novel, respectively (Task 2). Head maps show ERP scalp topography at the indicated latencies. Scaling of head maps is separately set to the maximum and/or minimum of each response to better display the fine details of each component's scalp topography. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

was observed for the LP or any other ERP component in either hemisphere.

Figure 17 compares representative ERP responses to EXP and CON stimuli when the outer (unbounded) regions were seen as figure and categorized respectively as familiar or novel during Task 2 of Experiment 2. N170 amplitudes for the EXP condition were greater than for the CON condition from $\sim 150 - 190$ ms at site P3, P4, P5, P6, P8, P10, PO3, PO4, PO5, PO6, PO7, PO8, PO10, O1, OZ, O2, O10 (maximum significance at PO6: $t(23) = -4.78$; $t_{\text{critical}} = -2.65$, $p < 0.05$, two-tailed). Thus during Task 2 the N170 amplitude differentiated successful vs. unsuccessful shape recognition of the outside regions of EXP and CON silhouettes.

LP amplitude differences remained the same as for Task 1; CON responses were greater than EXP responses over the 250 – 375 ms interval at sites P5, P7, P8,P9, P10, PO5, PO7, PO8, PO9, PO10, O1, OZ, O2, O9, and O10 (maximum significance at PO9: $t(23) = -9.33$; $t_{\text{critical}} = -2.84$, $p < 0.05$, two-tailed). Thus LP responses reflected the configural cue differences between EXP and CON silhouettes, regardless of which side of the silhouette was assigned figural status, or the successful or unsuccessful perception of the meaningful shapes in the EXP stimuli. As in Task 1, no major latency differences were found other than a small delay (~ 3 ms) of the CON P1 component relative to the EXP P1 at site O1 ($t(23) = -9.33$; $t_{\text{critical}} = 2.69$, $p < 0.05$, two-tailed);

Figure 18 compares representative ERPs to EXP and CON stimuli evoked during Task 1(black lines) and Task 2 (red lines). Recall that in Task 1 the inner bounded regions were seen as figure and categorized as novel, while in Task 2 the outer unbounded regions were seen as figure and categorized as familiar or novel (respectively). No between-condition P1 amplitude differences were observed ($ps > 0.1$), and the overall magnitude of the Task 2 P1 response (after collapsing across EXP and CON conditions) was approximately equivalent to the P1 response evoked during Task 1 ($ps > 0.1$). N170 and the LP amplitudes, however, were significantly different during Task 2 than Task 1 over most of the posterior sites (after collapsing across EXP and CON conditions). The N170 was larger at sites O9 O10 P6 PO8, O1 and O2 (max significance at O2: $t(23) = 3.47$; $t_{\text{critical}} = 2.75$, $p < 0.001$, two-tailed); the LP was smaller at all indexed sites (max significance at O1: $t(23) = -7.02$; $t_{\text{critical}} = -2.65$, $p < 0.001$, two-tailed). These ERP changes were accompanied by significant N170 latency delays ($\sim 3 - 7$ ms) for Task 2 vs. Task 1

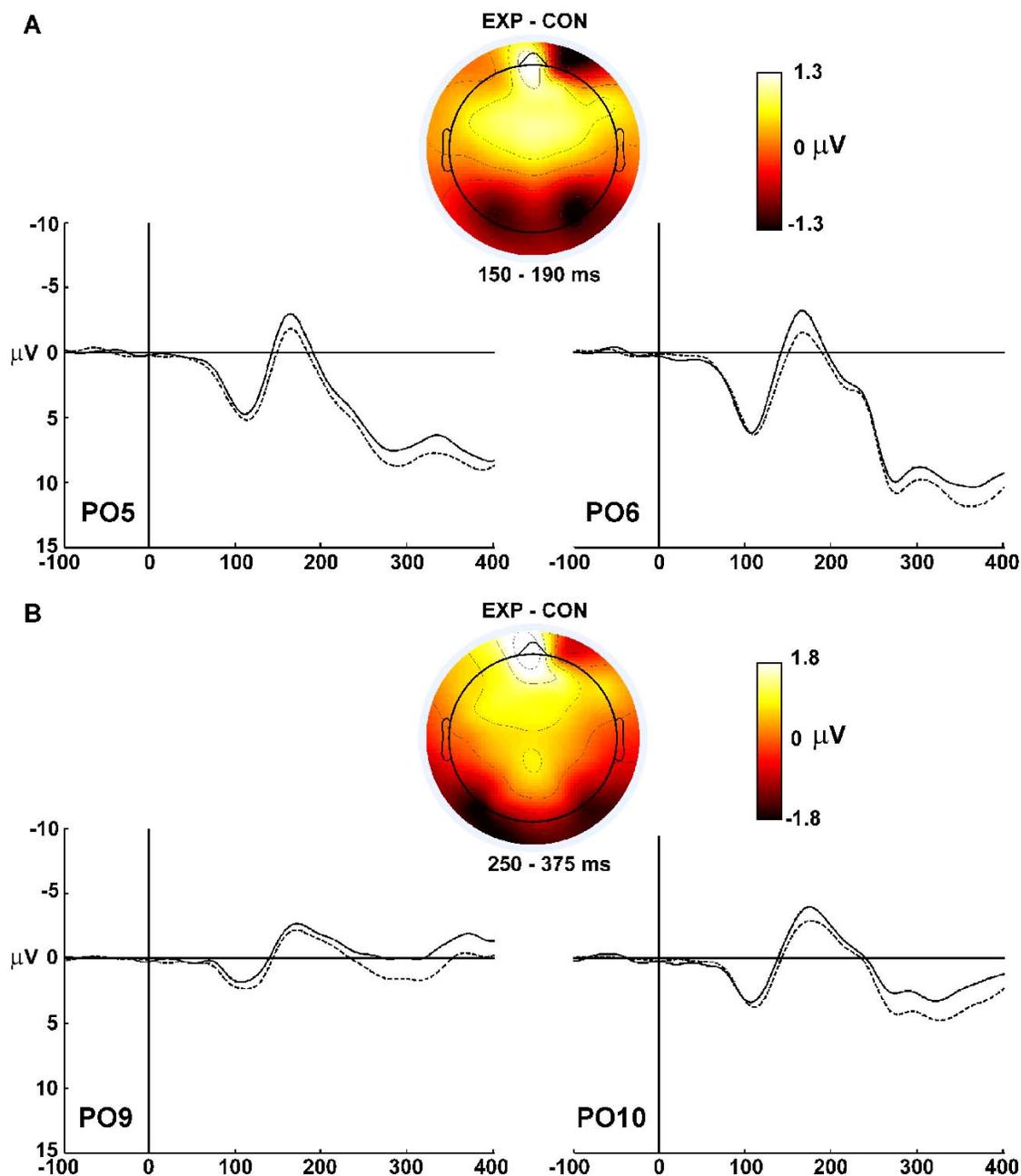


Figure 17. Comparison of Experiment 2, Task 2 ERP responses to EXP (solid black line) and CON (dashed black line) stimuli when the outer (unbounded) regions were categorized as familiar and novel, respectively. A) ERP waveforms at sites PO5 and PO6. Inset: Scalp topography of EXP – CON difference waveform averaged over the indicated interval. B) ERP waveforms at sites PO9 and PO10. Inset: Scalp topography of EXP – CON difference waveform averaged over the indicated interval. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

responses at sites P6, P8, P10, PO3, PO5, PO6, PO7, PO8, PO9, PO10, O1, O2, O10 (all $p > 0.05$, two-tailed; maximum delay of 7 ms at P6, $t(23) = 3.91$, $t_{critical} = 2.61$. $p < 0.002$, two-tailed). The Task 2 LP component was also delayed relative to the Task 1 LP at site P6 (difference = 3 ms, $t(23) = 2.88$, $t_{critical} = 2.82$. $p < 0.04$, two-tailed).

3.3 Experiment 2 - Discussion

Experiment 2 provides behavioral and electrophysiological evidence that EXP and CON stimuli are processed differently during the shape categorization task. The Task 1 behavioral data, obtained when participants were unconscious of the familiar shapes along the outside of EXP silhouettes, replicated the original finding of Experiment 1 that RTs to EXP stimuli categorized as novel were faster than to similarly categorized CON stimuli. This behavioral difference was accompanied by a decreased positive LP for EXP vs. CON stimuli over posterior scalp sites. For Task 2, participants were instructed to reverse the figure along the silhouette edges in order to see the outsides of the silhouettes as familiar (EXP) and novel (CON) shapes. The performance of this task was accompanied by an overall increase in N170 amplitude, with a greater N170 response for EXP than CON stimuli, and an overall decrease in LP responses. Between-condition differences in LP response replicated those seen in Part1 (CON > EXP).

The processing differences underlying the results of Experiments 1 and 2 could be due to differential unconscious (Task 1) and conscious perception (Task 2) of the familiar shapes depicted by the outside regions of the EXP stimuli. The behavioral and electrophysiological differences do correlate with the presence or absence of past

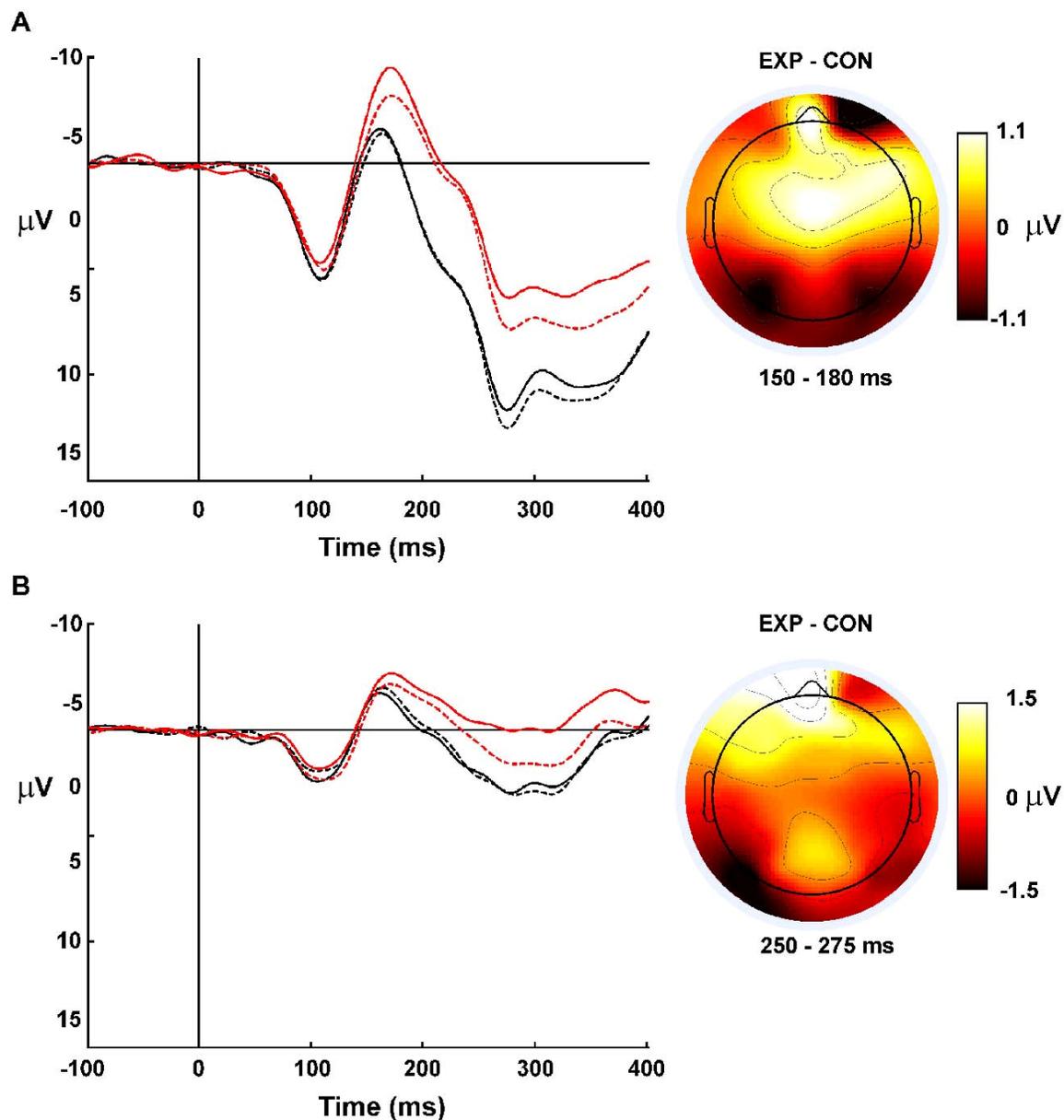


Figure 18. Comparison of Experiment 2, Task 1 (black lines) and Task 2 (light red lines) ERP responses to EXP and CON stimuli when the inner (bounded) regions were categorized as novel (EXP, black solid line; CON, dashed black line), and when the outer (unbounded) regions were categorized as familiar (EXP, light red solid line) and novel (CON, light red dashed line). A) ERP waveforms at site PO8. Inset: Scalp topography of $(\text{EXP} - \text{CON})_{\text{Task 2}} - (\text{EXP} - \text{CON})_{\text{Task 1}}$ difference waveform averaged over the indicated interval. B) ERP waveforms at site PO9. Inset: Scalp topography of EXP - CON difference waveform averaged over the indicated interval. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

experience cues in the outside areas of novel silhouettes (EXP, CON). Even so, such an interpretation is not yet totally compelling, as the patterns of data observed in Experiments 1 and 2 raise some questions.

First, the finding of faster RTs to EXP than CON stimuli during Task 1 is unexpected. One might expect that it would take longer to resolve the greater competition present for the EXP stimuli than for CON stimuli, and thus that RTs would be longer for EXP than CON stimuli, as observed by Peterson and Lampignano (2003) and Peterson and Enns (2005). As mentioned in Section 2.3, however, if participants based their judgments on the overall salience of the silhouette shape representations, then this might lead to a different pattern of RTs than observed in previous studies, assuming such representational salience was reduced in the EXP relative to the CON condition due to the greater mutual inhibition present to the former. This possibility will be discussed in more detail in Section 6.

Second, the finding of greater accuracy at categorizing EXP than CON stimuli as novel is similarly curious. One might have expected that EXP stimuli would be more difficult to categorize because implicit activation of shape memory cues could bias familiarity decisions towards “familiar” responses. As to be discussed in Section 6, however, if the salience of the EXP stimuli representations is reduced, then this could lead them to be perceived as more “novel” than the CON silhouettes. Third, neural responses associated with figure-ground segregation have been found to occur around ~ 100 ms in monkeys and humans (Lamme, Van Dijk, and Spekreijse, 1992; Lamme, 1995; Lamme, Super, and Spekreijse, (1998); Lamme, 2000; Super, Spekreijse, and Lamme,

2001). If the observed Late Potential differences reflect greater inhibition present in the processing of EXP stimuli, then why are such differences occurring later in time (~250 – 350 ms) and not earlier in time during the P1 and N170 responses? In addition, why do these LP differences persist even during Task 2 when participants attempt to reverse the silhouette figure to consciously see the meaningfully shaped contours of the EXP stimuli?

Before trying to piece together an explanation of these results in terms of the competitive model, it is important to verify that they could not be due to differences in low-level image properties between EXP and CON conditions in these experiments. It is possible that differences in such properties could affect subject task strategies (consciously or unconsciously). Furthermore, early ERP responses are very sensitive to such properties and property differences (VanRullen and Thorpe, 2001). If the present stimuli differ in one or more low-level properties, then the pattern of results observed across Experiments 1 and 2 may be artifactual. An analysis of these stimulus properties is presented in the next section.

4. STIMULUS ANALYSIS

4.1 Experiments 1 and 2 – Stimulus Analysis Methods

To assess possible stimulus differences between experimental stimuli, the low-level properties of luminance, contour length, and global spatial frequency were computed for CON, EXP, and for comparison, FAM stimuli. These values were then subjected to between-condition two-sample t-tests separately for each property. These three key properties were chosen for analysis because they have been shown to influence ERPs and behavior alike. For example, the P1 and N170 ERPs component have been shown to be sensitive to luminance (Johannes et al., 1995), while the N170 is sensitive to spatial frequency (Goffaux, Gauthier, and Rossion, 2003). Contour length is also an important property to assess in the present context because the total amount of configural cue competition across an edge may be proportional to the length of the edge. Thus a mismatch in edge lengths across conditions could lead to ERP and/or RT differences, or lack thereof.

Luminance was computed for each stimulus in terms of the total area (in pixels) of the white center regions of the silhouettes (in Experiment 2 recall that the silhouettes were white against a black background). This computation was based upon the assumption that for these monochromatic binary images, each “on”- (white) pixel produces a single quanta of luminance. Total stimulus luminance may then be expressed as the total number of pixels multiplied by the luminance quanta. Thus calculating the total stimulus area is equivalent to counting the total number of pixels contained within the white regions of each stimulus, which in turn is equivalent to indexing the total

luminance of the stimulus. Pixel numbers were computed using specially written MATLAB scripts implementing the *bwarea* function of the MATLAB Image Processing Toolbox.

Contour length was computed by first extracting out the perimeter of each stimulus (using the MATLAB Image Processing Toolbox *bwperim* function), and then counting the total number of pixels composing that perimeter (using the *bwarea* function). Spatial frequencies were computed using a previously published method (Trujillo et al., 2005). Two-dimensional Fourier transforms were performed on FAM, CON, and EXP stimuli. The resulting spatial frequency power values were summed across horizontal and vertical frequency ranges to yield summed values for each horizontal and vertical frequency. These two sets of values were then squared and summed, creating two global spatial frequency power statistics, one for horizontal and one for vertical frequencies.

4.2 Stimulus Analysis Experiments 1 and 2 – Results and Discussion

Table 6 shows the computed stimulus property values for each stimulus type. Table 7 shows results of the between-condition t-tests performed on the computed values. It is clear from the tables that the critical EXP and CON stimuli significantly differed from each other for all of the properties save vertical spatial frequency. Moreover, for all properties except contour length, EXP stimuli differed more from FAM stimuli than CON stimuli did. Thus it is possible that a portion of the EXP vs. CON ERP and

	FAM	CON	EXP
Total Area	34495.53 ± 2949.21	56044.18 ± 2152.63	62778.01 ± 1326.66
Contour Length	1700.00 ± 126.98	1582.87 ± 61.25	1814.81 ± 48.24
Spatial Frequency			
<i>Horizontal</i>	2.90 ± 0.18	4.49 ± 0.18	5.52 ± 0.14
<i>Vertical</i>	3.09 ± 0.16	3.35 ± 0.12	3.55 ± 0.08

Table 6. Computed low-level stimulus property values of luminance/total area (pixels), contour length (pixels), and spatial frequency (arbitrary units).

