Neurophysiological evidence for the influence of past experience on figure–ground perception

Logan T. Trujillo
Department of Psychology, The University of Texas at Austin, Austin, TX, USA

John J. B. Allen
Department of Psychology, University of Arizona, Tucson, AZ, USA

David M. Schnyer
Department of Psychology and Institute for Neuroscience, The University of Texas at Austin, Austin, TX, USA

Mary A. Peterson
Department of Psychology, University of Arizona, Tucson, AZ, USA

A fundamental aspect of perceptual organization entails segregating visual input into shaped figures presented against shapeless backgrounds; an outcome termed “figure–ground perception” or “shape assignment.” The present study examined how early in processing past experience exerts an influence on shape assignment. Event-related potential (ERP) measures of brain activity were recorded while observers viewed silhouettes of novel objects that differed in whether or not a familiar shape was suggested on the outside—the groundside—of their bounding edges (experimental versus control silhouettes, respectively). Observers perceived both types of silhouettes as novel shapes and were unaware of the familiar shape suggested on the groundside of experimental silhouettes. Nevertheless, we expected that the familiar shape would be implicitly identified early in processing and would compete for figural status with the novel shape on the inside. Early (106–156 ms) ERPs were larger for experimental silhouettes than for control silhouettes lacking familiarity cues. The early ERP difference occurred during a time interval within which edge-segmentation-dependent response differences have been observed in previous neurophysiological investigations of figure–ground perception. These results provide the first neurophysiological evidence for an influence of past experience during the earliest stages of shape assignment.

Keywords: perceptual organization, evoked potentials, electrophysiology, shape and contour, visual cognition


Introduction

The visual world we experience consists of a rich and varied collection of shapes. Visual shapes typically appear as distinct figures whereas regions of the visual field adjacent to the bounding edges of figures appear to be locally shapeless and to continue behind the figure as backgrounds (Rubin, 1915/1958). Furthermore, bounding contours are typically perceived to be “owned by,” or “assigned to,” the region that is seen as a shaped figure. Thus the perception of shape necessarily implies the perception of depth, two perceptual attributes that together compose figure–ground perception. The primary focus of this paper is the shape perception component of figure–ground perception, henceforth referred to as “shape assignment.”

Contemporary theorists assume that shape assignment results from inhibitory cross-edge competition between either contour or surface region representations encoding opposite sides of an edge (Craft, Schütze, Niebur, & von der Heydt, 2007). The side of an edge that wins the competition is seen as a shaped figure while the side that loses the competition is seen as an unshaped ground. Contour-based cross-edge competition is thought to occur between low-level representations encoding the ownership of an edge by the regions on either side (Craft et al., 2007; Qiu, Sugihara, & von der Heydt, 2007; von der Heydt, Zhou, & Friedman, 2003; Zhou, Friedman, & von der Heydt, 2000). Surface- or region-based competition is thought to occur between higher level representations of regional shape properties on opposite sides of an edge (Peterson, 2003; Peterson, de Gelder, Rapcsak, Gerhardtstein, & Bachoud-Levi, 2000; Peterson & Skow, 2008; Peterson & Skow-Grant, 2003; Vecera & O’Reilly, 1998). The most well-known region-based properties are the standard Gestalt configural cues (Peterson et al., 2000; Peterson & Skow, 2008), including relative area (the relative sizes of different visual regions), 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). Attention can also bias competition between two sides of an edge in a manner that can influence contour ownership (Kienker, Sejnowski, Hinton, & Schumacher, 1986; Qiu et al., 2007).

This paper considers another competing influence on shape assignment—past experience with the shape of a contour-bounded region; that is, the familiarity or meaningfulness of a contour-bounded region in terms of resemblance to previously encountered shapes and objects. Importantly, regions on either side of an edge have different shapes when seen as figure, implying that the familiarity of a bounding contour is relative to the side to which it may be assigned. Originally controversial, the idea that past experience can compete with other cues to influence figure–ground perception has found much empirical support. For example, the probability that one of two neighboring regions of visual space is seen as the shaped figure as opposed to the unshaped ground increases when that region portrays a familiar object (Peterson & Gibson, 1994a; Peterson, Harvey, & Weidenbacher, 1991). Furthermore, response times (RTs) to match novel figures are longer when previously seen shapes are suggested along the outside (groundside) of their borders (Peterson & Enns, 2005; Peterson & Lampignano, 2003). Two additional RT studies (Peterson & Kim, 2001; Peterson & Skow, 2008) found that observers were slower to respond to a familiar shape similar to one that had been suggested on the grounds of a previously shown figure than to a control shape, as predicted within a competitive framework. Importantly, most of the above findings were obtained even though participants were unaware of the familiar shapes they would have perceived had the groundside won the cross-edge competition.