	EXP vs CON	EXP vs FAM	CON vs FAM
Total Area	2.66 *	8.75 ***	5.90 ***
Contour Length	2.97 **	0.85	-0.83
Spatial Frequency			
<i>Horizontal</i>	4.55 ***	11.31 ***	6.28 ***
<i>Vertical</i>	1.36	2.54 *	1.32

Table 7. Between-condition t-tests between computed low-level stimulus property values. The *, **, and *** symbols indicate tests significant (respectively) at the $p < 0.05$, $p < 0.01$, and $p < 0.001$ (two-tailed) or greater significance levels ($df = 41$).

behavioral differences could be due to the influence of low-level stimulus differences across conditions.

EXP and CON stimuli also differed from FAM stimuli along several of these properties (except contour length and spatial frequency). At first glance this should not pose a problem, in that FAM stimuli were only used as part of the cover task within which the EXP and CON stimuli were presented, and thus ERPs to FAM stimuli were not critical to the present analysis (and thus not computed). Nonetheless, it remains possible that the behavioral results observed across Experiments 1 and 2 were indirectly influenced by the greater similarity of CON stimuli to FAM stimuli in terms of total area and/or horizontal spatial frequency.

For example, Figure 19 plots total area vs. accuracy (Figure 19A) and vs. RT (Figure 19B) for FAM (black triangles, dashed black line), CON (red squares, red solid line) and EXP (black circles, black solid line) stimuli categorized during Task 1 of Experiment 1. Figure 20 plots horizontal spatial frequency power vs. accuracy (Figure 20A) and RT (Figure 20B) for these same stimuli categorized during Task 1 of Experiment 1. These figures show that FAM and CON stimuli tended to be smaller in area and horizontal spatial frequency than EXP stimuli, and that participants made more errors and took longer to respond to small area/spatial frequency CON stimuli than large area/spatial frequency CON stimuli. Similar findings (not shown) were observed for accuracy rates and RTs of Experiment 2, Task 1. This pattern suggests that participants may have confused a subset of CON stimuli for FAM stimuli because of their similar stimulus properties, and as a result took longer to categorize that subset as novel. This possibility could explain the faster RTs to EXP vs. CON stimuli observed across Experiments 1 and 2.

One way to test this possibility would be to remove the most extreme-valued CON stimuli from the analysis and observe the effect on RT differences. Figure 21 shows Task 1 RTs from Experiment 1, after removing the eight most extreme-valued CON silhouettes across both total area and horizontal spatial frequency power; Table 8 shows the accuracy rates. As can be seen from the figure and table, the basic pattern observed in Experiment 1 remains FAM RTs are shorter than NOVEL RTs (428 ± 16 ms vs. 452 ± 21 ms, respectively; $t(22) = 3.80$, $p < 0.05$, two-tailed), and CON RTs are greater than EXP RTs (463 ± 21 ms vs. 445 ± 20 ms, $t(22) = 5.46$, $p < 0.01$, two-tailed). When this

analysis is applied to the Task 1 data of Experiment 2, a similar pattern of RTs were observed (Figure 22 and Table 9): FAM RTs are shorter than NOVEL RTs (492 ± 19 ms vs. 531 ± 25 ms, respectively; $t(23) = 2.94$, $p < 0.01$, two-tailed), and CON RTs are greater than EXP RTs (536 ± 25 ms vs. 526 ± 26 ms, $t(22) = 2.32$, $p < 0.025$, two-tailed). Note that the accuracy rates for these two experiments remained similar to what was found before the removal of the extreme-valued CON stimuli. Experiment 1 Task 1 accuracy rates did not differ between FAM and NOVEL conditions, but did differ between EXP and CON conditions ($p < 0.01$, two-tailed), while Experiment 2 Task 1 accuracy rates were significantly different between FAM and NOVEL ($p < 0.05$, two-tailed) and EXP and CON stimuli ($p < 0.01$, two-tailed).

4.3 Improving the Stimuli: Analysis, Results, and Discussion

The above results suggest that the behavioral effects observed in Experiments 1 and 2 are not purely due to stimulus artifacts, but also express high-level processing differences between the EXP and CON stimuli. A similar analysis could also be done to see if the ERP effects of Experiment 2 could or could not be explained by stimulus differences. Alternatively, one could remake the stimuli so that they differed as little as possible in the stimulus properties. This was the method chosen here. Since the EXP and CON stimuli were of the central interest in this study, the primary goal of this procedure was to completely equate these two stimulus types with each other as a group in terms of the several key stimulus properties analyzed earlier. Equating the FAM stimuli with the

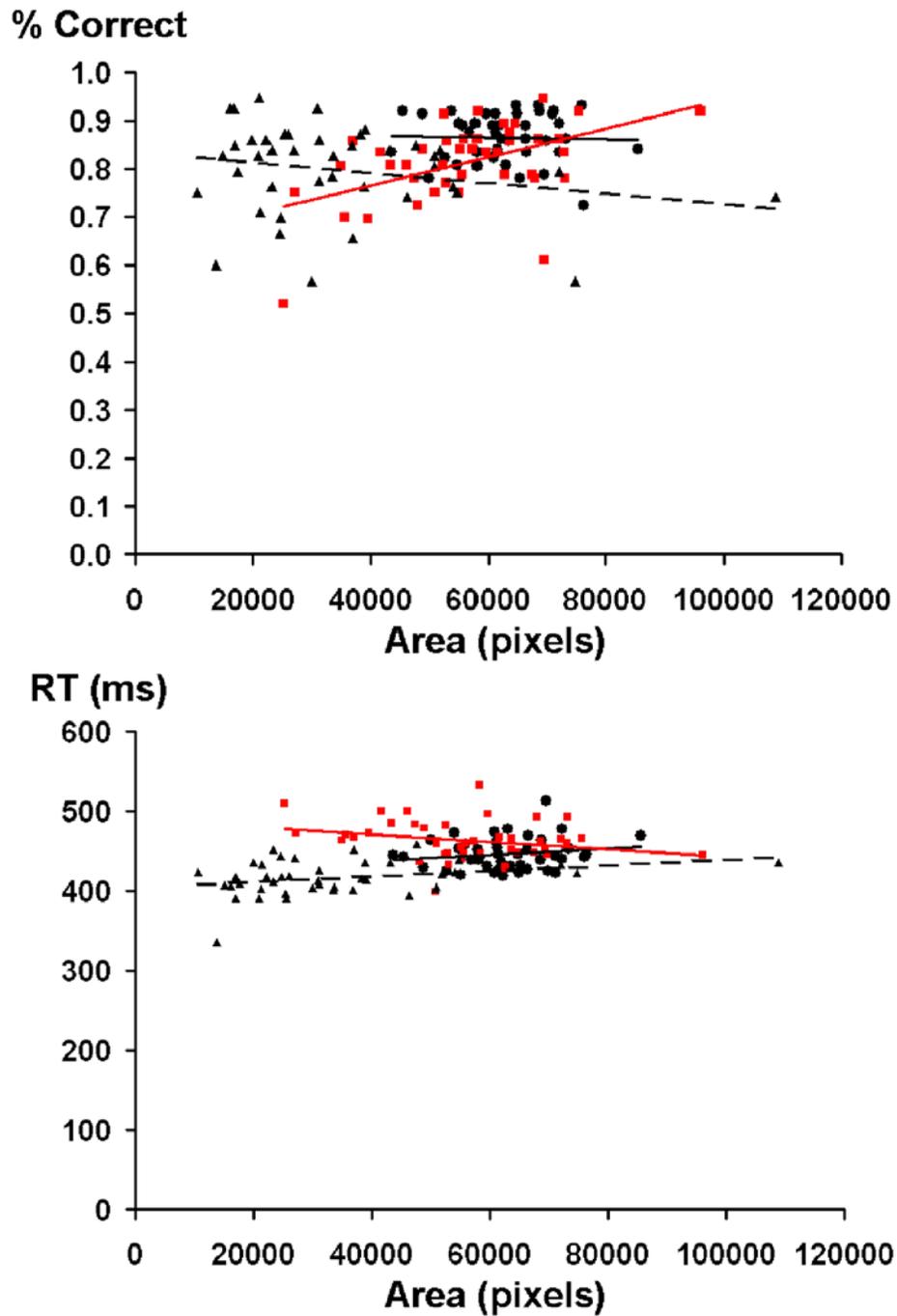


Figure 19. Experiment 1, Task 1 accuracy rates (top) and RTs (bottom) as a function of total stimulus area. Lines indicate least-squares fit to data. FAM = black triangles, dashed black line; CON = light red squares, light red solid line; EXP = black circles, black solid line.

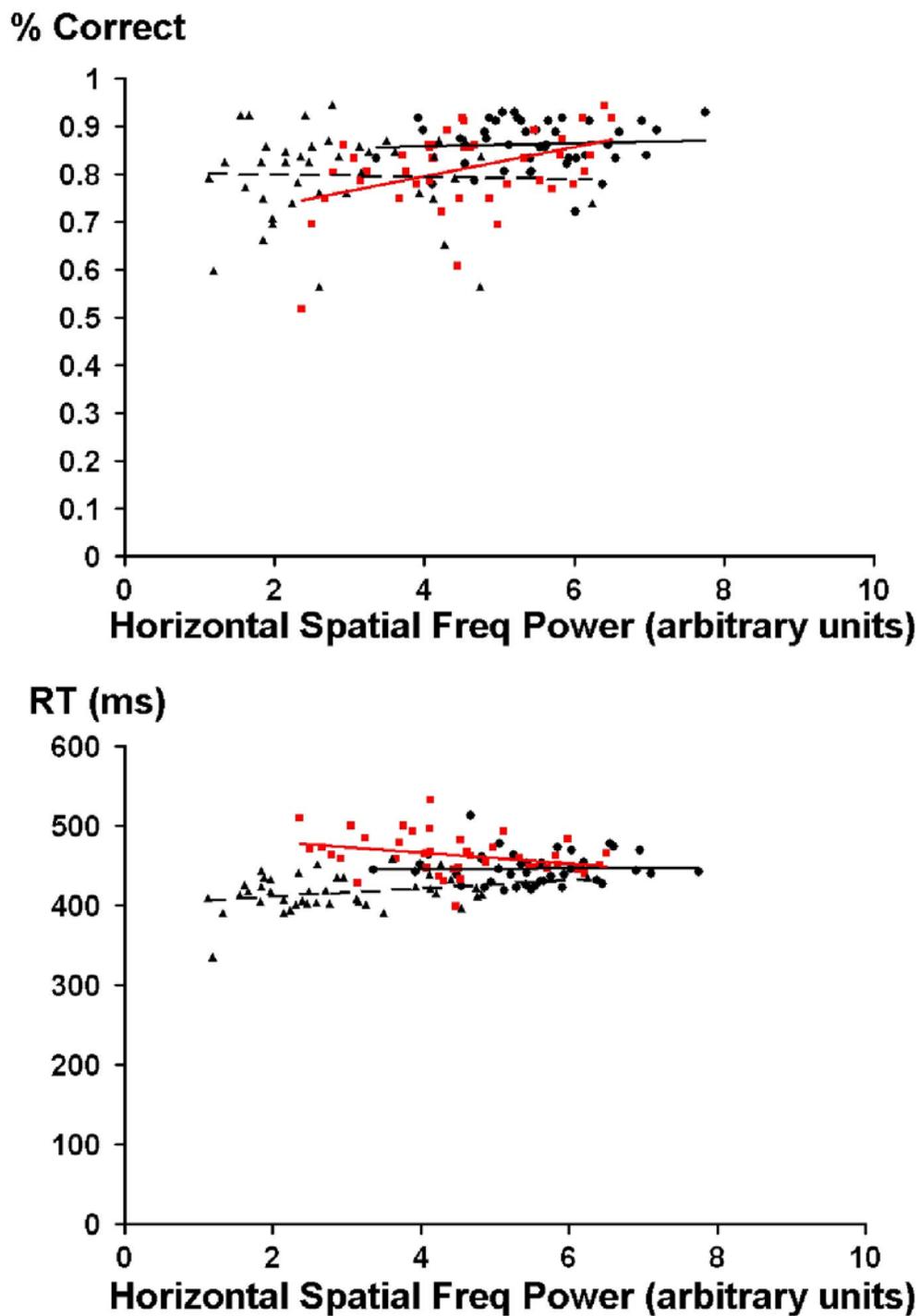


Figure 20. Experiment 1, Task 1 accuracy rates (top) and RTs (bottom) as a function of horizontal spatial frequency power. Lines indicate least-squares fit to data. FAM = black triangles, dashed black line; CON = light red squares, light red solid line; EXP = black circles, black solid line.

EXP and CON stimuli in a complete manner was difficult because large changes in some stimulus properties (e.g. contour length, width) would distort some of the FAM stimuli in a manner that rendered them as unrecognizable. Nonetheless, FAM stimuli were closely equated as possible to the NOVEL stimuli so that categorization decisions were based on recognition rather than difference in stimulus properties.⁷

The stimulus equating procedure involved changing the key properties of the stimuli (via Adobe Photoshop) and then computing t-tests between conditions. This process was repeated on a trial and error basis until a matched set of EXP and CON, and to a lesser extent, FAM stimuli were created. In order to facilitate the matching process, one stimulus was removed from each EXP and CON set, bringing each set to $N = 40$ stimuli; two stimuli were removed from the FAM set ($N = 40$) (see Appendix A for a listing of objects portrayed by the FAM stimuli and the unbounded regions of the EXP silhouettes in Experiment 3). FAM, EXP, and CON stimuli were analyzed in terms of luminance, contour length, spatial frequency, and vertical width. In addition, the configural cue of convex area was assessed for EXP and CON stimuli by computing the amount of convex intrusions from the center (bounded) silhouette regions into the outside (unbounded) regions, and vice-versa. Convex areas were identified by eye in Adobe Photoshop as intrusions of an edge into the inner or outer region of the silhouette; these intrusions were delineated by hand according to points of minimum and maximum curvature along the bounding contour. These area maps were then saved as bitmaps and

⁷ Such rough equation of FAM and NOVEL stimuli in terms of stimulus properties should not be an issue with respect to the present investigation since brain responses to the former were not of interest in this study.

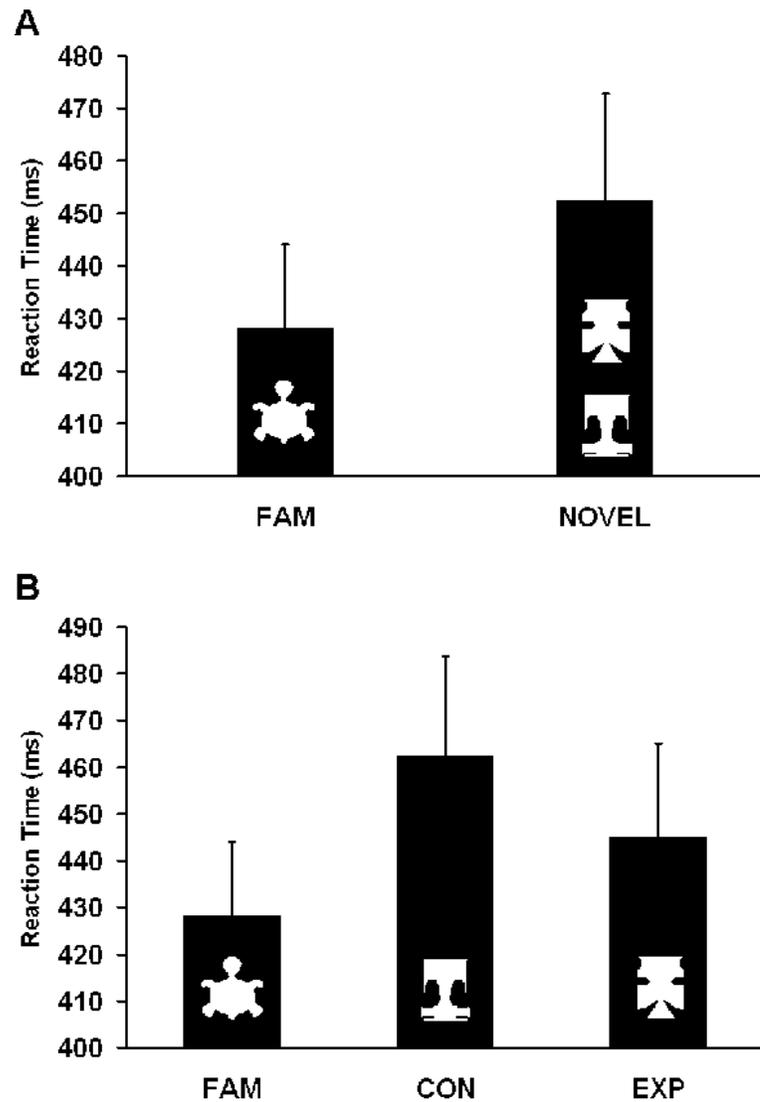


Figure 21. A) Reaction times (in ms) to categorize FAM stimuli as “familiar” and NOVEL (EXP & CON) stimuli as “novel” in Task 1, Experiment 1 after removing extreme stimuli (see text). B) RTs after separating responses to EXP and CON stimuli.

Response	<i>“Familiar”</i>	<i>“Novel”</i>		
	FAM	CON	EXP	EXP & CON
% Correct	82% ± 3%	84% ± 3%	89% ± 2%	87% ± 2%

Table 8. Accuracy rates for Experiment 1, Task 1 after trimming extreme CON stimuli.

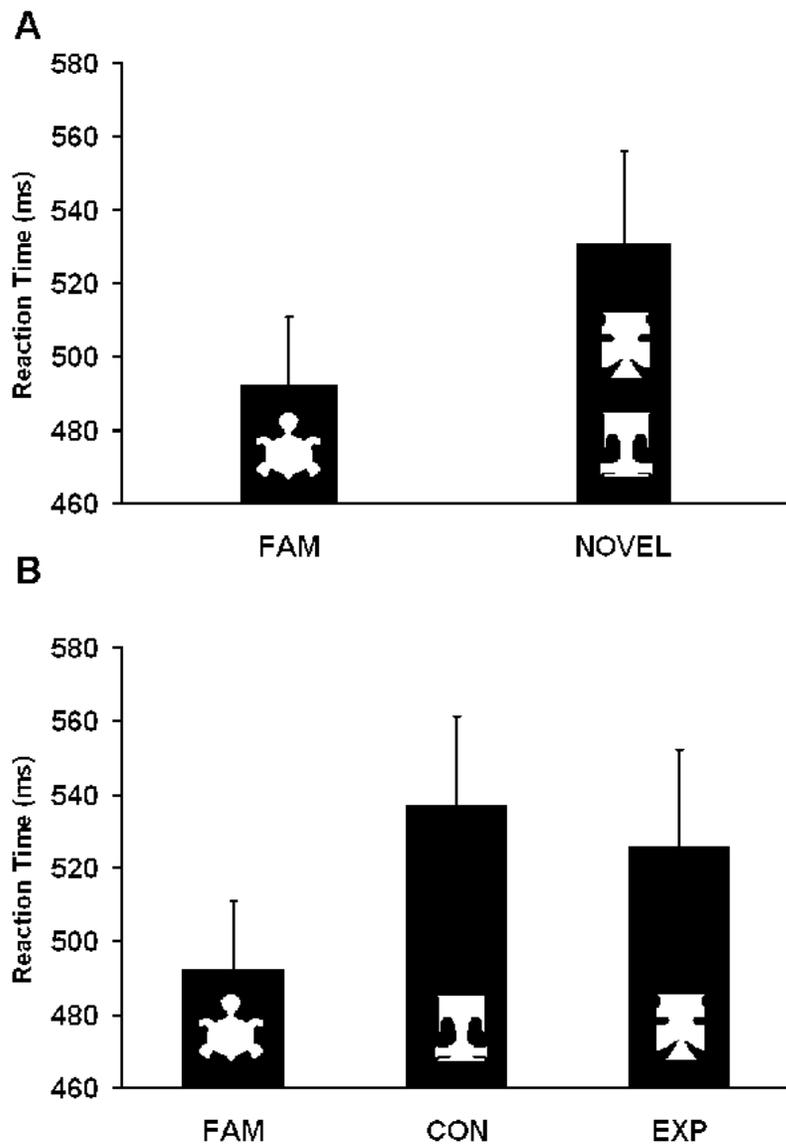


Figure 22. A) Reaction times (in ms) to categorize FAM stimuli as “familiar” and NOVEL (EXP & CON) stimuli as “novel” during Task 1, Experiment 2 after removing extreme stimuli (see text). B) RTs after separating responses to EXP and CON stimuli.

Response	“Familiar”		“Novel”	
	FAM	CON	EXP	EXP & CON
% Correct	89% ± 3%	95% ± 1%	97% ± 1%	96% ± 1%

Table 9. Accuracy rates for Experiment 2, Task 1 after trimming extreme CON stimuli.

then analyzed via MATLAB scripts specially written for this purpose (using the *bwarea* function).

Table 10 shows the computed stimulus property values for each stimulus type. Table 11 shows the results of the between-condition t-tests performed on the computed values. It is clear from the tables that EXP and CON stimuli no longer differ from one another in terms of image properties or the configural property of convex area. Although EXP and CON stimuli did differ from FAM stimuli in terms of horizontal spatial frequencies, the three stimulus types were equated along all other stimulus properties. Furthermore, for EXP and CON stimuli the outside (unbounded) regions of each stimulus type contained more convex area intruding into the central white regions than vice-versa (EXP: Outer, 11535.37 ± 877.52 pixels vs. Inner, 9436.35 ± 1012.06 pixels, $t(39) = -1.74$, $p < 0.05$, one-tailed; CON: Outer, 11200.00 ± 868.24 pixels vs. Inner, 9036.75 ± 811.36 pixels, $t(39) = -1.96$, $p < 0.05$, two-tailed). This validates the claim made in Section 1.3 that the configural cue of convexity is operating along the outside regions of the silhouettes. However, EXP and CON stimuli did not differ in terms of the relative differences in convex area between central and outside regions of the silhouettes ($t(39) = 0.04$; see Table 11, bottom row). Thus the EXP and CON stimuli had equivalent cross-edge competition from the cue of convexity favoring the outside. The EXP and CON stimuli were matched for all configural cues considered in this paper (area, convexity, symmetry, enclosure) except the cue of past experience (operative on the outside of the edge for EXP stimuli only).

Finally, it should be noted that the improved EXP and CON stimuli were broken up into two sub-sets A and B, as in Experiments 1 and 2 (see Appendix A). Each sub-set was also matched across EXP and CON conditions in terms of each stimulus property of interest (all p s > 0.1).

	FAM	CON	EXP
Total Area	45113.92 ± 2116.45	48304.59 ± 2016.42	47642.75 ± 2095.31
Contour Length	1784.04 ± 101.72	1762.68 ± 60.14	1726.70 ± 54.92
Horizontal Span	304.65 ± 13.08	291.78 ± 8.24	280.15 ± 8.84
Spatial Frequency			
<i>Horizontal</i>	3.64 ± 1.07	4.84 ± 1.34	4.71 ± 1.31
<i>Vertical</i>	3.56 ± 1.02	3.45 ± 0.56	3.34 ± 0.61
Convex Area			
<i>Inner</i>	N/C	9036.75 ± 811.36	9436.35 ± 1012.06
<i>Outer</i>	N/C	11200.00 ± 868.24	11535.37 ± 877.52
<i>Inner - Outer</i>	N/C	-2163.24 ± 1102.62	-2099.02 ± 1203.00

Table 10. Computed stimulus property values of luminance/total area (pixels), contour length (pixels), horizontal span (pixels), spatial frequency (arbitrary units), and convex area (pixels). N/C indicates properties that were not computed for FAM stimuli.

	EXP vs CON	EXP vs FAM	CON vs FAM
Total Area	-0.23	0.85	1.09
Contour Length	-0.44	-0.50	-0.18
Horizontal Span	-0.96	-1.55	-0.83
Spatial Frequency			
<i>Horizontal</i>	-0.42	4.41*	4.01*
<i>Vertical</i>	-0.82	-0.63	-1.18
Convex Area			
<i>Inner - Outer</i>	0.04	N/C	N/C

Table 11. Between-condition t-tests between computed stimulus property values. The * symbol indicates tests significant at the $p < 0.05$ (two-tailed) or greater significance level ($df = 39$). N/C indicates statistical tests not calculated because the relevant FAM properties were not computed.

5. EXPERIMENT 3 - OVERVIEW

The purpose of Experiment 3 was to use the improved figure-ground stimuli to replicate the behavior and electrophysiological findings of Experiments 1 and 2. If the previous findings are replicated using these stimuli, then the differences in cognitive processing of the stimuli are most likely due to the past experience cues present in the EXP stimuli and not the CON stimuli. If instead the findings of Experiments 1 and 2 are not replicated in Experiment 3, then the differences observed in the previous experiments likely arose from differences in low-level image properties. This experiment differed from the previous experiments, however, in that masks were not utilized in Task 2. This was done in order to make the high-denotative regions of the EXP stimuli easier to see and thus facilitate categorization performance in Task 2.

5.1 Experiment 3 - Methods

5.1.1 Participants

Thirty undergraduate participants (19 female, 11 male; 2 left-handed, 28 right-handed; mean age = 18.8 ± 0.26 years) were recruited from the University of Arizona's undergraduate subject pool. Three participants were removed from further analysis due to technical difficulties with their EEG recordings. Of the remaining 27 participants, there were 11 Seers (5 females, 6 males; 1 left-handed, 10 right-handed; mean age = 18.64 ± 0.24) and 16 Non-Seers (12 females, 4 males; all right-handed; mean age = 18.88 ± 0.43). Only the Non-Seers' data were analyzed; the Seers' data were not analyzed further. All participants were screened to ensure normal visual acuity, and were fully

informed of the experimental methods and proceedings before their consent to participate was obtained. The new experimental protocol was reviewed and approved by the Institutional Review Board for Human Studies at the University of Arizona.

5.1.2 Stimuli and Procedure

The stimuli used were the improved set previously described in Section 4.3. Visual angles were the same as in Experiment 1; viewing distance was 80 cm. The remaining design, task, and procedures of Experiment 3 Tasks 1 and 2 were identical to those of Experiment 2, save for the parameters specified here. Silhouette and mask exposure durations were 175 ms and 255 ms (masks were used in Task 1 only). Five different masks were used in Task 1, with each mask following each silhouette equally often; the same set of masks was used in all experimental conditions. Participants categorized silhouettes using two joystick buttons held one in each hand and had 2300 ms to make a response before the stimulus presentation program advanced to the next trial. Inter-trial intervals varied from 1452 ms to 4158 ms.

Post-experiment questioning was the same as in Experiments 1 and 2 (see Appendix D for a sample of the Experiment 3, Task 1 and Task 2 post-experiment questions), however the stimulus recognition task (see Appendix D) revealed that during Task 1 the 16 Non-Seers retained in this experiment did not reliably remember seeing familiar shapes depicted by the unbounded regions of the EXP silhouettes ($P(A) = 0.52 \pm 0.04$). During Task 2, participants remembered seeing many familiar shapes depicted in the unbounded regions of the EXP silhouettes ($P(A) = 0.79 \pm 0.01$). As in Experiments 1

and 2, the Experiment 3 P(A) measure for Task 2 was greater than in Task 1 ($(P(A))_{\text{Task 2}} - P(A)_{\text{Task 1}} = 0.28 \pm 0.04$; paired $t(23) = 7.33$, $p < 0.001$), again supporting the claim that participants actually saw familiar shapes in the unbounded regions of the EXP stimuli during Task 2, but did not see such shapes during Task 1.

5.1.3 Behavioral Data Analysis

The same behavioral measures (RT/% correct) and analyses used in Experiments 1 and 2 were used in Experiment 3.

5.1.4 EEG Recordings and Data Analysis

The recording and analysis methods and parameters were the same as in Experiment 2.

5.2 Experiment 3 - Results

5.2.1 Behavior

In Task 1, participants were faster at categorizing FAM stimuli as familiar than NOVEL stimuli (EXP and CON) as novel (FAM – NOVEL difference = -28.30 ms, $p < 0.01$, two-tailed; see Figure 23A), and more accurate at categorizing NOVEL stimuli as novel than FAM stimuli as familiar ($p < 0.01$, two-tailed; see Table 12). Comparison between EXP and CON trials shows that participants were faster to categorize EXP stimuli as novel than CON stimuli as novel (EXP – CON difference = -7.85 ms, $p < 0.05$,

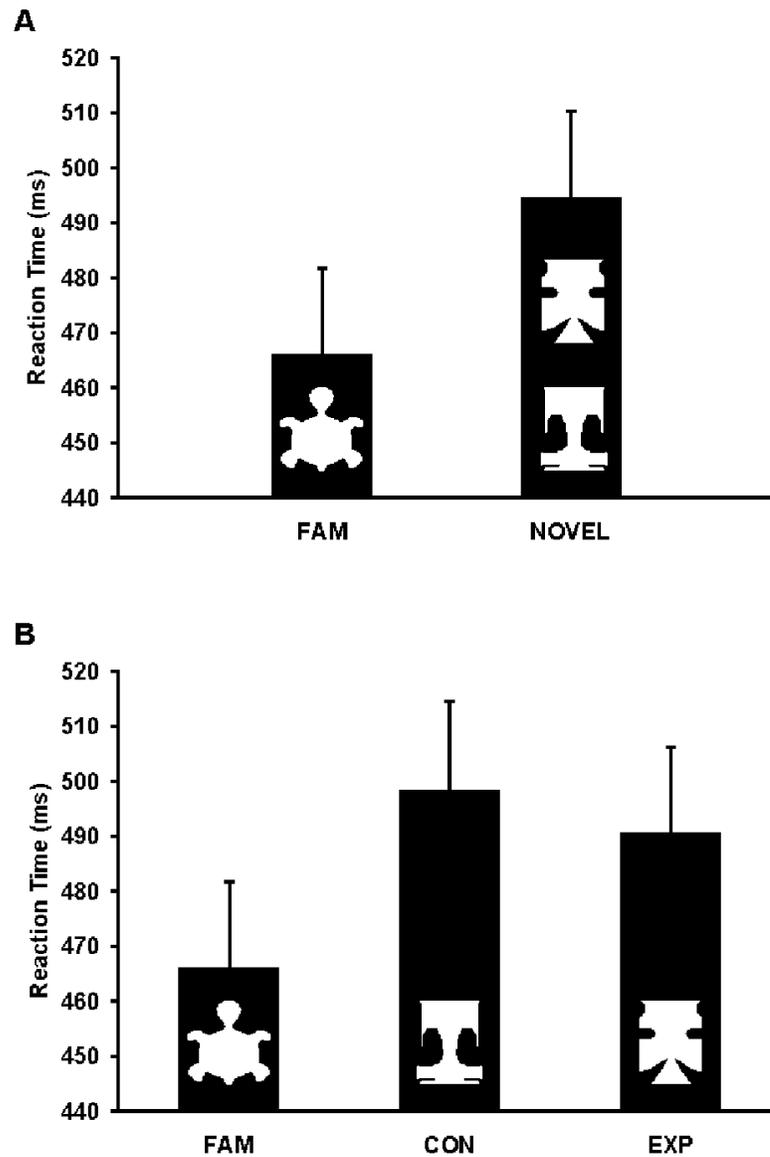


Figure 23. A) Reaction times (in ms) to categorize FAM stimuli as “familiar” and NOVEL (EXP & CON) stimuli as “novel” during Task 1, Experiment 3. B) RTs after separating responses to EXP and CON stimuli.

Response	“Familiar”		“Novel”	
	FAM	CON	EXP	EXP & CON
% Correct	90% ± 1%	95% ± 1%	97% ± 1%	96% ± 1%

Table 12. Accuracy rates for Experiment 3, Task 1.

Response	<i>“Familiar”</i>	<i>“Novel”</i>
	EXP	CON
% Correct	73 ± 3 %	86 ± 3 %

Table 13. Accuracy rates for Experiment 3, Task 2.

two-tailed; see Figure 23B). Furthermore, participants categorized EXP trials more accurately than CON trials ($p < 0.05$, two-tailed; see Table 12). During Task 2, participants more accurately categorized CON stimuli as depicting novel shapes in their outside unbounded regions than EXP stimuli as depicting familiar shapes in their outside unbounded regions ($p < 0.01$, two-tailed; see Table 13). Furthermore, participants' accuracy in these categorizations was above chance (EXP and CON: $p < 0.001$, two-tailed), although they were slightly biased to categorize the silhouettes as “novel” overall (“novel” = 56.5% of trials; “familiar” = 43.5% of trials). Reaction times to categorize the outsides of EXP stimuli were significantly faster than to categorize the outsides of CON stimuli (606 ± 25 ms vs. 659 ± 39 ms, respectively; $p < 0.05$, two-tailed).

5.2.2 ERP Analysis

Overall the ERPs evoked during Task 1 in response to improved EXP and CON stimuli were very similar to those evoked during Task 1 of Experiment 2. Figure 24 shows representative ERP responses to EXP and CON stimuli when the inner (unbounded) regions were categorized as novel during Task 1 of Experiment 3; Table 14 and Figure 25 compares these responses. There was a small, but reliable P1 amplitude difference at right hemisphere sites PO4 and PO6 (Figure 25B, D), where the EXP P1 was greater than the CON P1 (PO4: $t(15) = 3.04$, $t_{\text{critical}} = 2.97$, $p < 0.05$, two-tailed; PO6:

$t(15) = 2.97$; $t_{\text{critical}} = 2.97$, $p < 0.06$, two-tailed). Other significant between-condition amplitude differences did not emerge until $\sim 200 - 225$ ms post-stimulus during the onset of the positive LP over posterior scalp sites (Figure 25C, D). LP amplitudes in response to EXP stimuli were significantly smaller than for CON stimuli from $\sim 265 - 340$ ms at PO5, PO6, O1, and OZ (all $ps < 0.05$, two-tailed except sites PO4 and O2, $p < 0.06$; maximum significance at site PO5: $t(15) = -3.46$; $t_{\text{critical}} = -3.04$, $ps < 0.05$, two-tailed). Thus, as in Experiment 2, the Task 1 LP responses reflected the differences in past experience cues between EXP and CON silhouettes, as processed unconsciously.⁸ No significant between-condition latency differences were observed for the positive LP or any other ERP component in either hemisphere, although the latencies of all three ERP components were slightly shorter in Experiment 3 than in Experiment 2 (see Table 14).

Figure 26 shows representative ERP responses to EXP and CON stimuli when the outer (unbounded) regions were seen as figure and categorized as familiar or novel (respectively) during Task 2 of Experiment 3; Figure 27 along with Table 14 compares these responses. No P1 differences were observed ($ps > 0.1$), and the overall magnitude of the P1 response evoked in response to Task 2 (after collapsing across EXP and CON trials) was near equivalent to the P1 response during Task 1 ($ps > 0.1$). N170 amplitudes, however, were greater to EXP stimuli when the outsides were accurately categorized as familiar than to CON stimuli when the outsides accurately categorized as novel from ~ 140

⁸ An early pilot experiment was run using the improved stimuli and differed from Experiment 3 in that masks were used in Task 2. That experiment tested 6 Non-Seers, and inclusion of their Task 1 data in the present analysis (total $N = 22$) topographically spreads the significance of the LPP effect to include significant differences at additional sites PO3, PO4, PO7, P5 and O2 ($ps < 0.05$, two-tailed). This increase in the LPP effect came with a restriction of the P1 effect to site PO4 only ($p < 0.05$); N1 findings were unaffected.

	P1				N170				LP			
	Amplitude		Latency		Amplitude		Latency		Amplitude		Latency	
Task 1	PO5	PO6	PO5	PO6	PO5	PO6	PO5	PO6	PO5	PO6	PO5	PO6
FAM	6.78	8.46	104	102	-1.66	-0.79	146	150	13.18	15.72	313	275
CON	6.96	7.88	102	97	-2.39	-2.60	144	147	13.48	16.25	309	273
EXP	7.10	8.64	103	101	-1.97	-2.02	144	147	12.49	15.61	311	270
Task 2												
CON	7.12	8.56	102	97	-5.10	-7.44	150	154	0.14	-1.91	305	313
EXP	6.87	8.19	103	98	-5.51	-8.92	155	155	1.72	-0.71	289	295

Table 14. Representative ERP component peak amplitudes (μV) and associated latencies (ms) for P100, N170, and a late potential that was positive during Task 1 and predominantly negative during Task 2.