The above-cited evidence suggests that the familiarity of contour shape, established through past experience, is one of the factors entering into the competition for figural status. The stage of processing at which past experience influences shape assignment is unknown. Investigators have long debated whether past experience exerts an influence at low or high levels of visual analysis occurring early or late in the course of processing (e.g., Baylis & Driver, 2001; Driver & Baylis, 1995; Palmer, 1999; Peterson & Gibson, 1994a; Vecera & O’Reilly, 1998). Most previous studies based their conclusions in favor of early versus late influences on response latency data and/or figure–ground reports, indirect measures of processing order and latency. To our knowledge, there is one single-unit recording study in primates investigating this issue (Baylis & Driver, 2001), which found anterior inferotemporal (IT) activity, at least at the level of cytoarchitectonic region TE, to reflect a stage of processing beyond the level at which shape assignments occur. The study found individual TE cell responses to be highly consistent across contrast and mirror reversals of asymmetric black and white silhouettes, but not for figure–ground reversals across silhouette contours. This suggests that these IT neurons were not sensitive to the contour alone, but to the shape of the contour relative to the adjacent figure region to which it is bound, that is after shape assignment has occurred. This observation sets an upper bound on the level of the visual hierarchy at which past experience effects may operate; anterior IT cortex, being sensitive to complex and abstract shapes over large receptive field sizes (Desimone, Schein, Moran, & Ungerleider, 1985; Logothetis, Pauls, & Poggio, 1995; Tanaka, 1996), is placed at the highest levels of the visual hierarchy.

The above observation also poses a puzzle in that if the past experience effect implies a degree of access to pre-existing representations, then such access must occur at a level below the level where whole shapes and objects are encoded. One suggestion is that only partial configurations, rather than whole objects, need to be accessed for a significant influence on shape assignment to take place, with such partial object representations coded in posterior cortical regions such as V4 or the TEO region of posterior IT (Peterson, 2003). Although object recognition studies have reported very early (50–100 MS) human ERP and MEG responses to be sensitive to faces and to illusory contour stimuli (George, Jemel, Fiori, & Renault, 1997; Linkenaer-Hansen et al., 1998; Murray, Imber, Javitt, & Foxe, 2006; Murray et al., 2002; Seeck et al., 1997; Thierry, Martin, Downing, & Pegna, 2007), to our knowledge, no study has examined the relationship between past experience and shape assignment at earlier stages of the visual hierarchy.

The experiments reported in this paper use a high-temporal-resolution neurophysiological technique—event-related potentials (ERPs)—to investigate whether past experience influences early stages of shape assignment. Prior neurophysiological investigations of figure–ground segregation have identified an early period of processing, one of two critical processing stages in the segregation of simple figures from grounds. The first stage is held to entail edge segmentation, contour formation, and boundary ownership, all initial steps in shape assignment. The second stage is held to entail global figure–ground segregation. Evidence for these stages originally came from primate single-cell studies investigating figure–ground segregation by studying contour ownership or surface segregation. The first class of studies (Craft et al., 2007; Qiu et al., 2007; von der Heydt et al., 2003; Zhou et al., 2000) has found cells in V1, V2, and V4 to be modulated by whether contours are owned by, or assigned to, the particular adjacent region ultimately seen as figure. The onset of this modulation has been observed to occur as early as 25 ms (Zhou et al., 2000). The second class of studies (Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999; Supér, Spekreijse, & Lamme, 2001; Zipser, Lamme, & Schiller, 1996) found V1 neurons to give a strong response to an edge between two adjacent regions approximately 80–125 ms post-stimulus onset. Approximately 25–35 ms later, these neurons gave a stronger
response when their receptive fields contained a figure rather than a background. It is believed that these figure–ground-related effects reflect the influence of feedback signals from higher cortical levels, as they are abolished under anesthesia (Lamme, Zipser, & Spekreijse, 1998). This conclusion is consistent with human electrophysiological and fMRI evidence suggesting that feedback from high- to low-level cortical areas plays a role in the selection of the figure region to be further processed in lateral occipital cortex (Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006; Scholte, Jolij, Fahrenfort, & Lamme, 2008).

Further evidence for an early and a late processing stage was provided by Heinen, Jolij, and Lamme (2005) whose human participants discriminated between two kinds of texture-defined stimuli: “frame” stimuli, which portrayed a frame through which a background was visible, and “stack” stimuli portraying three stacked surfaces. Heinen, et al. found that discrimination performance was impaired when transcranial magnetic stimulation (TMS) was applied to early visual cortex during two time periods: 130–160 ms post-stimulus and 250–280 ms after stimulus onset, but not when it was applied during other time periods. They argued that TMS likely disrupted edge segregation in the early time frame and figure–ground segregation in the later time frame. Disrupting either of these processes would impair perceptual discrimination.

Additional evidence that an early stage of processing is critical for figure–ground perception comes from ERP experiments that used a subtraction technique to isolate responses associated with the perception of a textured figure on a larger textured field from those associated with an empty textured field alone (Bach & Meigen, 1990, 1992, 1997; Caputo & Casco, 1999; Lamme, van Dijk, & Spekreijse, 1992, 1993). In these studies, early ERP differences emerged at approximately 100 ms and peaked approximately 140–160 ms after stimulus onset (Caputo & Casco, 1999; Caputo, Romani, Callieco, Gasperi, & Cosi, 1999; Lamme et al., 1992). Caputo and Casco (1999) found that the early differential ERP responses for figures versus undifferentiated texture fields were insensitive to stimulus manipulations that enhanced figure–ground discrimination. Therefore, they attributed their early differences to initial edge segmentation (a similar estimate of the temporal course of edge or contour perception comes from the illusory contour literature, e.g., Murray et al., 2006, 2002. See Discussion section for more details).