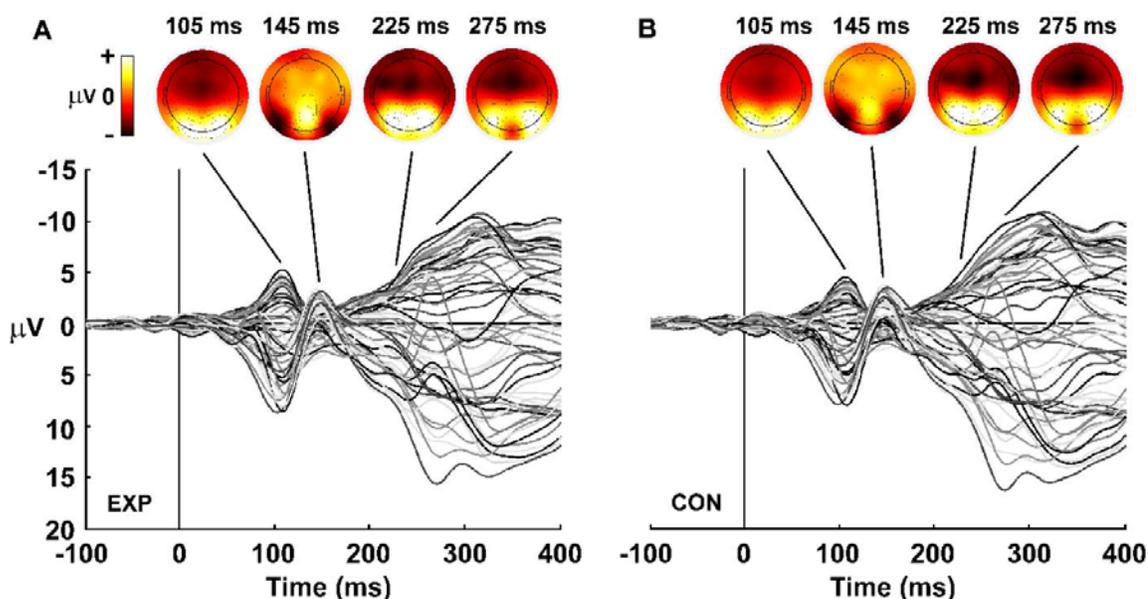


Figure 24. Grand-average ERP waveforms at all scalp sites to EXP (A) and CON (B) stimuli categorized as novel during Task 1 of Experiment 3. Head maps show ERP scalp topography at the indicated latencies. Scaling of head maps is separately set to the maximum/minimum of each response to better display the fine details of each component's scalp topography. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

to 180 ms at sites P4, P6, PO6, and PO8 (maximum significance at PO6: $t(15) = -3.85$; $t_{\text{critical}} = -2.91$, $ps < 0.05$, two-tailed). Thus, as for Task 2 of Experiment 2, Experiment 3 Task 2 N170 amplitudes differentiated successful vs. unsuccessful conscious shape recognition of the outside regions of EXP and CON silhouettes. In addition, overall N170 amplitudes (after collapsing across EXP and CON trials) were significantly larger during Task 2 than Task 1 at sites P4, P6, P8, PO8, and PO10 (see Figure 23; all $ps < 0.05$, two-tailed; max significance at PO10: $t(15) = -3.93$; $t_{\text{critical}} = -2.92$, $p < 0.05$, two-tailed), similar to the overall N170 amplitude increase observed in Experiment 2.

In contrast to Experiment 2, Late Potential amplitudes differed between Tasks 1 and 2 of Experiment 3. During Task 2, the LP response was predominantly negative for right hemisphere sites and only slightly positive over posterior left hemisphere sites (Figure 26). This morphological change is most pronounced in Figure 28 which shows representative ERPs to EXP and CON stimuli evoked during Task 2 (red lines), when the outer regions were seen as figure and categorized as familiar or novel (respectively), to ERP responses evoked during Task 1 (black lines), when the inner regions were categorized as novel. Indeed, the LP was larger and more positive during Task 1 than during Task 2 (after collapsing across EXP and CON conditions) at all indexed sites except site P1 (max significance at PO6: $t(15) = 12.27$; $t_{\text{critical}} = 2.56$, $p < 0.001$, two-tailed).

Furthermore, comparing across Task 2 of Experiments 2 and 3 (after collapsing across EXP and CON conditions) over the interval of overlap (~ 250 – 275 ms) confirms

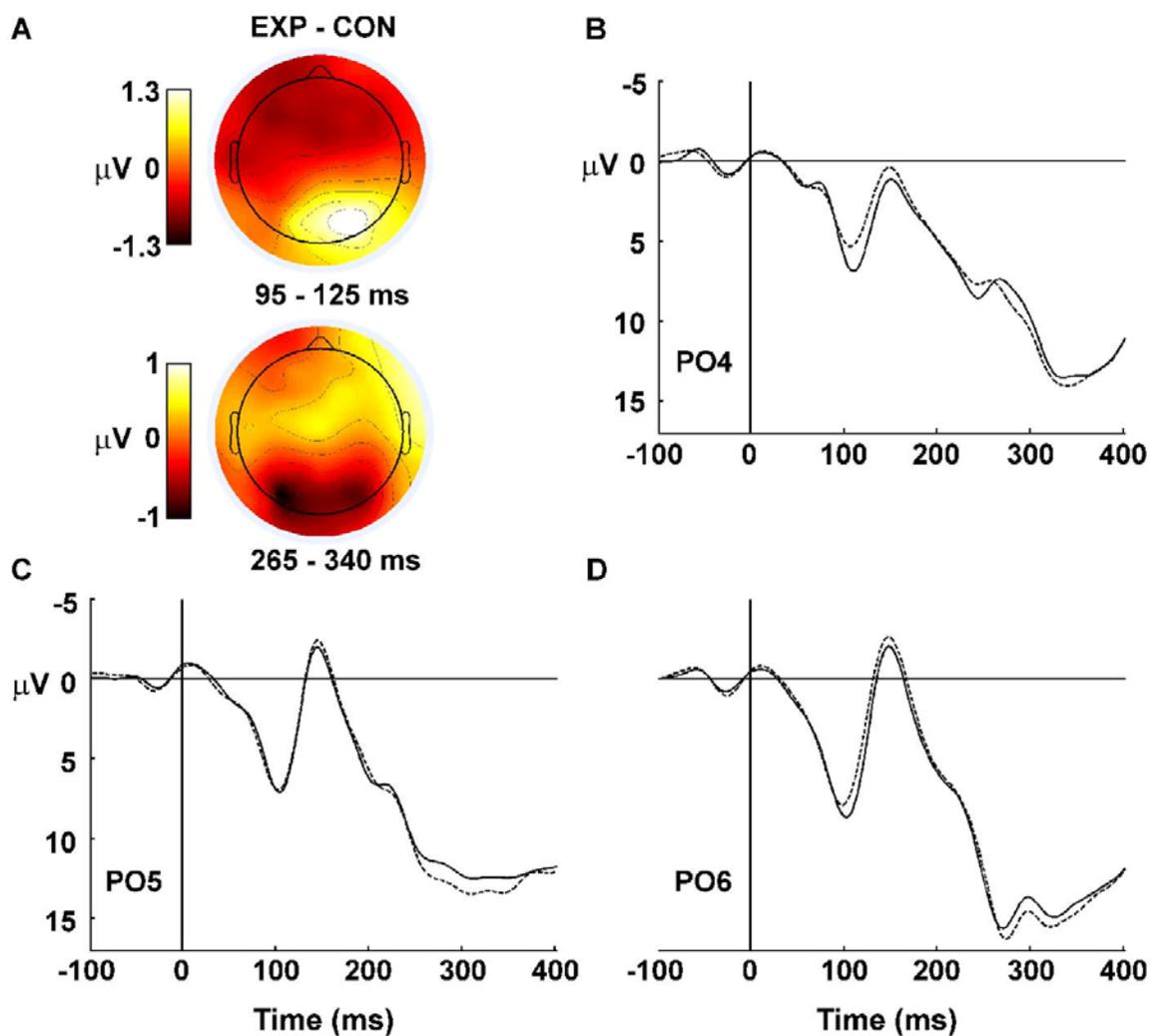


Figure 25. Comparison of Experiment 3, Task 1 ERP responses to EXP (solid black line) and CON (dashed black line) stimuli when the inner (bounded) regions were categorized as novel. A) Scalp topography of EXP – CON difference waveform averaged over the indicated interval. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline. B) ERP waveforms at site PO4. C) ERP waveforms at site PO5. D) ERP waveforms at site PO6.

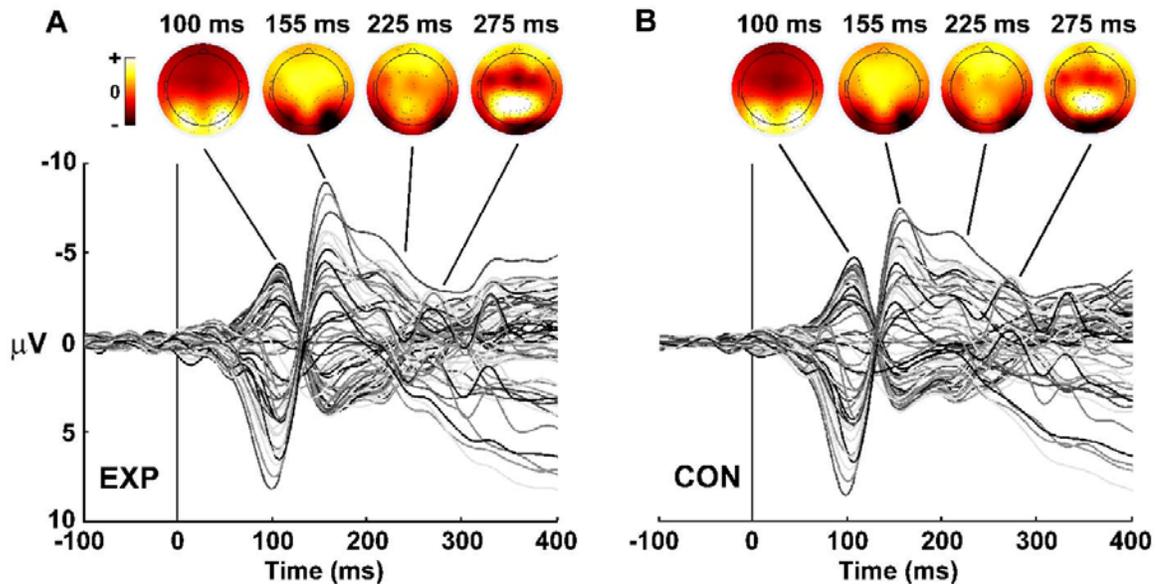


Figure 26. Grand-average ERP waveforms at all scalp sites to EXP (A) and CON (B) stimuli when the outer (black) regions were categorized as familiar and novel, respectively (Task 2). Head maps show ERP scalp topography at the indicated latencies. Scaling of head maps is separately set to the maximum and/or minimum of each response to better display the fine details of each component's scalp topography. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

that the Late Potential in Experiment 2 is larger and more positive than that in Experiment 3 at all indexed scalp sites except P1, P2, P3, and P9 (all p s < 0.05, two-tailed; maximum significance at site O1: two-sample permutation $t(38) = 5.32$; $t_{\text{critical}} = 2.22$, $p < 0.001$, two-tailed). Nonetheless, the LP still differed between conditions, as CON responses were more negative than EXP responses over the 225 – 275 ms interval at sites P3, P5, PO5, and PO7 (see Figures 27 and 28; all p s < 0.05, two-tailed except site PO7, $p < 0.1$; maximum significance at PO5: $t(15) = -3.06$; $t_{\text{critical}} = -2.83$, $p < 0.05$, two-tailed).

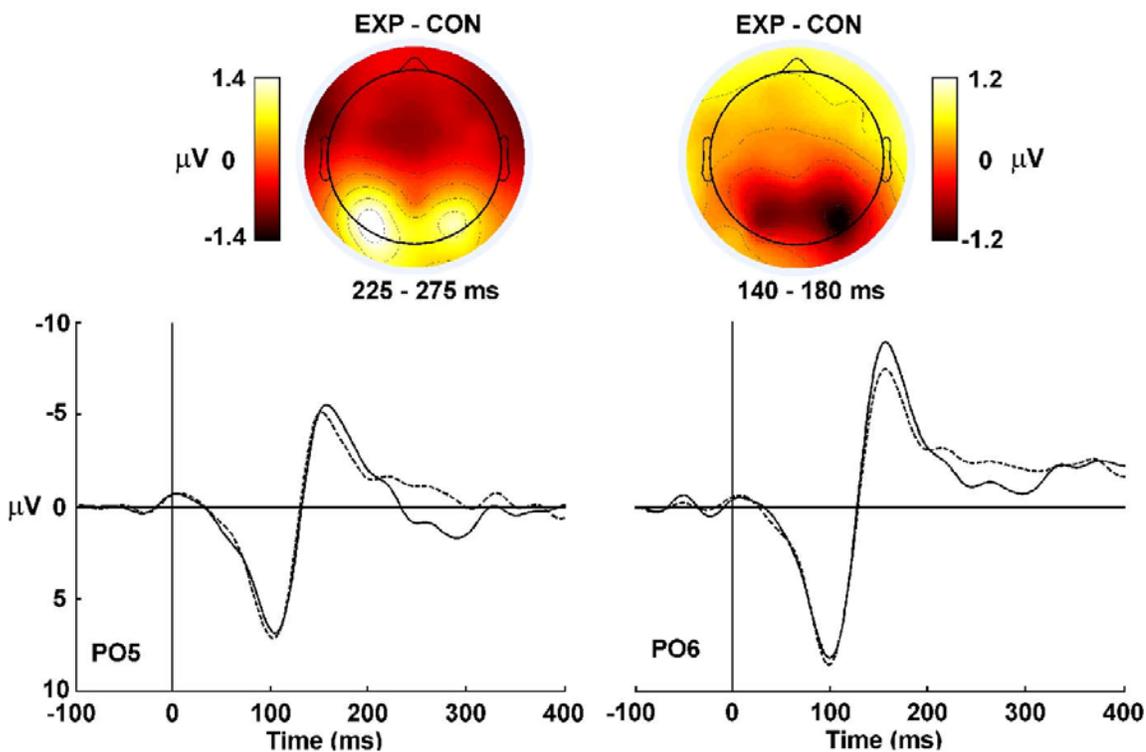


Figure 27. Comparison of representative Experiment 3, Task 2 ERP responses to EXP (solid black line) and CON (dashed black line) stimuli when the outer (black) regions were categorized as familiar and novel, respectively. ERP waveforms are shown at sites PO5 (left) and PO6 (right). Inset: Scalp topography of EXP – CON difference waveform averaged over the indicated interval. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

Finally, as during Task 1, no major latency differences were found for Task 2 ERP responses ($p > 0.1$, two-tailed). There were significant N170 latency delays ($\sim 3 - 7$ ms), however, for Task 2 vs. Task 1 responses at sites P5, P6, P7, P8, P9, PO3, PO5, PO6, PO7, PO8, PO9, PO10, O1, O2, O9, O10 (all $p > 0.05$, two-tailed; maximum delay of 7 ms at PO7, $t(16) = 4.79$, $t_{\text{critical}} = 2.92$, $p < 0.001$, two-tailed), again similar to what was observed in Experiment 2.

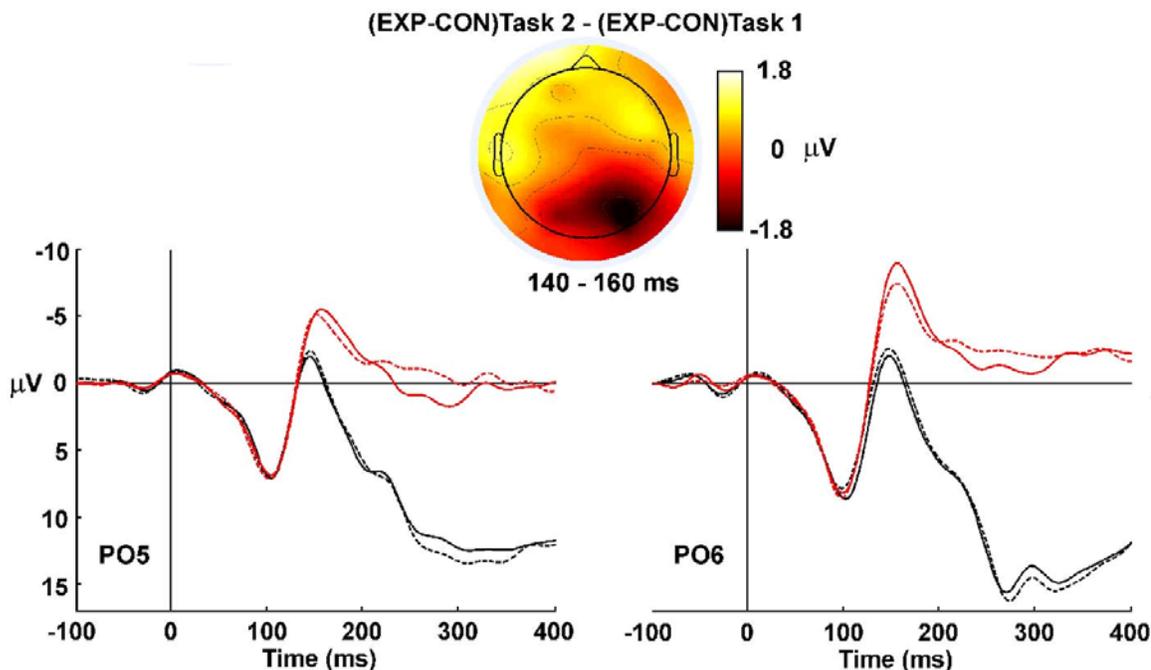


Figure 28. Comparison of Experiment 3 ERP responses to EXP and CON stimuli when the inner (bounded) regions were categorized as novel (Task1: EXP, black solid line; CON, dashed black line), and when the outer (unbounded) regions were categorized as familiar (Task 2: EXP, light red solid line) and novel (CON, light red dashed line). ERP waveforms are shown at site PO5 (left) and PO6 (right). Inset: Scalp topography of $(\text{EXP} - \text{CON})_{\text{Task 2}} - (\text{EXP} - \text{CON})_{\text{Task 1}}$ difference waveform averaged over the indicated interval. Light colors indicate positive increases and dark colors indicate negative increases with respect to the pre-stimulus baseline.

5.3 Experiment 3 - Discussion

The results of Experiment 3, Task 1 provide further behavioral and electrophysiological evidence that EXP and CON stimuli were processed differently during this shape categorization task. As in Experiments 1 and 2, RTs to EXP stimuli categorized as novel were faster than to similarly categorized CON stimuli during Task 1, when participants were unconscious of the familiar shapes along the outside of EXP silhouettes. This behavioral difference was accompanied by a decreased positive LP for

EXP vs. CON stimuli over posterior scalp sites, replicating the Task 1 LPP findings of Experiment 2. In contrast to the latter, the P1 ERP component was larger for EXP vs. CON stimuli during Task 1. This suggests that processing differences between the two types of stimuli may emerge as early as 100 ms.

Importantly, these behavioral and electrophysiological results were obtained using well-matched stimuli that eliminate confounds arising from mismatched low-level stimulus properties and configural cues (see Section 4.3).⁹ Furthermore, the results were obtained in the absence of conscious awareness of the cues to past experience present in the EXP stimuli. This indicates that the processing of EXP stimuli during Task 1 shape categorization was accompanied by unconscious access to pre-existing shape representations that did not occur, or occurred to a much lesser degree, to CON stimuli. Thus past experience influenced the perception of these stimuli as figural shapes.

The larger overall N170 amplitudes for EXP and CON responses during Task 2 relative to Task 1 suggest that the N170 component differentiated the top-down reversal of figure against the bottom-up bias of the configural cues. Participants were required during Task 2 to reverse the figure along the silhouette edges in order to see the outsides of the silhouettes as familiar (EXP) or novel (CON) shapes. This figure reversal required the overcoming of the bias in cue constellation which otherwise would bias the center bounded regions to be seen as figure. The fact that participants were able to successfully categorize the outsides of the silhouettes indicates that they overcame this bias to see

⁹ The unchanging behavior of the LPP across Task 1 of Experiments 2 and 3 suggests that this component is relatively unaffected by differences among the stimulus properties analyzed in this study. Nonetheless, the P1 differences observed across Experiments 1 and 2 vs. Experiment 3 are consistent with a sensitivity to such stimulus differences so that between-condition effects are artificially induced or true effects hidden (as may have been the present case).

these regions as figure. The N170 component appeared to be the only ERP component that reflected this figure reversal, in that it was the only component that was larger during Task 2 relative to Task 1 for both EXP and CON stimuli. N170 amplitudes also discriminated between the successful and unsuccessful conscious access to shape memories, as evidenced by the greater responses to EXP versus CON stimuli in Task 2 of Experiment 3.

Experiment 3 Task 2 Late Potential amplitudes in response to EXP and CON stimuli were predominantly negative and reduced in amplitude relative to the Task 2 LPP responses observed in Experiment 2. Furthermore, the late potential still differentiated EXP and CON stimuli in Task 2, but now CON LP responses were more negative than EXP responses, whereas before CON LP responses were more positive than EXP responses. These differences in late potential amplitude and morphology across experiments are likely due to absence of pattern-masking of the silhouettes in Task 2 of Experiment 3 because a positive LP is present with masking (Tasks 1 and 2 of Experiment 2, Task 1 of Experiment 3). It is unlikely that this difference reflects the stimulus property differences of the EXP and CON stimuli used in Experiment 2 because later potentials are less affected by such changes in stimulus properties. Task 1 LP magnitudes were slightly larger in Experiment 3 than Experiment 2 ($\sim |0.29| \mu\text{V}$ averaged across sites PO5 and PO6; see Tables 5 and 14), suggesting that LP responses are not entirely insensitive to stimulus differences (although such a difference could be also be due to individual-participant factors such as small differences in skull thickness or electrode placement). This disparity, however, is not large enough to account for the

large positive LP present in Experiment 2 Task 2 that was not present in Task 2 of Experiment 3. It is more likely that the positive LP is related to the early processing of the masks, as in both Experiments 2 and 3 the appearance of the positive Late Potential appears ~ 100 ms after the onset of the masks and offset of the silhouettes.

Nonetheless, the between-condition Late Potential differences observed in these experiments indicate that these mask-related potentials are differentially affected by the processing of the EXP and CON stimuli. These differences are not explainable in terms of differences among the masks because the same set of masks was used in each condition. What is not immediately clear is why the amplitude differences switch in polarity with the presence or absence of masking, and how these differences are related, if at all, to the differential mutual inhibition of the preceding silhouettes. Understanding this result will require further consideration of the neural processes underlying the perception of the silhouettes and their relationship to the PIMOCA framework of figure-ground segregation. This will be discussed in the General Discussion (Section 6).

6. GENERAL DISCUSSION

6.1 More Evidence for the Influence of Past Experience on Figure-Ground Segregation

Taken together, the three experiments reported in this dissertation provide further evidence for an influence of past experience on figure assignment. Task 1 of Experiment 3 provide the first electrophysiological evidence for the processing of past experience cues by demonstrating ERP differences when object memory representations were accessed on the groundside of an edge during processing (EXP stimuli) as compared to when they were not (CON stimuli). Note that there was no conscious perception of the shapes along the unbounded regions of the EXP stimuli under these circumstances; both EXP and CON stimuli were quickly and accurately classified as novel. The P1 ERP response was greater for EXP versus CON stimuli (Task 1, Experiment 3) demonstrating that the consequences of object memory access can manifest as early as 100 ms. Importantly, the fact that this finding was observed after controlling for low-level image properties across conditions confirms that these results are not due to stimulus artifacts.

The LPP ERP response was larger for CON than EXP stimuli (Task 1, Experiments 2 and 3) indicating that such differential access to object memories also affects later brain responses (~300 ms). The fact that this finding manifested regardless of whether low-level image properties were equated across conditions (Experiment 3) or not (Experiment 2) indicates that such a late stage of processing is relatively insensitive to differences among such image properties (although perhaps not entirely insensitive; see Section 5.3 above).

Finally, these ERP differences were accompanied by faster reaction times to categorize EXP than CON stimuli as novel relative to an additional group of silhouettes (FAM) categorized as familiar shaped objects (Task 1, Experiments 1 – 3). This task may be considered to be a direct behavioral index of the processes leading to the perception of the silhouettes as shaped figures. Thus the present behavioral results add to the large amount of behavioral evidence (e.g. Peterson et al., 1991; Peterson and Gibson, 1994; Peterson and Kim 2001, Peterson and Enns, 2005; Peterson and Skow, submitted; see Section 1.3 and 1.4 for discussion) demonstrating access to object memories during figure-ground segregation.

6.2 ERP Correlates of the Unconscious versus Conscious Perception of Object Shape

Experiments 2 and 3 also demonstrated different patterns of P1, N170 and Late Potential ERP activity when participants perceived a familiar shape on the outside of the EXP silhouettes (Task 2) versus when they did not, i.e. when instead the outside was perceived as a shapeless ground (Task 1). These differences in perception map onto access to the object representations that did (Task 2) versus did not (Task 1) result in conscious perception of a familiar shape. First, EXP versus CON P1 differences present in Task 1 of Experiment 3 were eliminated in Task 2. Second, in Task 2, when the outer (unbounded) regions of the EXP silhouettes were seen as shaped figures, N170 ERP responses were greater when participants saw those regions as depicting familiar versus novel shapes (Experiments 2 and 3). These N170 differences took place in the context of generally enhanced N170 magnitudes for both EXP and CON stimuli during Task 2 as

compared to Task 1. This overall N170 enhancement most likely reflects top-down task-induced influences involved in reversing the figure against the bottom up bias in configural cues; such a reversal is necessary in order to see the outsides of the silhouettes as shaped figures.

Third, the Late Potential responses (LPP, LNP) observed in Experiments 2 and 3 also differed according to the conscious perception of the outer regions of the EXP stimuli as familiar shapes versus the conscious perception of these regions in CON stimuli as novel. The polarity of this difference, however, depended upon whether or not a mask was used in Task 2. When a mask was used (Task 2, Experiment 2) LPP responses were more positive when the outer regions of the CON stimuli were seen as novel than when the same regions of the EXP stimuli were seen as familiar. When a mask was absent (Task 2, Experiment 3), the late response was primarily negative (LNP), but was more negative for CON stimuli seen as novel than EXP stimuli seen as familiar. This indicates that the polarity of this difference is in some way related to the processing of the masks (to be discussed in more detail in Section 6.5 below).

A remaining question is whether the late ERP differences observed across Experiments 2 and 3 reflect activity of a neural correlate of consciousness (NCC) for conscious perception of object shape. Recall from Section 1.5.2 that according to the method of contrastive analysis (Baars, 1997), states of consciousness are directly contrasted with states of unconsciousness. Thus any differentially active brain responses to experimental and control stimuli of Task 2 relative to Task 1 should then correspond to activity reflective of a NCC. Given this criteria, it is unlikely that the P1 or Late

Potential responses reflect a neural correlate of consciousness; the former because no P1 differences were observed in Task 2, the latter because EXP versus CON Late Potential differences are present in both Tasks 1 and 2.

It is easier to make a case for the N170 ERP component as a NCC because a difference in N170 activity between EXP and CON stimuli only emerges in Task 2 when the known shapes sketched by the outer regions of the EXP silhouettes are consciously seen as familiar. Recall that the N170 response was significantly larger for EXP than CON stimuli during Task 2. Such a difference is not present in Task 1 when the past experience cues in the EXP stimuli processed are unconsciously. Thus according to the assumptions of the contrastive analysis method, it is reasonable to conclude that the differential Task 2 N170 response may reflect activity of a NCC for conscious perception of object shape. Note that this conclusion is not weakened by any ERP differences arising purely from the figure reversal required to perform Task 2. This is because what matters in the comparison between Task 1 and 2 is the EXP versus CON difference across the two tasks. Any top down effects (or lack thereof) of figure reversal should be subtracted out when computing the difference in response between the two stimulus types, for a given task.

Although the N170 response likely reflects activity of a NCC for conscious perception of familiar object shape, further research is needed to determine to what degree the N170 reflects activity of a NCC and what neural systems contributing to the N170 qualify as a NCC. The definition of a NCC given in Section 1.5.2 requires a neural system the states of which must be sufficient for the corresponding states of

consciousness, with no subset of the system by itself sufficient for consciousness. It cannot be determined from the present data if the N170 response reflects such a minimally sufficient neural system or if it reflects the combination of NCC activity with neural activity representing other cognitive processes. Indeed the present data suggests that the latter possibility may be the case because the N170 response also signaled successful figure-ground reversal; overall N170 responses (collapsed across EXP and CON conditions) were larger when participants were required to reverse the figure against a biased cue configuration to see the outer silhouette regions as figure (Task 2) than when they were not so required (Task 1). Future research might be able to disentangle these two types of neural activity by use of EEG source analysis methods.

Another qualification on the status of the N170 component as reflecting activity of a NCC for the perception of familiar shape (within the context of the present task) is the fact that consciousness research has not yet established what kind of neural activity instantiates a NCC. Various leading proposals for the NCC have included increases in high-level neural activity (Crick and Koch, 1995; 1998; 2000), neural synchrony (Singer, 2000), global differentiation and integration of reentrant neural activity (Edelman and Tononi, 2000a,b), and 2nd-order interactions among 1st-order object and self representations (Damasio, 1999; 2000). On the face of it, the findings observed here are consistent with Crick and Koch's proposal in that the N170 response is known to originate from higher-level medial temporal areas that may include the fusiform gyrus (Hermann, Ehrlis, Muehlberger, & Fallgatter, 2005; Itier and Taylor, 2004a,b). However further analyses of neural synchrony, reentrant neural activity, and N170 cortical sources

are necessary to rule out other the other competing hypotheses. Such analyses are beyond the scope of the present paper, but are a fruitful direction for further research.

6.3 Evidence for Mutual Inhibition?

What has not yet been established is whether these ERP and behavioral findings are consistent with the competitive model presented in Section 1.2. That is, are these findings consistent with the occurrence of mutual inhibition during cross-edge competition, inhibition that may survive the competition for some period of time? Section 6.4 begins to address this question by first considering how competition and inhibition would be instantiated cognitively and behaviorally. How competition and inhibition might be instantiated neurally and electrophysiologically is discussed in Section 6.5.

6.4 A Model of Evidence-Accumulation Modulated by Competitive Inhibition

In order to correctly model the behavioral findings established in the present study, it is important to be clear about the nature of the shape categorization tasks given to the participants and how it compares to the tasks of the studies reviewed in Section 1.4. The present study used two tasks (Task 1 and Task 2) in which decisions about object/shape familiarity were required; such an object decision was also required in the tasks of Peterson and Kim (2001) and Peterson and Skow (submitted) suppression studies. Recall that these studies showed that once object memories are inhibited during the processing of a prime stimulus, then it takes longer to reactivate those object

memories during the processing of a probe stimulus that matched in basic level category. However, the shape categorization tasks of the present study differed from the task of the previous suppression studies in that participants categorized unprimed silhouettes. Thus Task 1 measured the behavioral consequences of competition outcome rather than suppression¹⁰, while Task 2 measured the behavioral consequences when such competition was affected by top-down influences of task set.

The present study also differs from the previous studies investigating cross-edge competition (Peterson and Lampignano, 2003; Peterson and Enns, 2005) in that the latter used same/different tasks to index the competition. Recall that the priming studies of Peterson and Lampignano (2003) and Peterson and Enns (2005) showed that memories for figure regions of prime stimuli bounded by unique articulated contours competed with other configural cues when the same contours were assigned to figure regions of a probe stimulus that was previously a ground region on prime trials. These studies found that competition increased RTs to determine whether two probe stimuli were the same or different. The direction of this difference (longer RTs when competition was present vs. not) is opposite in direction to the RT differences observed in Task 1 of the present object detection task (shorter RTs when competition is present versus not).

Peterson and Enns (2005) concluded that, in their task, the different shapes suggested on the opposite side of the edges of the probes had the potential to interfere with the required same/different responses. That is, evidence accumulated for

¹⁰ Although the stimuli were repeated throughout Task 1, it is assumed here that short-term suppression effects were not relevant because mutual inhibition has been found to be short-lived (e.g. Peterson and Kim, 2001). However, it is possible that previous exposures of a stimulus

same/different responses while the memory representation of the familiar shape potentially present on the unbounded (ground) side was still activated. Therefore in order to be accurate, participants had to delay responding in the experimental condition relative to the control condition. This suggests that decision responses could be made before figure-ground segregation is finalized, but that certain conditions (e.g. the experimental condition) would require a further progression towards figure-ground resolution than other conditions (e.g. the control condition) (Peterson and Lampignano, 2003; Peterson and Enns, 2005).

While decision responses can certainly be made before figure assignment, it is not clear that this could explain the difference in RT patterns between the present shape categorization task and the previous same/different tasks. A similar theoretical argument as for Peterson and Enns (2005) could be made about the present task: evidence accumulated for familiar/novel responses while the representation of familiar shape potentially present on the unbounded (ground) side of the EXP stimuli was still activated. Decision responses could be still be made before figure-ground segregation is finalized in the present task, but even if this were so, RTs to categorize EXP silhouettes were not longer relative to RTs to categorize CON stimuli. This might indicate that the figures of EXP stimuli were resolved more rapidly than CON stimuli (inconsistent with previous claims, e.g. Peterson and Lampignano, 2003; Peterson and Enns, 2005), or that there is some further difference between the present and previous studies that leads to the conflicting patterns of results. This latter option is the position taken in this paper and will be explored in the remainder of this section.

One possible difference between the present and previous studies may be that although both the present and previous studies of cross-edge competition required the perception of shape in order for participants to successfully perform the task, they differed in terms of the number of shapes perceived and, more importantly, what types of judgments or comparisons had to be made about them. The present study involved the perception of a single figure followed by a familiarity judgment as the figure representation was compared to object representations stored in long-term memory. In contrast, the same/different task required the perception of, and comparison between, two shapes in working memory from which a similarity judgment is made. These two types of comparison processes (long vs. short term memory) may follow different time courses depending on whether or not competition is present at the level of object memory representations. That is, the effect of competition on the ability to perform a task may be different when two shapes are compared to each other in working memory as compared to the case of a single shape compared with long-term memory representations. The former case may involve additional competition between representations of the two shapes to be compared that is nonlinearly dependent upon the competition during figure assignment of each shape individually. A further difference between the present task and the tasks of Peterson and Lampignano (2003) and Peterson and Enns (2005) is that the latter experiments assessed memory for novel borders that had been viewed on prime trials only once before the probe trials, whereas the present task examined the consequences of accessing preexisting memories of portions of similar basic-level objects. The mechanisms mediating memory for past experience with a previously seen

border may follow different time courses than those mediating memory for basic level objects. Additional research is needed to settle these issues further, but one advantage in using the present task paradigm to theorize about the effects of mutual inhibition and competition on figure assignment is that it is an intrinsically simpler and more tractable situation (i.e. competition during the resolution of a single figure representation).

How then should the behavioral findings of the present task be understood in terms of cross-edge competition and mutual inhibition? Following Peterson and Enns (2005), it will be assumed in the present model that evidence is accumulated in order to perform the familiar/novel judgments of the present task. Instead of assuming anything about figural resolution times, however, the present model will instead assume that the evidence accumulation determining the participants' perception of familiarity is driven by the overall activation of a perceptual representation. In evidence-accumulation models of decision-making, evidence is accumulated by participants over time until some threshold is reached or some internal time limit met, at which point a decision is made and response generated (Sanford, 1972; Ratcliff, 1978, 1980; Smith, 2000; Smith et al. 2004).