Caputo and Casco (1999) also observed a second negative deflection of the ERP difference wave that peaked approximately 200–260 ms post-stimulus onset. The latency of this later differential response was shorter when figure–ground segmentation was enhanced after figural line elements were aligned parallel to, rather than perpendicular to, the orientation of the segregation edge, a stimulus manipulation that results in enhanced figure–ground perception. Accordingly, they interpreted the later response as related to the goodness of global figure–ground segmentation. Further support that figure–ground distinctions per se are evident in a later time frame was reported by Scholte, Witteveen, Spekreijse, and Lamme (2006), who observed differential magnetoencephalographic (MEG) responses between checkerboard and homogenous texture stimuli at approximately 193–240 ms post-stimulus onset.

Although these previous neurophysiological experiments have provided much information regarding the processing stages of figure–ground perception, none of them can shed light on the issue of when past experience influences shape assignment, as none included manipulations of familiarity. The present study compared neural responses to stimuli that differed in terms of whether or not past experience entered into the competition for figural status, but did not differ in terms of the type of figure perceived as a result of the competition. Specifically, ERPs were recorded while human observers categorized three types of silhouette figures as depicting novel versus familiar shapes (Figure 1A). For all silhouette types, the Gestalt configural cues of small area, symmetry, and enclosure favored the interpretation that the figure lay on the inside of the silhouette. Half the silhouettes depicted familiar objects (i.e., well-known animals and objects, samples are shown in Figure 1A, top row). Familiar objects were included so that subjects had to make a decision when viewing the silhouettes. ERP responses to familiar silhouettes are not of theoretical interest (see below for further explanation). The other half of the silhouettes portrayed novel objects; these were the critical silhouettes (Figure 1A, middle and bottom rows). The novel silhouettes were divided into two types: experimental and control novel silhouettes. For experimental silhouettes (Figure 1A, middle row), a portion of a familiar object was suggested on the unbounded (outside) side of the silhouette’s edge; hence, the shape property of familiar configuration was placed in competition with the properties favoring the interpretation that the bounded silhouette was the figure. In contrast, control silhouettes (Figure 1A, bottom row) suggested novel objects along the outside as well as the inside of their bounding edges and thus were expected to produce less cross-edge competition than the experimental stimuli. Experimental and control novel shapes were equated for a variety of low-level and high-level stimulus attributes (Peterson & Gibson, 1994a; Peterson & Kim, 2001; see also Appendix A), save the presence or absence of a familiar configuration on the outside of their bounding contour.

Despite the familiar configuration suggested on the outside of the experimental stimuli, observers were expected to perceive the bounded insides of both experimental and control silhouettes as novel figures because the preponderance of shape properties supported that interpretation. (Results conformed with these expectations; see below. Note that unlike the readers of this paper, experimental participants were naive as to the manipulations that distinguished between experimental
and control silhouettes.) In addition, the silhouettes were presented in brief masked exposures (see Procedure section) in order to prevent eye movements that would change the balance of cues, perhaps resulting in the conscious perception of the familiar shapes along the outsides of the experimental silhouettes. It was important for participants to not see the shapes on the outside of experimental silhouettes so as to avoid confounding any effects of past experience with effects related to conscious recognition of the familiar shapes. Nevertheless, it was hypothesized that the shape memories corresponding to these familiar configurations would be accessed during stimulus processing as the shape properties on both sides of the silhouette edges were analyzed. It was predicted that neurophysiological changes associated with shape memory access and/or the consequences of such access (i.e., competition) would be observed in differences between the ERPs recorded for experimental and control silhouettes.

The central question is when in the course of processing would differences between experimental and control silhouettes be observed? Would differential processing be evident early in processing, or only later? The search for these ERP changes took place primarily within the two time periods identified by previous research as critical to figure–ground segregation (as well as in a later period during which we observed qualitative differences in our data), but it was not certain whether such past-experience-dependent differences would be observed early or late in processing. A straightforward hypothesis might predict that if past experience plays a role in the outcome of shape assignment—that is, in the construction of a visual figure—then experimental vs. control ERP differences should emerge early in time before this outcome takes place. Nevertheless, it is also possible that the different silhouette types, which were expected to both be perceived as novel shapes, might also produce differential responses in the second processing period previously interpreted to reflect global figure–ground segmentation. Moreover, we did not predict a direction for experimental versus control ERP differences during either processing stage, as the stimuli compared in our study—stimuli differing in the amount of cross-edge competition induced by the presence versus absence of a familiar configuration competing with the small, closed, symmetric novel configuration—were very different from those compared in the previous ERP and MEG research—stimuli in which a simple figure was present or not against a uniform textured field. Since the hypotheses regarding the direction and the time course of the ERP differences were non-directional, the initial exploratory experiment (Experiment 1) was followed by a confirmatory experiment (Experiment 2) that gauged the repeatability of effects observed in Experiment 1.

Methods

Participants

**Experiment 1**

Thirty-nine students were recruited from the University of Arizona undergraduate subject pool; the data from 5 participants were removed due to technical difficulties with their EEG recordings (N = 4) or near-chance task performance on the categorization task (N = 1). The data from an additional 11 subjects were not analyzed because they reported seeing familiar shapes in the outsides of the silhouettes (see Post-experiment questioning section). Thus the data from 23 participants (18 females;
all right-handed; mean age = 20.70 ± 1.24 years) who were classified as not perceiving the familiar configuration suggested on the outside of the experimental silhouettes were retained in the Experiment 1 analysis. All participants were screened to ensure normal visual acuity and were fully informed of the experimental methods and proceedings before they consented to participate. This study was approved by the Institutional Review Board for Human Studies at the University of Arizona.