Although the time to make a decision depends on the information content of the accumulated evidence, it is also affected by the rate of evidence accumulation and this in turn depends on the signal strength of incoming stimuli. The present model takes this idea further by supposing that the rate of evidence accumulation also depends on the signal strength of the visual representation formed in response to the stimulus, representations that can be strengthened or weakened according to the presence or absence of competition and mutual inhibition. Thus the framework presented here combines the

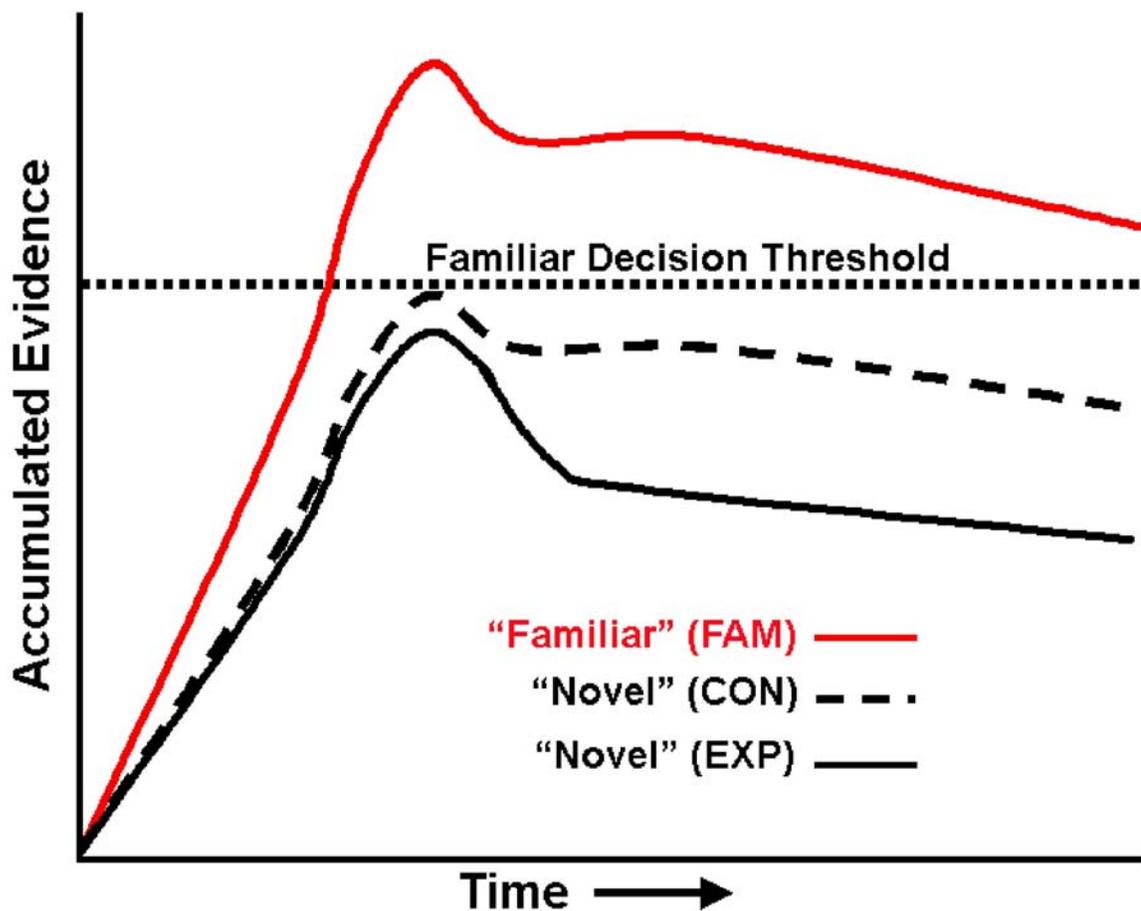


Figure 29. Time course of evidence accumulation during Task 1 according to the EA|CI model. Solid light red line = accumulated evidence leading to categorization of FAM stimuli as “familiar”; Dashed black line = accumulated evidence leading to categorization of CON stimuli as “novel”; Solid black line = accumulated evidence leading to categorization of EXP stimuli as “novel”; Dotted black horizontal line = threshold to categorize stimulus as “familiar”.

PIMOCA model with standard models of evidence accumulation to result in an *evidence accumulation modulated by competitive inhibition* model (hereon referred to as the EA|CI model).

In the EA|CI model (Figure 30) the “evidence” accumulated by the decision-making stage is the output of the figure assignment stage, output that contains

information reflecting the degree of familiarity imparted to the perceived shapes of the silhouettes. Participants base their decisions on this information. “Familiar” decisions are made when shape processing output supersedes a threshold for a “familiar” decision to be made; if output activity does not meet this threshold then a “novel” decision is made. In the case of the FAM silhouettes, shape processing is assumed to be robust and rapid because the central regions of the stimuli are biased to be seen as figure while actually depicting familiar shapes. Thus the outputs of the shape assignment stage are equally robust and rapidly pass the threshold to generate a “familiar” decision by participants.

The novel silhouettes (EXP and CON) do not generate such salient output because they do not depict familiar shapes. The shapes of the EXP and CON silhouettes do vaguely resemble familiar shapes, however, consistent with previous findings that people can be biased to judge novel silhouette shapes as familiar (McBeath, Schiano, and Tversky, 1997). Thus the novel shapes produce outputs that come near, but do not exceed the threshold to decide “familiar”. So it becomes difficult to decide if the EXP and CON stimuli depict familiar or novel shapes, leading to longer RTs to categorize them as “novel”. This explains the longer RTs to novel than familiar silhouettes observed in all three experiments reported here. Nonetheless, there is greater mutual inhibition present for EXP stimuli than CON stimuli (see Section 1.3) that reduces the figure assignment output strength of the former to a level that is even lower than for CON stimuli (Figure 30). Thus although NOV silhouettes are difficult to disambiguate from FAM silhouettes, EXP silhouettes are easier to disambiguate than CON stimuli, and it thus becomes

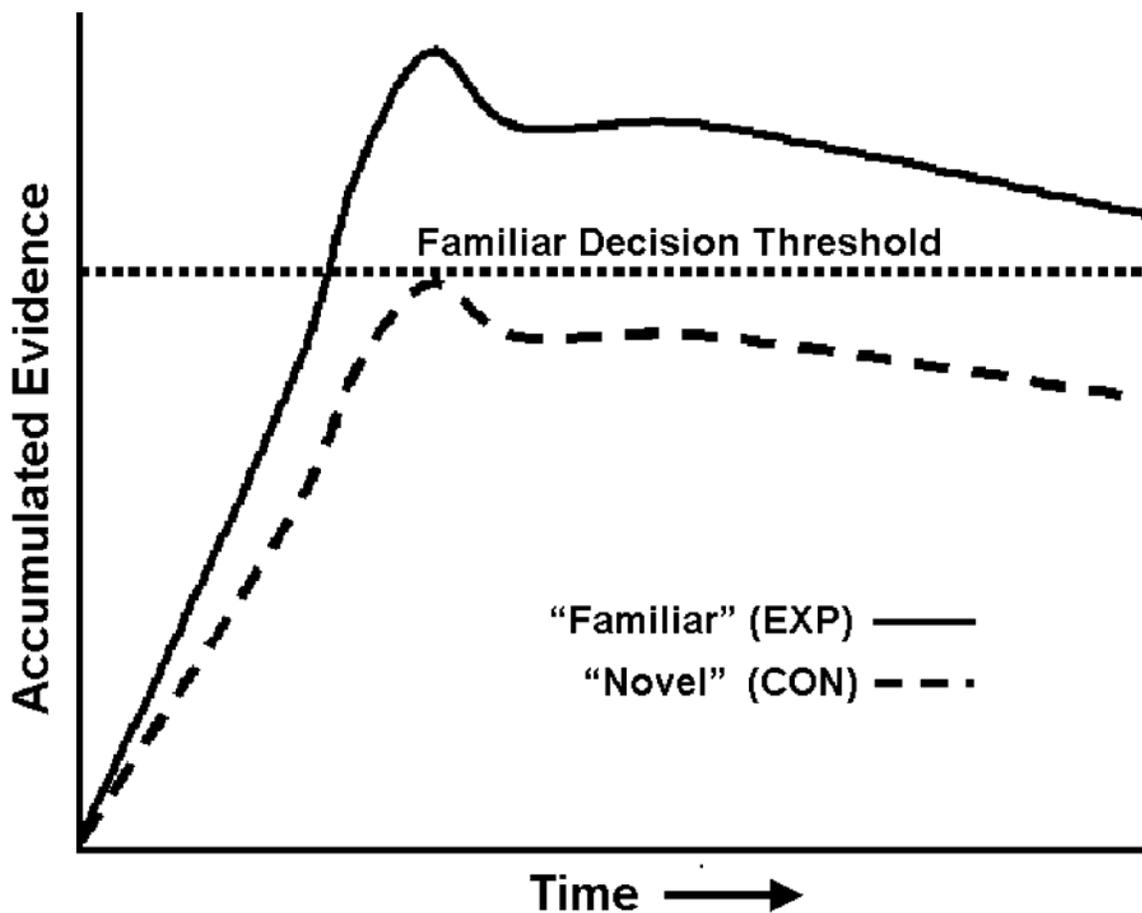


Figure 30. Time course of evidence accumulation during Task 2 according to the EA|CI model. Solid black line = accumulated evidence leading to categorization of EXP stimuli as “familiar”; Dashed black line = accumulated evidence leading to categorization of CON stimuli as “novel”; Dotted black horizontal line = threshold to categorize stimulus as “familiar”.

evident sooner to participants that EXP silhouettes won’t exceed the threshold to decide “familiar”. This would lead to faster RTs to categorize EXP than CON stimuli, as observed during Task 1 of all three experiments.

The EA|CI model can also be applied to the behavioral findings of Task 2 (Figure 30). Task 2 involves a similar sequence of shape/figure assignment, familiarity decision, and motor response as in Task 1, but now the familiarity decision is made in the outer

regions of the silhouettes. In order for the familiar shapes to be perceived consciously, the regions on the outside of the bounded silhouettes must be seen as figures. For this to occur, the cues favoring the outside as figure must win the cross edge competition. This likely happens because the observer musters an intention to see the outside as figure (in response to the task set), and perhaps deploys attention to the outside regions. Both intention and attention affect figure assignment (Peterson & Gibson, 1994; Peterson, et al., 1991). Reversal is probably more likely to occur for EXP than for CON stimuli because in the former case, past experience also favors the outside as figure. In this case, figural shape assignment is robust and rapid for EXP stimuli because the figure regions now depict familiar shapes, and thus the output of the shape assignment stage is equally robust and exceeds the threshold to rapidly generate a “familiar” decision. As in Task 1, however, Task 2 CON responses approach, but do not exceed the threshold to decide “familiar”. Thus it becomes difficult to decide if the CON stimuli figure regions depict familiar or novel shapes, leading to longer RTs to categorize as them as “novel”, as observed during Task 2 across all three experiments (although only significantly so in Experiment 3).

Thus the EA|CI model accounts for the RT findings of both Tasks 1 and 2 in terms of differing representation strengths for each type of stimulus: strong (FAM), weak (EXP), and intermediate (CON). Strong representations are more likely to be familiar objects, while intermediate representations (CON) may be either familiar or novel. Weak representations (EXP) may also be familiar or novel, but are more likely to be novel. This explains not only the RT patterns for Task 1, but also the finding that accuracy rates to

categorize EXP stimuli as novel are greater than for CON stimuli. In the case of Task 2, there are only two representation strengths, strong (EXP) and weak (CON), but the weaker strength remains close enough to the familiarity threshold that it becomes more difficult, and time-consuming, for participants to decide “novel”. The low accuracy rate to categorize EXP stimuli as “familiar” observed during Task 2 across all three experiments suggests, however, that representation strengths did not pass the familiarity threshold for these stimuli on a significant portion of trials. This could be due to a failure to reverse the silhouettes, as well as from failure to recognize a shape as familiar once a reversal has occurred. The low accuracy rates may also indicate that some stimuli have weaker past experience cue strengths than others, and/or that it might be difficult to recognize the shape from just a fragment, especially without any evidence of occlusion consistent with the perception of just a shape fragment. Participants, however, were more accurate without a mask (Experiment 3 Task 2) than with a mask (Experiment 2 Task 2); this difference between experiments may have occurred simply because it takes more time for evidence to accumulate than was available with a mask.

The EA|CI model is consistent with the evidence for cross-edge competition gathered in the priming studies involving object decisions reviewed in Section 1.4. Competition-induced inhibition of object memories during the processing of primes can outlast the competition itself, and thus affect the processing of subsequently presented stimuli. In the case of the suppression studies of Peterson and Kim (2001) and Peterson and Skow (submitted), this ongoing inhibition and suppression of object memories impedes the ability to recognize a subsequently presented line drawing when the latter

matches the object memory at the basic level, as observed by longer RTs to categorize the probe drawing as familiar. While it is still unclear how the EA|CI model relates to the findings of Peterson and Lampignano (2001) and Peterson and Enns (2005) (see earlier discussion on pp. 114-116), the EA|CI model is consistent with the early investigations of the role of past experience in figure assignment that assessed conscious figure judgments (e.g. Peterson et al, 1991; see Section 1.3) in that the usual predictions of the PIMOCA model still apply (i.e. the probability of perceiving a given side as figure is increased when cues to past experience are added to more strongly cue that side). What the EA|CI model does suggest is that the figure judgments in such tasks might be influenced by the strength of a figure-ground representation. Investigation of this possibility should be a subject for future research.

6.5 A Neural Conception of the EA|CI Model

6.5.1 Representation Strength: From Behavior to Neural Activity

The final question remaining to be discussed within this dissertation is how the EA|CI model can be used to understand the electrophysiological findings obtained in this study. To accomplish this requires further elucidation of the concept of representation strength introduced in the previous section.

In the EA|CI model, the strengths of cognitive representations are quantified in terms of their salience with respect to some decision process. High salience equals high strength; low salience equals low strength. A simple assumption to make when transitioning to a neural model is that the salience of a cognitive representation is

represented in terms of the overall activation strength of the neurons coding for that representation. Thus high salience equals high neural activation; low salience equals low neural activation. It follows that when looking for a neural correlate of competition and mutual inhibition, one should look for activation patterns that follow the hypothesized salience levels for each stimulus type based on the behavioral findings (see Section 6.4, above). That is, stronger representation strengths arising under conditions of weak mutual inhibition should be associated with strong neural activations, while weak representation strengths arising from conditions of strong mutual inhibition should be associated with weaker neural activation patterns. For the rest of this paper, this guiding principle shall be called the Representation Strength Equivalency assumption.

6.5.2 Representation Strength: From Neural Activity to Electrophysiology

Applying the Representation Strength Equivalency assumption to the present data is complicated by the biophysical nature of ERPs as measures of neural activity. This section briefly elucidates this issue.

6.5.2.1 ERP Changes Due to Competition-Induced Changes in Raw Neural Activation

A given ERP source reflects a mixture of excitatory and inhibitory synaptic electric potential activity arising from large populations of neurons synchronized in their firing (Nuñez and Srinivasan, 2006). This synchronization leads to constructive summation among synaptic electrical potentials of a given type (excitatory, inhibitory),

while leading to destructive summation between potentials of opposite type. Any measurable electric potential at the scalp surface then reflects the final balance of constructive and destructive summation among synaptic potentials.

This balance of constructive and destructive summation is affected by (at least) three factors. First, strong inhibition of excitatory neurons coding for a perceptual or cognitive representation leads to reduced activity of those neurons relative to weak inhibition. This activity difference manifests both in terms of raw activation (firing rate) as well as the numbers of cells that are active. Second, inhibitory and excitatory synaptic potentials are opposite in polarity; thus the more inhibition for a given figure representation, the more inhibitory synaptic activity there is, which should then lead to greater destructive summation between the synaptic potentials associated with the latter and those associated with excitation; smaller destructive summation occurs when there is less inhibitory synaptic activity. Third, excitatory and/or inhibitory neurons firing in or out of phase with each other will also lead to constructive or destructive summation, respectively, and there is evidence that suggests that changes in inhibition levels affects the synchronization of neural populations (Traub, Jefferys, and Whittington, 1999). In any of the above cases it is reasonable to interpret the amplitude of the ERP (relative to baseline)¹¹ as reflecting the magnitude of neural activation. That is large ERP magnitudes indicate a strong amount of neural activation (greater constructive summation), while smaller ERP values indicate a small amount of neural activation (greater destructive summation).

¹¹ Note that these ERP amplitudes are measured with respect to a pre-stimulus baseline, and so amplitudes of a given polarity are bounded by some maximum value and a zero (baseline) value.

Now consider the prediction of the PIMOCA model (Section 1.2) that weak cue competition equals weak mutual cross-edge cue inhibition and strong cue competition equals strong mutual cross-edge cue inhibition, along with the assumption of Representation Strength Equivalency (Section 6.5.1), in which the overall strength of a perceptual or cognitive representation is proportional to the overall strength of a neural representation. These two starting points together suggest that the presence of strong competition and mutual inhibition should be expressible in terms of inhibition among competing neuronal representations, inhibition that should serve to reduce the overall neural activation.

The obvious neurophysiological candidates for implementation of this inhibition are the cortical inhibitory neurons linked within the main network of excitatory neurons coding the neural representation. The reduction in neural activity would manifest as a general reduction in excitatory firing rates and/or desynchronization of cell firings in time. This in turn would lead to a reduction in the strength and constructive summation of the synaptic potentials, and an increase in destructive summation through the electrical cancellation of excitatory and inhibitory synaptic potentials, and the overall change in the balance of constructive and destructive summation would then lead to a decreased EEG signal.

Therefore, the presence of strong mutual inhibition relative to weak mutual inhibition should lead to low neural activity, which in turn should be accompanied by a lower ERP signal. That is, ERP responses indicative of strong mutual inhibition of configural cues across an edge (e.g. Task 1 EXP stimuli) should be characterized by

decreased amplitudes relative to when little or no mutual inhibition is present (e.g. Task 1 CON stimuli).

6.5.2.2 ERP Changes Due to Competition-Induced Changes in EEG Source

Configuration

Changes in ERP amplitude, however, may reflect more than just variations in synaptic potential summation. Such differences may also reflect changes in EEG source configuration. For example, suppose that an ERP source of an overall given polarity and/or dipole orientation (reflecting an overall combination of excitatory and inhibitory activity) is operating during one condition of a particular task, but another condition involves activation of another EEG source of opposite polarity or orientation to the first source. Such a situation would produce ERP changes that are not indicative of a change in neural activation strength, but instead reflect differences in source polarity or orientation. This situation could be further complicated if the second condition involved both sources being activated simultaneously, in which case their opposite polarity potential fields would lead to the electrical cancellation of the two source activities, and again produce ERP changes that are not indicative of a change in source strength.

It is unlikely that between-condition competition-related ERP changes observed in the present study arise from a change in EEG source configuration. This assumption is motivated, in part, by previous findings of the sources and behavior of the three ERP components measured in this study (see Section 6.5.3), and by the highly similar topographies for each ERP component across conditions within a single experiment (see

Figures 14 and 24). While the Task 2 Late Potential topographies do change between Experiments 2 and 3, they remain relatively similar across conditions. Nonetheless, Task 2 did require the reversal of figure against a bottom-up cue bias by the participants, and thus recruited top-down process to a larger degree than Task 1. It may be possible that this change in task set across Task 1 to Task 2 could have involved the activation of another neural source originating the top-down influences. It may also be possible that the overall N170 increase and LP amplitude decrease seen in Task 2 relative to Task 1 could be due, in part, to the onset of such a source and the consequences this would have to the overall bioelectric potential summation. An obvious candidate for the location of such a source would be in the frontal cortices, which are known to be involved in executive decision making, task monitoring, and the initiation of attention (Stuss and Knight, 2002).

The above conjectures could be tested by an analysis of the frontal EEG signals measured in this study in conjunction with a rigorous source localization analysis, a subject for future research beyond the scope of the present study. It is unlikely that the mere bioelectric presence of these possible sources and the impact on the overall source configuration differed across conditions because the source topographies of Task 2 did not appear to change qualitatively between conditions. The presence of such an additional source, however, may have still have led to a difference in ERP signals due to its' affect on the activity of other ERP sources through long-range interactions. This is the subject of the next sub-section.

6.5.2.3 ERP Changes Due to Competition-Induced Changes in Interactions

Among Multiple EEG Sources

Electrical cancellation aside, a further reason for a change in ERP amplitude is that two neural sources may interact with one another through medium- or long-range connections such that the activity of one source is modulated by the activity of the other or vice-versa; such modulation between two or more sources could be reciprocal as well. This activity modification may occur when the sources are simultaneously coactive, or it may persist after the initiating source has ceased being active.¹² Differential ERP activity may result if the interactions between neural sources are different according to the presence of competition and mutual inhibition. For example, suppose two sources are interacting such that the activity modulates the activity of the other source. If a greater degree of competition-induced inhibition is operating on the modulating source, thus reducing its activity and signal output, this would then lead to a change in activity of the second source. Which direction this change goes would depend on the nature of the modulation of the initial source. It is clear that an analysis of competition-induced changes in such interactions becomes increasingly intractable with increasing number of sources.

¹² The latter may occur through hysteresis, in which neuronal membrane potentials remain elevated after excitatory input is removed, or through accommodation, in which the neuronal excitability is reduced after a period of inhibition (O'Reilly and Munakata, 2000).

6.5.3 What Do the Present ERP Changes Reflect?

The discussion of Section 6.5.2 shows that there are at least four possibilities for the between-condition changes in ERP amplitude observed in the present study: 1) changes in ERP source activation strengths (either by changing the strength and/or relative balance of excitatory and inhibitory synaptic potentials, and/or by changing the degree of synchronized firing among a neural population); 2) changes in the ERP source configuration; 3) changes in the long-range modulatory interactions among two (or more) coactive neural sources; and 4) some combination of the above. The subject of the next three sub-sections is to consider which possibility best explains the changes observed in the three ERP components (P1, N2, LP) observed in this study.

6.5.3.1 The P1 Response

The general scalp topography of the P1 responses observed in this study was temporo-occipital, and thus consistent with previous findings of an origin for the P1 in extra-striate cortex (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001). There is also evidence that the P1 originates from volume-conducted signals of two spatially distinct bilateral source configurations, partially co-active in time, at least when evoked by simple grating stimuli (Di Russo et al., 2001). These cortical locations are consistent with source analyses of attention-related P1 and associated fMRI responses (Mangun et al., 1998).¹³ This observed consistency in source configuration suggests that P1 changes

¹³ While these findings conflict with a recent current source density (CSD) analysis localizing photorealistic face-related P100 responses to the fusiform gyrus (Herrmann et al., 2005b), that study may be vulnerable to spatial inaccuracies given the small number of recording electrodes (N = 21) used.

most likely involve changes in source activity rather than changes in source configuration (although there may still be hemispheric differences in source activity). These findings do not rule out the possibility that P1 responses may be modulated by higher-level sources, however.

In the present study, the P1 amplitudes of Task 1 Experiment 3 were larger in response to EXP relative to CON stimuli. This could indicate that EXP neural activity was inhibited less than CON stimuli at this stage of processing. Neural network models often distinguish feedforward versus feedback inhibition (O'Reilly and Munakata, 2000), in which the former “anticipates” the effect the input will have on a set of excitatory cells and compensates accordingly, while the latter, acting at the same hierarchical level as the excitatory units to be inhibited, responds to the actual activity of the excitatory cells. It is possible that the initial activation of an object memory could have temporarily overwhelmed feedforward inhibition until eventually feedback inhibition won out over time. Furthermore, since P1 responses are known to originate from extra-striate sources, if the P1 reflects the initial activation of an object memory, then this would indicate that such memory representations extend to lower levels of the visual system (~ V2, V3, V4) than previously thought (Peterson, 2003).

Finally, it is unlikely that these P1 responses reflect the effect of a modulatory source. The task set was to categorize the central bounded regions of the silhouettes as figure, in accordance with the bias of configural cues, and thus did not require figure reversal. Thus attention was centrally focused, although it remains possible that attention was “captured” (Yantis, 1996) by the presence of the object shapes in the unbounded

silhouette regions. This interpretation would be consistent with the established finding that the P1 reflects attention to space and objects (Mangun and Hilyard, 1991; Luck, Hilyard, Mouloua, Woldorff, Clark, and Hawkins, 1994; Mangun, Buonocore, & Girelli, 1998; Valdes-Sosa, Bobes, & Rodriguez, 1998). The present observation that P1 responses can be sensitive to high-level cues such as past experience is also supported by studies showing a P1 sensitivity to faces (Herrmann, Ehlis, Ellgring, and Fallgatter, 2005a; Hermann, Ehlis, Muehlberger, & Fallgatter, 2005b; Itier & Taylor, 2002, 2004b; Halit, de Haan, & Johnson, 2000; Trujillo, Peterson, and Allen, submitted), although these reports have not gone uncontested (e.g., Rossion et al., 1999, Latinus & Taylor, 2005).

There were no P1 amplitude differences in Task 2 of Experiment 3, suggesting equal mutual inhibition across conditions in which the outside unbounded regions of the stimuli as seen as meaningful (EXP) and novel (CON) shaped figures. Now the task set is to work against the bottom-up cue bias to assign figure to the unbounded regions. This additional top-down influence may have served to equalize the inhibition across conditions.

6.5.3.2 The N170 Response

The lateral occipital-temporal scalp topography of the N170 responses observed in this study was similar to that previously observed for N170 responses to faces and objects (Bentin, Allison, Puce, Perez, and McCarthy, 1996; Sagiv and Bentin, 2001; Bentin et al., 1996; Rossion, Curran, and Gauthier, 2002). Source analyses indicate that

the N170 sources are localized in part to ventral temporal regions including the fusiform gyrus (Hermann et al. 2005a), a region known to be highly face sensitive (Kanwisher, McDermott, and Chun, 1997). Other studies (e.g. Itier and Taylor, 2004a) suggest that activity in the superior temporal sulcus also contributes to the N170 and that activity in this region is responsible for much of the face selectivity of the N170, with the fusiform region mediating the non-face selective N170 source component. Faces were one among the many object shapes depicted by the unbounded regions of the EXP silhouettes (see Appendix A). It is likely, however, that since the overwhelming majority of the depicted objects were not faces the N170 response measured here mainly reflects processes attributed to the common fusiform source. This, together with the fact that the present N170 scalp topographies did not change between conditions, suggests that it is unlikely that the present between-condition N170 differences involve a change in EEG source configuration.

The present N170 responses were not different between-conditions in Task 1, a situation involving greater mutual inhibition for EXP than CON silhouettes. One explanation for this null finding could be that any N170 increases arising from the activation of an object memory were masked by the greater inhibition during the EXP condition through the destructive summation of excitatory and inhibitory potentials (see Section 6.5.2). That the N170 might reflect the activation of object memories is supported by previous findings that the N170 can be selective for different object categories (Itier and Taylor; 2004b), especially when viewers have expertise with an object category (Rossion et al., 2002). However, the absence of N170 differences for

Task 1 may also be simply due to the fact that the activated object memory lost the cross-edge competition during the EXP condition by the onset of the N170. Furthermore, if it is assumed that N170 indexes conscious perception of familiar shape (see Section 6.2), then one would expect no differences between EXP and CON stimuli since both were perceived as novel stimuli in Task 1. This assumption is consistent with the fact that the N170 was greater in Task 2 when the unbounded regions of the silhouettes were seen as a familiar object shapes (EXP) than not (CON). Alternatively, these Task 2 N170 differences could arise from a reduction in mutual inhibition for the EXP silhouettes via the influence of top-down processes involved in the reversal of figure; this reduction in mutual inhibition could also be partially responsible for the general increase in Task 2 N170 amplitudes. Nonetheless, it may also be possible that the overall N170 increase in Task 2 relative to Task 1 is due, in part, to the overall changes in bioelectric potential summation that may arise from the presence of the neural source(s) originating the top-down modulation (as discussed in Section 6.5.2.2).

6.5.3.3 The Late Potential Response

The Late Potential response observed in the present study is perhaps the most difficult to understand, as its behavior changes both with stimulus condition (EXP, CON), task set (Task 1 vs. Task 2), and the presence or absence of a mask (i.e. Experiment 3, Task 1 vs. Task 2; Experiments 2 vs. 3, Task 2). The LP responses of Task 1 present the simplest case, as masks were present in both conditions across Experiments 2 and 3 under a task set to categorize the central bounded regions of the silhouettes as

familiar or novel. Under this condition, even though both EXP and CON stimuli were correctly classified as novel, the LP was smaller and less positive for EXP than CON stimuli. A straightforward interpretation of this finding suggests that the LP response were lower in the EXP condition due to a decrease in neural activity arising from cross-edge competition. However, it is clear that this late positive component represents the activity of at least two separate source configurations, the source(s) associated with the later processing of the EXP and CON silhouettes and the source(s) associated with the early processing of the masks. What is not immediately clear is if the decrease in neural activity occurs for one or both sources and whether this decrease occurs through the modulatory influence of one source on the other, as discussed next.

These alternatives may be disentangled by a careful analysis of the time course of the processing of the silhouettes. Silhouettes are presented for 167 ms in Experiment 2 and for 175 ms in Experiment 3. The silhouettes elicit P1 and N170 responses. Around the time of the N170 response the silhouette is removed and replaced by a mask. It takes approximately 50 ms for signals from the retina to reach the visual cortex (DiRusso et al., 2001), so the onset of the P1 response to the mask should be observable in the ERP traces ~ 217 ms after silhouette onset for Experiment 2 and ~ 225 ms for Experiment 3. The peak of the P1 response to the mask should then occur ~ 267 ms for Experiment 2 and ~275 ms for Experiment 3. These predicted timelines coincide with the time at which late positive potentials were observed in Experiments 2 and 3 (see Figures 14 and 24).

By the time the P1 to the mask reaches its zenith ~ 275 ms after silhouette onset, one would expect the high-level processing of the silhouette to be still ongoing, although

this activity may have ceased earlier if enough relevant shape information had been extracted from high-level visual representations so that a decision about a silhouette's familiarity could be made. Nonetheless, it is highly likely that signals originating from the high-level processing of the silhouettes are influencing the early processing of the mask through the extensive feedback projections known to connect high- and low-level visual cortical regions (Salin and Bullier, 1995). This conclusion is supported by previous findings that the responses of low-level V1 neurons in primates are enhanced when a figure rather than a ground lies within their receptive fields, with this enhancement manifesting ~ 100 ms after stimulus presentation (Lamme, Rodriguez, & Spekreijse, 1999; Zipser, Lamme, & Schiller, 1996). The modulation of low-level neural activity by feedback from high-levels could be accomplished in two ways: 1) excitatory feedback could directly couple with low-level neurons so as to drive activation to increased levels (e.g. increased firing rates and/or synchronization); or 2) high-level feedback could release the lower level units from lateral inhibition (as assumed by Roelfsema, Lamme, Spekreijse, and Bosch (2002) to model the findings of Lamme et al., 1999; 1996).¹⁴

Thus, if the activity of the neurons mediating the high-level processing of the silhouettes during Task 1 is reduced through the greater mutual inhibition of the EXP stimuli relative to the CON stimuli, then this should lead to a reduction of feedback to the lower visual levels in the EXP condition. In the case of direct excitatory feedback,

¹⁴ One objection to the role of feedback connections in neural computation is that such feedback appears to be diffuse and non-specific in connectivity with the lower levels (Salin and Bullier, 1995). That is, these feedback connections "broadcast" the signals from high-levels to all neurons at the lower level. This does not pose a problem, however, in that only the low-level neurons that are active during this time are modulated by the high-level signals (Roelfsema et al., 2002); neurons that are not active or, at least, not as strongly driven by input stimuli appear to be relatively unaffected by the high-level signal.

reduced feedback would lead to less excitation of mask-related neural activity at lower-levels. In the case of indirect excitatory feedback (e.g. Roelfsema et al., 2002), reduced feedback would lead to a decrease in the degree to which low-level cells are released from lateral inhibition, yielding greater inhibition of the early processing of the mask in the EXP relative to the CON condition. In either case, reduced feedback should lead to a reduced LP response, exactly as observed in Task 1 of Experiments 2 and 3. Importantly, these observations are not confounded by any potential stimulus differences among the mask stimuli, as the same set of masks was presented in EXP and CON conditions. Hence, the decreased Task 1 LP response to EXP relative to CON stimuli most likely arises from a reduction in neural activity at high-levels (due to inhibitory competition) combined with low-level neural activity reductions resulting from a decreased modulation of the low-level source by the high-level source.

Now consider the Task 2 LP responses, which were different across Experiments 2 and 3 (Figures 18 and 28). In Experiment 2 the Task 2 Late Potential was positive as in Task 1, due to the processing of the masks (i.e., the LP reflects the P100 to the mask combined with the later waveforms reflecting processing of the silhouette). Although the overall magnitude of the LP was reduced with respect to Task 1, EXP LP responses were still reduced with respect to CON LP responses. In Experiment 3 the Task 2 LP was predominantly negative due to the absence of a mask and associated P100 response, although the magnitude of this response was again reduced for EXP vs. CON stimuli. What do these reductions in Task 2 EXP vs. CON LP responses reflect?

One possibility is that participants saw the outside regions as figure from the outset, but were able to find familiar shapes in the EXP stimuli more rapidly than for CON stimuli. This is predicted by the EA|CI model (Section 6.4) and is supported by the faster RTs to categorize the unbounded regions of EXP stimuli as familiar than CON stimuli as novel in Task 2 of Experiment 3. It follows that the high-level neural activity associated with the processing of the EXP silhouettes may have also terminated earlier than the neural activity in the CON case, which persisted during a continued attempt to find familiar shapes in the CON stimuli. This possibility is supported by the fact that the Experiment 3 Task 2 LP polarity is negative, maximal over similar scalp locations as the N170, and thus consistent with a more ventral source in visual cortex. This hypothesis is also consistent with the general morphology of the N170 to LP transition for Experiment 3 Task; the EXP LP transitions rapidly to baseline while the CON LP remains greater than baseline. In Experiment 2 Task 2 when a post-stimulus mask was presented, this early termination of high-level activity in the EXP condition might reduce or eliminate high-level feedback, thus reinstating inhibition at the lower visual levels during the early processing of the masks in the EXP condition. Thus for both experiments, the continuation of processing in the CON condition that was terminated earlier in the EXP condition could explain the reduced LP magnitude for EXP relative to CON conditions of Task 2.¹⁵

¹⁵ Is it possible that this explanation could account for the LP effects of Task 1 instead of differential mutual inhibition? This is not likely because in Task 1 participants categorized the central bounded regions of both EXP and CON stimuli as novel shaped figures in accordance with the configural cue biases of the silhouettes, which was equated for both stimulus types (see Section 4.3). Thus the task set should not have compelled participants to consciously extend their time spent processing a stimulus in either condition

An alternative possibility is that that some mutual inhibition of object memory representations might still persist, despite the influence of the task set of Task 2. According to the PIMOCA model such mutual inhibition might occur if the participants' first percept of a silhouette was consistent with the cues favoring the center (i.e., the outside was seen as ground and the familiar shape representation accessed on the outside was inhibited), and subjects had to reverse the figure-ground organization in order to see the familiar shape on the outside. Unfortunately there is no way to tell from the present experiment whether the first figure-ground determination was center as figure that was overcome by the observer, or whether past experience and strategies employed in the service of the task set caused the outside to be initially be seen as figure and then maintained over time. No records of first-perceived figure-ground organization (central bounded region or outside unbounded region) were recorded in this study. The two competing explanations for the cause of the observed LP differences might be tested by modifying the present task to include reports of first-perceived figure-ground organization.

One remaining difficulty with understanding the between-condition differences in LP response is the following: if there are two source configurations active, one at the high-level (e.g. fusiform and higher regions) and one at the low-level (e.g. extra-striate regions) then might not the between-condition differences in the LP arise simply from differential electrical cancellation between the two sources across conditions and not involve modulatory interactions between the sources via neural feedback? This problem

(although this time would certainly be influenced unconsciously by the presence of mutual inhibition in the manner already described previously).

appears especially relevant since the ERPs associated with high-level processing (e.g. N1) exhibit a negative polarity while the low-level ERPs (e.g. P1) exhibit a positive polarity, with the rough orientations of these sources collinearly oriented in part. This could be approximately modeled as two positive dipole oriented in opposite directions, with the low-level responses (e.g. the P1 source in extra-striate cortex) corresponding to the positive end of the posteriorly pointing dipole and the high-level ventral responses corresponding to the negative end of the other dipole pointing in an ventral and anterior direction¹⁶. A comparison of the Task 2 LP findings across Experiments 2 and 3 indicates this possibility is unlikely however.

Consider low- and high-level EEG sources L_{CON} , $L_{EXP} > 0$ and H_{CON} , $H_{EXP} > 0$ that are roughly collinear¹⁷ in the direction of their equivalent dipoles, but oriented in opposite directions. To a first approximation¹⁸, the total Late Potential response for each condition is then $LP_{CON} = L_{CON} - H_{CON}$ and $LP_{EXP} = L_{EXP} - H_{EXP}$, and the between-condition difference is then $\Delta LP = LP_{CON} - LP_{EXP} = (L_{CON} - H_{CON}) - (L_{EXP} - H_{EXP}) = (L_{CON} - L_{EXP}) + (H_{EXP} - H_{CON})$. The P1 amplitudes generated by the masks should not

¹⁶ It should be noted that polarity and orientation of ERPs and ERP sources are not absolute, but relative to the particular electrical reference with respect to which evoked potentials are calculated and, to a lesser degree, the manner of baseline correction (see Footnote 11). What is most important to the present argument is that whatever the absolute values are of these properties, they are oppositely valued and thus likely to lead to destructive summation.

¹⁷ In the case when equivalent dipoles representing the low-level and high-level LP sources are not collinear, the following argument would still hold if one assigns one dipole as a reference and then considers the components of each dipole that project onto the axis formed by the vector orientation direction of the other dipole. These projections would then still cancel (although to a lesser degree than in the collinear case). If the dipoles are at right angles to each other, then there is no electrical cancellation, and any between-condition changes do not arise from electrical cancellation stemming from changes within a single source.