**Experiment 2**

Thirty-six students were recruited from the University of Texas at Austin undergraduate subject pool; the data from 3 participants were removed due to EEG recording technical difficulties. The data from an additional 7 participants were not analyzed because they reported seeing familiar shapes in the outside of the silhouettes (see *Post-experiment questioning* section). Thus the data from 26 participants who were classified as not perceiving the familiar configuration suggested on the outside of the experimental silhouettes were retained in the Experiment 2 analysis (19 females; 22 right-handed; mean age = 18.46 ± 0.36 years). All participants were screened to ensure normal visual acuity and were fully informed of the experimental methods and proceedings before they consented to participate. This study was approved by the Institutional Review Board for Human Studies at the University of Texas at Austin.

**Stimuli**

**Experiments 1 and 2**

There were 80 small, mirror symmetric, enclosed white silhouettes (H: 4.7°; W: 1.8°–9.4°) depicting on the inside of their bounding contour shapes not previously encountered by the participants. These novel silhouettes were divided into 40 experimental silhouettes (samples in Figure 1A, middle row) whose vertical edges suggested a portion of a familiar (nameable) object along the outside (see *Appendix B* for a list of objects depicted by the outside of the experimental silhouettes) and 40 control silhouettes (samples in Figure 1A, bottom row) whose vertical edges suggested a novel shape along the outside as well as the inside of the bounding edge. Experimental and control silhouettes were equated on low-level features (luminance, spatial frequency, contour length, and stimulus size; see *Appendix A*) plus properties known to affect figure–ground perception (enclosure, symmetry, convexity, area; Peterson & Gibson, 1994a; Peterson & Kim, 2001) to eliminate stimulus differences that might differentially affect ERP responses between conditions. Experimental and control silhouettes were each divided into two 20 silhouette subsets (Sets A and B; see *Appendix B*), with presentation balanced across subjects. Approximately equal numbers of animate and inanimate objects were portrayed on the outsides of the experimental stimuli in the two subsets. All stimuli were created in Adobe Photoshop (Adobe Systems, San Jose, CA; [www.adobe.com](http://www.adobe.com)).

An additional 40 white silhouettes (H: 4.7°; W: 1.8°–9.4°) were created from photos and artwork. On the insides of their closed boundaries these familiar silhouettes depicted nameable, animate and inanimate objects, animals, plants, and symbols previously encountered by participants outside the laboratory (samples in Figure 1A, top row; see *Appendix B* for a list of objects depicted by the familiar silhouettes). The familiar silhouettes were included for the subjects’ task, which was to categorize each silhouette, shown individually, as a novel or a familiar shape as quickly and as accurately as possible. This cover task served two functions. First, it ensured that the bounded silhouettes engaged the participants’ attention. Second, it allowed us to assay whether participants perceived both experimental and control silhouettes as “novel,” as expected if the insides of both types of silhouettes won the competition for figural status. An important aspect of our design was that ERP responses to the two critical types of novel silhouettes would be assessed under conditions where they received the same classification response, thus ensuring that any observed ERP differences were not due to differences in stimulus categorization. The primary comparisons of interest in this paper involve comparisons between experimental and control novel silhouettes because those two types of stimuli were carefully matched for stimulus features, and because they received the same classification response. We did not compare ERPs for familiar and novel silhouettes because we expected they would be classified as members of different categories and thus might produce ERP responses reflective of differential categorization processes and not the influence of past experience per se. Furthermore, it was not possible to match the familiar and novel silhouettes in terms of stimulus characteristics (see *Appendix A*).

**Procedure**

**Experiments 1 and 2**

In each of 4 blocks of trials, subjects viewed 40 familiar silhouettes intermixed with 40 novel silhouettes (20 experimental and 20 control silhouettes). Silhouettes were presented one at a time for 175 ms (see Figure 1B) centered on a 20” CRT screen in Experiment 1 and a 20” LCD screen in Experiment 2 (60-Hz refresh rates for both experiments). Each stimulus was followed by a 250-ms mask. Five different white pattern masks (H: 4.7°; W: 9.4°) were used, with each mask following each silhouette equally often; the same masks were used in all conditions. Participants viewed the stimuli from a distance of 80 cm. For each silhouette, participants indicated their novel versus
familiar categorization response by pressing one of two buttons either held one in each hand (Experiment 1) or on a mouse pad held by both hands with a single response assigned to each hand (Experiment 2); left/right button assignment was balanced across subjects in both experiments. DMDX software (Forster & Forster, 2003) was used to record subjects’ categorization responses and time the stimulus presentations.

Before the experiment, participants underwent a block of 11 practice trials using familiar and control novel silhouettes not included in the experiment; they received feedback after incorrect responses on practice trials only. Between trials, a small cross appeared in the center of the screen on which participants were instructed to fixate their eyes; all silhouettes and masks were presented centered on fixation. Silhouettes were repeated across blocks, with the ordering of trials randomized for each block. Interstimulus intervals (ISIs) varied from 1452 ms to 3358 ms (SOAs ranged from 1627 to 3533). Participants had a 1500-ms time limit to respond to the stimuli.