¹⁸ This analysis does not take into account any distortions and/or non-linearity in the electrical cancellation due to spatially inhomogeneous electrical properties of scalp, skull, CSF, and brain tissue (Nuñez and Srinivasan, 2006).

have differed across-conditions because the masks were the same, so it is reasonable to assume that $LP_{CON} \approx LP_{EXP}$ and $\Delta LP \approx (H_{EXP} - H_{CON})$. Thus any between-condition Late Potential differences in the present study arising purely through electrical summation mainly do so because of a between-condition difference in the strength of the high-level source.

Most importantly, the direction of this difference must be the same whether a mask is present or not; that is, $\Delta LP_{\text{Experiment 2, Task 2}} = \Delta LP_{\text{Experiment 3, Task 2}}$. It is unlikely that the Late Potential differences observed here are related to high-level processing of the mask. The between-condition LP Task 2 differences observed in Experiment 2 unfold at an early point in the processing of the Experiment 2 masks (~100 ms post-mask onset), before mask-related signals can travel through the ventral visual pathway to reach high-level visual cortex to influence the behavior of high-level visual source(s) (in terms of polarity and/or magnitude changes). It might be possible that at some point in visual processing low-frequency mask-related information could be projected rapidly from early visual areas directly to the orbitofrontal cortex (OFC) and then back-projected to temporal cortex, carrying signals related to the most likely interpretation of the input image to be integrated with the bottom-up analysis (Bar, 2003; Bar et al., 2006). Nonetheless, since the masks were the same across EXP and CON conditions, the influence of any mask-related “expectation signals” upon high-level visual processing should not differ between conditions and thus should be subtracted out when calculating $\Delta LP_{\text{Experiment 2, Task 2}}$. Furthermore, the evidence that does exist for such a prefrontal route (Bar et al., 2006) suggests that such information reaches the OFC ~ 130 ms post-stimulus

onset (Bar et al., 2006), and would require at least 50 ms more for these signals to propagate back down to temporal cortex. This is much too late to account for the LP differences observed here, which again emerge ~ 100 ms post-mask onset.

Therefore, if the between-condition LP differences are due to between-condition differences in electrical summation, then $\Delta LP_{\text{Experiment 2, Task 2}} = \Delta LP_{\text{Experiment 3, Task 2}}$. How does this compare to the data gathered in Experiments 2 and 3? In Experiment 2 Task 2, $LP_{\text{EXP}} < LP_{\text{CON}}$, so $\Delta LP > 0$. In Experiment 3 Task 2, $|LP_{\text{EXP}}| < |LP_{\text{CON}}|$, but $LP_{\text{EXP}} > LP_{\text{CON}}$, so $\Delta LP < 0$; that is, the CON – EXP difference is now in the opposite direction as in Experiment 2. This contradicts the prediction of the electrical summation hypothesis, and thus renders it unlikely (within the validity of the present approximations) that the observed Task 2 between-condition differences arise *purely* from between-condition differences in the electrical cancellation of sources. Such differences must be present, of course, because the bioelectric activity of the high-level sources should be reduced under conditions of greater mutual inhibition (as discussed in Section 6.5.2.1). What the above argument suggests is that these differences are obscured by the much greater and oppositely directed between-condition changes that arise from the modulatory interaction between the high- to low-level LP sources.

Hence the general description of the Late Potential observed in this study is that of an ERP response arising out of the interaction between the processing of the silhouettes and the masks, and thus represents a combination of neural sources that interact to change their activity levels according to the degree of mutual inhibition present coupled with task set. How does this interpretation compare to previous interpretations of Late

Potentials observed in response to visual stimuli? The relationship is not clear. There have been several distinguishable positive ERP responses that have occurred in the general time frame (~ 230 – 400 ms) of the Late Potentials observed here, the most well-known of which is the P300 complex that occurs to oddball stimuli (Dien et al., 2004). The P300 tends to have a more parietal distribution than the LP observed in the present study, although there is some topographical overlap between the two responses. The scalp topographies of the present LP responses are more similar to that of a closure-related late ERP reported by Doniger et al. (2000; 2002). That study observed a positive potential emerging ~230 ms post-stimulus that remained positive over succeeding time points during unsuccessful recognition of a fragmented object, but that turned negative (reaching a minimum at ~293 ms) during the successful closure and subsequent recognition of fragmented objects. The present LP responses are also similar to a late positive responses observed by Latinus and Taylor (2005) over parieto-occipital sites in response to Mooney faces, fragmented black and white shapes that are seen as faces upon successful visual closure. The commonalities in scalp topography of these responses suggest that the present LP and these other Late Potentials may originate in partially overlapping neural processes. Further elucidation of this relationship, if any, would be a useful direction for future research.

6.5.4 Summary of the Neural Evidence for Mutual Inhibition

In summary, the EA|CI model suggests that the strongest neural evidence for mutual inhibition comes from observation of the Late Potential during Task 1, which is

reduced during processing of the EXP stimuli relative to the CON stimuli. The model suggests that the reduction in LP response arises from the greater inhibition of high-level visual cortical regions devoted to processing the cues to past experience present within the EXP stimuli. This effect of this inhibition is most apparent in the changes in low-level visual cortical activity modulated by the activity at high-levels, as when silhouette stimuli are followed by a mask (Experiments 2 and 3 Task 1). This decrease in high-level cortical activity can also be seen when a mask is not present (Experiment 3 Task 2), but the interpretation of the Task 2 LP is not clear (see Section 6.5.3).

The earlier ERP components (P1, N170) did not show any unambiguous signs of increased mutual inhibition. The greater P1 response to EXP than CON stimuli in Task 1 Experiment 3 suggests that inhibition of object memories is not strongly engaged early in processing, although such inhibition can be equalized for this component by top-down influences (Experiment 3 Task 2). The N170 observations show that whatever mutual inhibition may have been engaged for this component for EXP stimuli in Task 1, it is reduced or eliminated by top-down influences of task set during Task 2. Furthermore, all these effects can be explained either in terms of reductions or increases in neural activity due to fluctuations in mutual inhibition or the former coupled with the long-range interaction of coactive neural sources.

6.6 Future Directions

The EA|CI model well explains the behavioral and electrophysiological data reported here but this explanation is, in part, post-hoc. The data themselves are not questionable; the results presented in this dissertation have been highly reliable and replicable across several experiments and levels of methodological rigor. But more work is needed to fully confirm or disconfirm the predictions of the model discussed throughout Section 6.5.

6.6.1 Behavioral Directions

So far Task 1 has only been fully studied with use of a mask. How would the behavior change if silhouettes in Task 1 were not masked? Among Non-Seer participants, would RTs continue to be shorter for EXP than CON stimuli classified as novel? Removal of the mask would certainly increase the number of participants who are Seers, and some pilot work exists in support of this claim (Trujillo, in progress). Increasing the number of Seers, however, would allow a proper analysis of this experimental group. Would Seers elicit the same pattern of behavioral responses as Non Seers? Many Seers reported that they did not begin to perceive the objects depicted within the unbounded regions of the EXP stimuli until the middle of Task 1. Would early Task 1 trials show behavioral evidence of mutual inhibition that would change in later trials?

6.6.2 Electrophysiological Directions

As with the behavior, the Task 1 electrophysiology has also not been studied without use of a mask. How would the polarity, amplitude, and topography of the Late Potential change for Non Seers when silhouettes are not followed by masks compared to when they are (the present experiments). One prediction from the EA|CI model would be that the basic topography of negative potentials observed in Task 2 without a mask will also be present in Task 1 without a mask, with CON LP responses more negative than EXP LPs because the latter are more greatly inhibited. Detailed dipole and current source density source localization analyses applied to this data, in conjunction with source analyses on the data presented here could help to clarify this prediction, plus the several conclusions made throughout Section 6.5.3 regarding which possible origin(s) of ERP change applies to the ERP components measured in this study (Section 6.5.2). Finally, recall that in Section 6.5.3.3 the question was raised regarding whether the Task 2 LP differences reflect differences in mutual inhibition (arising if first-perceived figure-ground organization is of the central silhouette region that is then reversed to the outer regions), or differences in the length of processing devoted to the EXP and CON silhouettes (participants might work longer to perceive the unbounded regions of the CON stimuli as familiar). This question could be addressed by modifying Task 2 to include reports of first-perceived figure-ground organization and then calculating EXP and CON ERPs only for trials during which first-perceived figures were the outer regions of the silhouettes.

The EEG analyses could also be informed by adapting the basic task paradigm for use with functional magnetic resonance imaging (fMRI); indeed a preliminary experiment of this sort is currently in progress (Trujillo, Peterson, and Ryan, in progress). fMRI can measure the hemodynamic signature of neural activation with precise spatial resolution of cortical and sub-cortical sources. Such spatial precision can be used to check and improve the results of the EEG source analyses, as well as provide further information regarding the general relationship between the generators of EEG and fMRI signals in the cortex, and the more specific relationship under conditions of mutual inhibition. This enterprise would be best served through use of new technology that allows simultaneous measurement of EEG and fMRI because the current task paradigm is not as effective beyond one session of experiment participation, and thus does not allow for task repetition across imaging modalities. Participants learn to see the objects depicted by the EXP silhouettes during the course of the experiment, either as Seers in Task 1, or as a prelude to Task 2. Thus the current task paradigm does not allow for the acquisition of fMRI and EEG signals from a single subject. Simultaneous measurement of EEG and fMRI would solve this problem, because the need for task repetition across imaging modalities would be eliminated.

It is not clear, however, if the specific predictions the EA|CI model makes for EEG would apply to the fMRI case because these methods rely upon different biophysical principles and index different physiological processes. For example, while it was argued in Section 6.5.2.1 that mutual inhibition should lead to a decreased ERP response, it could be argued that such inhibition should lead to an increased fMRI

response. This is because the latter indexes blood-oxygen increases as the result of increased neural activity and the inhibitory neurons mediating the inhibition require oxygen just like the excitatory cells. An increase in inhibition should increase inhibitory cell activity to subsequently increase blood-oxygen uptake and supply, and therefore the related fMRI signal. What is unknown is whether the decrease in oxygen requirement from inhibited excitatory cell populations would serve to produce a change in fMRI signal given the oxygen requirement increase for the inhibitory cells. More theoretical work is needed to resolve this issue.

6.6.3 Computational Directions

Computational investigation of the EA|CI model would involve the creation of biologically-plausible models of figure-ground segregation that describe configural cue competition and mutual inhibition through neural networks that explicitly simulate excitatory and inhibitory synaptic potentials. There have been several neural network models of figure-ground competition proposed in the literature (e.g. Kienker et al., 1987; Vecera and O'Reilly, 1998; 2000; Roelfsema et al., 2002; see Section 1.2). Some of these models implement a role for past experience cues, some do not. Some models are more biologically plausible, some make no attempt to relate to neurobiology. These models do share a common principle that figure assignment is instantiated through some form of competition and inhibition. Nonetheless, to present knowledge no one has yet proposed a formal network model that accounts for past experience effects on figure assignment in a biologically plausible way. The development of a formal neural network treatment of the

PIMOCA model (Section 1.2) would be the first step towards computationally testing the plausibility of the EA|CI model proposed here.

Once a biologically plausible neural network description of the PIMOCA model is achieved, then the next step would be to extend the network to encompass shape familiarity judgments via evidence-accumulation based on the output of the PIMOCA network. This would then allow investigation to see if the behavioral results obtained in the present study could be reproduced by such a network. Importantly, the competition-induced synaptic potential changes of these networks could then be assessed for concordance with the EA|CI model. Such investigations could be supplemented by biophysically realistic simulations of synaptic potential summation in localized cortical sources under competition-induced changes in excitation and inhibition. These studies can then be used to extrapolate to ERP changes measured non-invasively from the scalp.

6.7 Conclusion

In conclusion, this dissertation has presented brain-based evidence for access to object memories during figure-ground segregation and shape perception. Early (P1) and late (Late Potential) ERP responses were differentially sensitive to silhouette stimuli containing cues to past experience even though those cues were perceived unconsciously (due to masked exposures). This ERP evidence is consistent with a competitive model of figure assignment in which configural cues compete for dominance across an edge to promote one side of the edge to be seen as figure. The neural evidence is also accompanied by behavioral evidence consistent with the competitive model,

assuming that shape decisions are based upon accumulation of evidence arising from the outputs of figure-ground processing. Furthermore, the present experiments have also provided evidence that a temporally-intermediate ERP response (the N170) is sensitive to the differences between conscious and unconscious perception of familiar shape. This ERP component may reflect activity of a neural correlate of consciousness.

Future experiments should attempt to replicate and extend these findings by examining the behavioral and ERP responses of participants (Seers) who become aware on their own of the cues to past experience present in the experimental stimuli. In addition, advanced EEG source localization and fMRI methods should be used to attempt to localize the neural sources underlying the ERP responses. Such localization efforts may be used to determine if the present ERP differences arise through inhibition-induced differences in neural feedback from high-level visual brain regions encoding object shape to low-level regions representing basic edge and surface properties. Finally, computational efforts should be orientated towards implementing a model of evidence accumulation modulated by competitive inhibition (EA|CI) in a biologically plausible manner. In turn, these models may be used to constrain biophysical models of the electrical properties of neural networks to see if such competitive inhibition would give rise to the ERP differences observed in the present study. Such efforts, in conjunction with the present study, will further current understanding of the role of past experience in figure assignment, as well as the neural and cognitive bases of conscious shape perception.

7. APPENDICES

7.1 Appendix A: Objects Portrayed within the Unbounded Regions of EXP Silhouettes.

Set A		Set B	
axe	hand	anchor	jet
butterfly	lamp	bunny	leaf
bell	pig	duck	Mickey Mouse
bone	palm	elephant	owl
boot	rhino	faucet	pineapple
bulb*	sprayer	flower	pine tree*
coffee pot	train	foot	seahorse
dog	umbrella**	guitar	snowman
eagle	woman	horn	teddy bear
face	wrench	house**	watercan
grapes		hydrant	

* - indicates stimuli used in Experiment 2 that were not included as part of the matched stimulus set of Experiment 3.

** - Umbrella and house EXP stimuli were switched to the opposite subset for Experiment 3 (umbrella: A → B; house: B → A) in order to improve the match in stimulus property values between subsets.

7.2 Appendix B: Objects Portrayed within the Bounded Regions of FAM Silhouettes.

apple		ram
bat	frog	scissors*
balloon (hot air)**	giraffe*	screw
birthday cake	goldfish	skull**
boat	graduating student**	spade
bottle	heart	spider
bug	ice cream cone	spoon*
bumblebee	jellyfish	star
cactus	key*	steer
castle	kite*	strawberry
cat	lion	syringe*
clover	lizard	telephone
crab*	lobster	tent
crown	missile**	tshirt**
dragonfly	octopus*	turtle
Eiffel tower*	penguin	wheel**
flame	race car	

* - indicates stimuli used in Experiment 2 that were not included as part of the matched stimulus set of Experiment 3.

** indicates stimuli used in Experiment 3 that were not included as part of the matched stimulus set of Experiment 2.

7.3 Appendix C: Post-Experimental Questionnaire- Experiments 1 and 2

7.3.1 Task 1 – Stimulus Sets A and B

1) What did you think the experiment was about? Did you have any thoughts or general impressions about the experiment while you were doing it?

2) Did you ever notice anything familiar in the black surrounds of the white silhouettes while they were on the screen?

If yes, describe all familiar objects you can remember seeing and when you first started seeing them.

7.3.2 Task 2 – Stimulus Sets A and B

1) At what point during Part2 did you feel that you reached a limit on the number of objects you could see in the black surrounding area of the silhouettes (i.e. at what point did you stop seeing new objects in the surrounds)? During the 1st three blocks, 2nd three blocks, 3rd three blocks, 4th three blocks, 1st half, 2nd half?

2) Did you have any strategy to try to see the objects in the surround?

3) Did it become easier to see objects in the surround as Part2 progressed in time?

4) Please list all the familiar objects you can remember seeing in the black surrounds of the stimuli during Part 2 of this experiment. During which blocks did you first see them (1st two blocks, 2nd two blocks, 3rd two blocks, 4th two blocks, 1st half, 2nd half)?

If yes, describe all familiar objects you can remember seeing and when you first started seeing them.

7.3.3 Stimulus Set A Item Recognition List – Task 1 and 2

Bell	Watch
Paintbrush	Pear
Axe	Eagle
Woman	Boot
Doorknob	Lamp
Fox	Kettle
Umbrella	Rain drop
Raccoon	Clothes-hanger
Carrot	Palm
Bone	Face
Hippo	Grapes
Butterfly	Hammer
Wrench	Hand
Tire	Rhino
Pants	Coffee pot
Walrus	Bowling pin
Spray bottle	Sea lion
Plate	Dog
Bulb	Chair
Pig	Snake
Train	

7.3.4 Stimulus Set B Item Recognition List – Task 1 and 2

Water-can	Pineapple
Anchor	Chair
Gorilla	Mickey Mouse
Television	Guitar
Bunny	Horn
Teddy-bear	Stapler
Crayon	Owl
Duck	Leaf
Car	Kangaroo
Snowman	Hydrant
Knife	Rat
Baby	Pine tree
Elephant	Hourglass
Cup	House
Seahorse	Jet
Tie	Diamond ring
Basket	Chopsticks
Faucet	Foot
Trashcan	Pillow
Tooth	Bike
Flower	

7.4 Appendix D: Post-Experimental Questionnaire- Experiment 3

7.4.1 Tasks 1 and 2 - Stimulus Sets A and B

The post-experimental questions for Experiment 3 were the same as for Experiments 1 and 2 (see Sections 7.2.1 and 7.2.2).

7.4.2 Stimulus Set A Item Recognition List – Task 1 and 2

Bell		Clothes-hanger
Paintbrush	Pants	Palm
Axe	Walrus	Face
Woman	Hydrant	Grapes
Doorknob	Plate	Hammer
Fox	Pig	Hand
House	Train	Rhino
Raccoon	Watch	Coffee pot
Carrot	Pear	Bowling pin
Bone	Eagle	Sea lion
Hippo	Boot	Dog
Butterfly	Lamp	Chair
Wrench	Kettle	Snake
Tire	Rain drop	

7.4.3 Stimulus Set B Item Recognition List – Task 1 and 2

Water-can	Flower
Anchor	Pineapple
Gorilla	Chair
Television	Mickey Mouse
Bunny	Guitar
Teddy-bear	Horn
Crayon	Stapler
Duck	Owl
Car	Leaf
Snowman	Kangaroo
Knife	Spray Bottle
Baby	Rat
Elephant	Umbrella
Cup	Hourglass
Seahorse	Bulb
Tie	Jet
Basket	Diamond ring
Faucet	Chopsticks
Trashcan	Foot
Tooth	Bike

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