Post-experiment questioning

We were only interested in analyzing data from participants who did not see the shapes on the outside of experimental silhouettes in order to avoid confounding any effects of past experience with effects related to conscious recognition of the familiar shapes. Therefore, after the experimental trials, participants were asked whether they saw any known shapes on the outsides of the silhouette edges; if they answered “yes,” they were asked to recall the shapes they had seen. To be certain they understood these questions, the experimenter showed them sample experimental silhouettes from the set they had not seen and pointed out the familiar shape suggested on the outside. During this questioning after Experiment 1, 11 participants (“Seers”) reported seeing familiar shapes in the outsides of the silhouettes, although they were unable to correctly recall more than a few of them (typically 2–3). The remaining 23 Experiment 1 participants (“Non-Seers”) neither responded “yes” to the initial question nor reported seeing familiar shapes on the outsides of the silhouettes when they were shown samples. Following Experiment 2, 7 participants were classified as Seers and 26 participants were classified as Non-Seers via the same procedure. Participants classified as Seers on the basis of these post-experiment questions were removed from further analysis for both experiments as there was no way to ascertain the number of trials during which they saw the familiar shapes on the outside, and therefore on how many trials their data might be expected to differ from those of the Non-Seers because they were aware of the familiar shapes on the outside of the experimental silhouettes.

To further assess the degree to which participants might have seen the familiar shapes in the grounds of the experimental silhouettes, all participants were asked to choose from a list of 40 objects they had seen on the outside of the silhouettes during the experiment. The list included the objects suggested on the outside of the experimental silhouettes and an equal number of matched foil objects not depicted by either the experimental or the familiar silhouettes (see Appendix B for a list foil objects). Recognition of the familiar shapes suggested on the outside of the experimental silhouettes was estimated via P(A), a non-parametric estimate of the proportion of the area under the receiver operating characteristic (ROC) curve for the case where only a single pair of hit and false alarm rates is available (McNicol, 1972). P(A) can range in value from 0 to 1. When the number of hits is equal to the number of false alarms, P(A) = 0.5; P(A) values above 0.5 indicate more hits than false alarms, while P(A) values below 0.5 indicate more false alarms than hits.

In Experiment 1, P(A) scores were 0.53 ± 0.05 for Seers and 0.53 ± 0.03 for Non-Seers, neither of which was significantly different from chance (assessed via one sample t-tests, ps > 0.25). Thus neither the Seers nor the Non-Seers of Experiment 1 chose the names of objects suggested on the outside of experimental silhouettes more often than those of foil objects not shown during the experiment. In Experiment 2, P(A) scores for the Non-Seers were 0.55 ± 0.04 and not different from chance (p > 0.17), while P(A) scores for Seers were 0.63 ± 0.05 and significantly different from chance (t(1, 6) = 2.74, p < 0.03, two-tailed). This P(A) finding indicating significantly greater hits vs. false alarms is consistent with the self-reports of Seers that they saw some of the shapes on the outsides of the silhouettes in Experiment 2, and thus supports the decision to remove the Seers from further analysis.

Behavioral data analysis

Experiments 1 and 2

The proportions of correct responses and the corresponding RTs were calculated for the shape categorization task. “Novel” responses were considered correct for both control and experimental novel silhouettes; “familiar” responses were considered correct for familiar silhouettes. Although the familiar stimuli were not of central interest in this study, we analyzed behavioral responses in order to ascertain that participants were satisfactorily performing the shape categorization task. Trials with reaction times ≥1500 ms or <200 ms were not included in the analysis. A total of 0.03% ± 0.02% and 1.1% ± 0.9% trials were rejected for this reason in Experiments 1 and 2, respectively. In addition, behavioral data analysis was restricted to trials free of EOG artifacts (see ERP data analysis section).

Statistical analyses of accuracy rates and RTs were carried out via two-way repeated measures ANOVAs with within-subjects factors of Block (1–4) and Silhouette Type. Two analyses were performed for each behavioral measure: (1) A comparison of “familiar” responses vs. “novel” responses (the latter were collapsed across
experimental and control trials). This analysis was performed in order to compare performance on the present task with other tasks in the object recognition literature requiring judgments of familiarity; and (2) a comparison of “novel” responses for experimental vs. control novel silhouettes. This was the central comparison of interest for the present study. The $p$-values of all within-subject tests involving more than two conditions were adjusted using the Greenhouse–Geisser correction for non-sphericity. For ease of interpretation, reports of all significant behavioral $F$-tests subject to Greenhouse–Geisser correction include uncorrected degrees of freedom, corrected $p$-values, and the Greenhouse–Geisser epsilon value $\epsilon$. All post-hoc comparisons were Bonferroni corrected.

### ERP data acquisition

**Experiment 1**

Sixty-four channels of scalp electroencephalographic (EEG) signals were recorded using sintered Ag/AgCl electrodes mounted in an electrode cap (Neuroscan, Compumedics, Charlotte, NC, USA; [www.neuroscan.com](http://www.neuroscan.com)) with 2 additional bipolar electrode pairs outside the cap to monitor vertical and horizontal eye movements. Cap recording sites included standard and extended 10–20 system locations (Figure 2A), recorded with respect to a linked-ear reference. Two pairs of Ag/AgCl bipolar recording leads were affixed to the outer canthi of both eyes and also to the superior and inferior orbit of the left eye. All channels were amplified with a gain of 2816 via a Neuroscan Synamps II amplifier system in DC mode at a sampling rate of 1000 Hz. Impedances were reduced below 5 kΩ.

**Experiment 2**

Sixty-nine channels of scalp EEG signals were recorded while subject performed the discrimination task, via active Ag/AgCl electrodes mounted in a BioSemi electrode cap (BioSemi Instrumentation, Amsterdam, The Netherlands; [www.biosemi.com](http://www.biosemi.com)). Recording sites in the cap included standard and extended 10–20 system locations (Figure 2B). Two additional electrodes were affixed to the inferior orbits of both eyes to monitor vertical electrooculographic (EOG) activity (e.g., eye movements and blinks); an additional electrode was also placed at the outer canthi of the left eye to monitor horizontal EOG. All channels were amplified by a Biosemi Active II amplifier system in 24-bit DC mode at an initial sampling rate of 2048 Hz (400-Hz bandwidth) decimated online to 256 Hz, with EEG signals recorded with respect to a common mode sense (CMS) active electrode placed between sites PO3 and POZ. As active electrodes make skin preparation redundant, electrode impedances were not measured; however, half-cell potentials of the electrode/gel/skin interface were kept between ±40 mV, following standard recommendations for the Active II system.

### ERP data analysis

**EEG pre-processing**

Continuous data were imported offline into MATLAB using the EEGLAB toolbox ([Delorme & Makeig, 2004](http://www.eeglab.org)) for the MATLAB computing software (The Math Works, Natick, MA, USA; [www.mathworks.com](http://www.mathworks.com)), where all subsequent analysis was performed via in-house scripts that utilized EEGLAB functions. Single 2000-ms EEG trials were extracted from the continuous record for correctly classified experimental and control trials; trials with RTs <200 ms or >1500 ms were also excluded from further analysis. These trials ranged from −750 ms to 1250 ms with respect to silhouette onset. Muscle and signal artifacts were removed from the raw EEG record by visual inspection. Experiment 2 trials were transformed to a linked mastoids reference for the purposes of artifact removal; Experiment 1 trials were left unchanged. Bad EEG channels were replaced using an EEGLAB-based spherical spline interpolation algorithm ([Perrin, Pernier, Bertrand, & Echallier, 1989, 1990](http://www.ncbi.nlm.nih.gov/pubmed)); [Perrin, Pernier, Bertrand, Giard, & Echallier, 1987; 1990](http://www.ncbi.nlm.nih.gov/pubmed); $m = 5$; 50 term expansion) applied to the remaining channels. No more than 2 channels (<3.2% of all channels) were interpolated for any given subject in Experiment 1 and no more than 5 channels (<7.3% of all channels) were interpolated for any given subject in Experiment 2. Next, Experiment 1 single trials were down-sampled to a 256-Hz sampling rate for comparability with Experiment 2 (between-condition differences in recording sampling rates was not intentional but due to differences in default recording parameters of the Neuroscan and BioSemi systems); no resampling was performed for Experiment 2 data. For both experiments, EEG data were then transformed to an FPZ reference (following [Bach & Meigen, 1992, 1997](http://www.ncbi.nlm.nih.gov/pubmed); [Lamme et al., 1992](http://www.ncbi.nlm.nih.gov/pubmed)), and then low-pass filtered (166-point FIR filter, 43-Hz half-amplitude cutoff, zero phase shift). Next, epochs were further truncated to the −200 to 600 ms range and

![Figure 2. Extended 10–20 scalp locations of EEG recording electrodes in (A) Experiment 1 and (B) Experiment 2. 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.](http://example.com/figure2.png)
baseline corrected to the −200 ms to 0 ms pre-stimulus interval.

EEG trials containing eye blinks and vertical/horizontal EOG activity were rejected from further analysis; additional horizontal and vertical EOG channels were computed offline for this purpose. The horizontal EOG channel was computed as the bipolar montage of the outer canthi EOG signals; the vertical EOG channel was computed from the bipolar montage of the superior and inferior orbit signals. EEG trials containing significant EOG activity > 50 µV or < −50 µV (after removal of the constant DC offset) were rejected from the analysis via an automatic algorithm written for MATLAB. For EEG trials used to estimate the early ERP components, EOG artifacts were rejected over the −200 to 300 ms interval. This choice maximized the number of retained trials, and thus signal-to-noise ratios of these small amplitude components. In addition, RTs for these trials entered into the behavioral analysis (see Behavioral data analysis section).

For EEG trials used to estimate the late stage of processing that included the masks, a larger signal-to-noise ratios of these small amplitude components. For EEG trials used to estimate the early ERP components, EOG artifacts were rejected due to excessive eye blink and/or saccadic EOG activity; for Experiment 2, averages of 0.1% ± 0.9% (short-rejection interval) and 18.9% ± 3.7% (long-rejection interval) Non-Seer EEG trials were rejected due to excessive eye blink and/or saccadic EOG activity; for Experiment 2, averages of 5.1% ± 0.9% (short-rejection interval) and 18.9% ± 3.7% (long-rejection interval) Non-Seer EEG trials were rejected for this reason. The efficacy of this rejection procedure was confirmed by examining the grand-average vertical and horizontal EOG potentials (computed after 43-Hz low-pass filtering; see above) in the −200 to 200−600 ms interval, which did not vary more than |±3 µV| to |±5 µV| in any condition for Experiment 1, and |±3 |V| to |±4 µV| in any condition for Experiment 2. As 0.1° of eye movement corresponds to approximately 1.6 µV EOG deviation (Lins, Picton, Berg, & Scherg, 1993), it was concluded that Experiment 1 and Experiment 2 participants produced residual average eye movements of less than 0.19° to 0.33°. Thus for both experiments, the residual eye movements were well below the center to horizontal edge distance (0.9°–4.7°) of the silhouettes.

Stimulus-locked ERPs were computed by averaging trials separately for the experimental and control stimuli for each subject. For Experiment 1, an average of 72.2 ± 0.8 trials per condition entered into the ERPs used to estimate the early ERP responses and 55.7 ± 2.2 trials per condition entered into the ERPs used to estimate the late ERP responses; for Experiment 2, averages of 66.1 ± 1.1 and 56.6 ± 2.1 trials per condition entered into the early and late ERPs, respectively.

Statistical analysis

In order to determine the spatiotemporal signatures of past experience influences on shape assignment, we computed point-wise non-parametric randomized permutation paired t-tests between experimental and control ERP responses corrected for multiple comparisons across electrodes and time points using a cluster-based method (Nichols & Holmes, 2002). This method allows the identification of the onset of differential responses between experimental and control conditions in a manner that is more conservative than standard parametric t-tests, as no assumptions of normality are required.

This statistical method consists of three steps. In Step 1, a statistical significance threshold is empirically determined for each data point independently. This is achieved by estimating a t-distribution from the data for each electrode and time point by computing t-statistics from each of 20,000 random within-subject permutations of data values across conditions under the null hypothesis. That is, on each permutation, a randomized subset of participants is selected to have their data exchanged across two experimental conditions before t-values are computed (under the null hypothesis, the t-value computed after this exchange is still an element of the null distribution). In this manner, a distribution of 20,000 t-values is created, and the two-tailed p = 0.05 primary threshold is determined for each data point. (It should be noted that accurate results can be achieved for random permutation tests by using a minimum of 10,000 permutation steps; see Blair & Karniski, 1993). In Step 2, these significance thresholds are used to determine the distribution of maximal cluster size of data points exceeding the significance thresholds under the null hypothesis. Step 2 is achieved by computing a second round of 20,000 permutations, where during each permutation the p = 0.05 thresholds determined in Step 1 are applied at each corresponding data point. T-values above these thresholds are divided into contiguous clusters and a maximal cluster size is determined for each permutation step, yielding a distribution of 20,000 maximal cluster values under the null hypothesis. In Step 3, the obtained distribution of maximal cluster sizes is used to hypothesis test the t-statistic cluster sizes obtained from the non-permuted data. T-statistic clusters calculated from the non-permuted data with sizes greater than the maximal cluster distribution’s p = 0.05 criterion cluster size are considered significant at the two-tailed level with strong control for type-I error.

In the present study, we first computed permutation tests for experimental and control data separately, testing for significant non-zero changes in ERP amplitude from baseline. As statistically significant above-baseline changes would be expected to occur for data points possessing high signal-to-noise ratios and not data points possessing low signal-to-noise ratios, these initial tests thus excluded the latter from further analysis. Data points that reached significance in these initial tests for experimental and/or control ERPs were then entered into an additional permutation analysis testing for differences between experimental and control conditions. The permutation tests were performed over all electrode sites for two
separate intervals: the 0–200 ms post-stimulus time range encompassing the early P1 and N1 ERP responses (see Figure 3) and the 200–600 ms post-stimulus interval encompassing the later response to the masks (Figure 3). Permutation testing was computed separately for these time intervals in order to increase the localizing power of the statistical cluster tests (Blair & Karniski, 1993; Guthrie & Buchwald, 1991) because the larger ERP response to the masking stimulus might lead to larger cluster sizes that would bias the estimated statistical distribution in a manner that could reduce the power to detect smaller effects in the early time interval. The division of these time intervals of

Figure 3. Grand-average (top row) experimental and (bottom row) control ERPs for (left column) Experiment 1 and (right column) Experiment 2. Waveforms for all channels are shown superimposed (Experiment 1: 64 channels; Experiment 2: 69 channels). Head maps display scalp topographies of P1, N1, P2, and P3 components at peak latencies and are displayed in normalized dimensionless units for ease of visual comparison across components; light/dark colors indicate ± values. Note that the P1 and N1 responses reflect early processing of the silhouettes alone, while the P2/P3 response reflects late silhouette processing plus early processing of the mask.
interest at 200 ms was chosen because it encompassed the early P1 and N2 ERP components at a time point midway between the presentation of the masking stimuli at 175 ms post-stimulus onset and 225 ms post-stimulus onset when visual signals related to the mask would be expected to reach visual cortex (assuming retina-to-cortex conduction delays of approximately 50 ms; cf. Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002).

The results of the permutation tests are displayed as intensity plots, where the x-, y-, and z-axes represent time, electrode, and t-value, respectively (Murray et al., 2002). The temporal endpoints of statistically significant data clusters were taken as the onset and offset of differences between experimental and control conditions. An omnibus test summarizing the overall between-condition differences was also performed by collapsing statistically significant cluster points across time and electrode dimensions for each participant before computation of a single permutation t-test on these collapsed values.

ERP visualization and localization

For graphic visualization, ERP waveforms were averaged across participants and electrodes demonstrating significant between-condition differences. ERP component scalp topographies were visualized by averaging ERP amplitudes over participants and time intervals demonstrating significant between-condition differences. These grand-average ERP waveforms and scalp topographies were displayed using algorithms from the EEGLAB MATLAB toolbox.

Information about the intracranial sources of past experience effects on shape assignment was estimated via current source density (CSD) topographic mapping. CSD analysis transforms raw EEG potentials into a measure of the radial current density at the scalp. CSD computation is known to reduce the effects of physical delays of approximately 50 ms; cf. Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002).

Results

Behavior

Experiment 1

Novel versus familiar categorization responses were highly accurate in Experiment 1 (see Table 1). A two-way ANOVA yielded a significant main effect of Block ($F(3, 66) = 11.96, p < 0.001, \varepsilon = 0.80$); overall accuracy (collapsed across all three Silhouette Types) increased with repetition only from Block 1 (89% ± 1%) to Block 4 (93% ± 1%; $p < 0.004$). A main effect of Silhouette Type was also significant ($F(1, 22) = 25.40, p < 0.001$); participants classified novel stimuli (96% ± 1%) more accurately than familiar stimuli (88% ± 2%). In addition, a significant Block × Silhouette Type interaction ($F(3, 66) = 8.19, p < 0.001, \varepsilon = 0.76$) indicated that accuracy to classify familiar stimuli slightly increased with repetition (Block 1 = 83% ± 2% to Block 4 = 91% ± 1%; $p < 0.004$). Classification accuracy for novel stimuli did not change with repetition ($p > 0.52$).

A second two-way ANOVA examined whether subjects were differentially accurate in classifying control versus experimental silhouettes as “novel.” No significant main effects or interactions were found ($ps > 0.13$): participants classified control and experimental silhouettes as novel shapes equally accurately across all four blocks of the experiment. Thus any additional behavioral or ERP effects observed in this experiment cannot be due to differences in categorization difficulty.

RTs for correct trials were rapid in Experiment 1 (≤512 ms; see Table 1). The two-way ANOVA performed on correct “familiar” and “novel” categorization RTs yielded a significant main effect of Block ($F(3, 66) = 16.55, p < 0.001, \varepsilon = 0.50$), indicating that overall RTs decreased across all 4 blocks (Block 1 = 559 ± 24 ms to Block 4 = 469 ± 15 ms; $p < 0.004$). A main effect of Silhouette Type was also significant ($F(1, 22) = 7.30, p < 0.013$); participants were faster to accurately categorize familiar (484 ± 15 ms) than novel silhouettes (507 ± 18 ms). The

<table>
<thead>
<tr>
<th>Accuracy</th>
<th>RTs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EXP</td>
</tr>
<tr>
<td>Experiment 1</td>
<td>97 (1)</td>
</tr>
<tr>
<td>Experiment 2</td>
<td>96 (1)</td>
</tr>
</tbody>
</table>

Table 1. Mean accuracy rates (%) and RT (ms) per experiment and condition. SE values in parentheses.
finding of faster “familiar” vs. “novel” responses replicates a well-established finding in the object recognition literature (e.g., Bülthoff & Bülthoff, 2003). There was no significant Block × Silhouette Type interaction ($F[3, 66] = 0.16, p > 0.85, \epsilon = 0.67$).

Within the novel silhouettes, RTs to correctly categorize experimental versus control silhouettes were compared via a second two-way ANOVA. A main effect of Block was significant ($F[3, 66] = 14.61, p < 0.001, \epsilon = 0.49$); RTs to classify both experimental and control silhouettes as “novel” decreased across blocks (Block 1 = 571 ± 27 ms to Block 4 = 479 ± 15 ms; $p < 0.004$). A main effect of Silhouette Type was also significant ($F[1, 22] = 4.89, p < 0.038$), but the Block × Silhouette Type interaction was not significant ($F[3, 66] = 1.03, p > 0.39, \epsilon = 0.76$). Participants were faster to categorize experimental silhouettes as “novel” (504 ± 17 ms) than control silhouettes (512 ± 18 ms). This result indicates that the presence of a familiar configuration on the outside of experimental but not control silhouettes did not induce response interference; had it done so, then correct “novel” RTs would have been longer for experimental than control silhouettes. Thus in the present research, this finding allows us to rule out differential response interference as an explanation for any differences in observed ERPs for experimental and control silhouettes.

**Experiment 2**

Categorization responses were also highly accurate in Experiment 2 (see Table 1). The repeated-measures ANOVA performed on “familiar” versus “novel” accuracy rates yielded a significant main effect of Block ($F[3, 75] = 3.85, p < 0.023, \epsilon = 0.75$); participant classification responses increased in accuracy for all three stimulus types across blocks (Block 1 = 89 ± 1% to Block 4 = 91 ± 1%; $p < 0.009$). A main effect of Silhouette Type was also significant ($F[1, 25] = 26.09, p < 0.001$); participants categorized novel stimuli (95% ± 1%) more accurately than familiar stimuli (86% ± 1%), indicating either that the familiar silhouettes were harder to recognize than the novel silhouettes or that participants had a bias to classify the stimuli as “novel.” There was no significant Block × Silhouette Type interaction ($F[3, 75] = 2.67, p > 0.08, \epsilon = 0.69$). The ANOVA comparing experimental and control accuracy rates yielded a trend toward a main effect of Silhouette Type ($F(1, 25) = 3.5, p = 0.073$), but the qualitative difference in accuracy rates to categorize experimental and control silhouettes was very small (approximately 1%; see Table 1) again indicating that any other behavioral or ERP effects observed in this experiment are unlikely to be due to differences in categorization difficulty. No other main or interaction effects were significant ($p > 0.69$).

Classification RTs were rapid (≤596 ms; see Table 1) but not as rapid as in Experiment 1. This was confirmed by collapsing across factors of Block and Silhouette Type to directly test overall RTs between the two experiments via a two-sample $t$-test. RTs in Experiment 1 (500 ± 16 ms) were significantly faster than in Experiment 2 (580 ± 19 ms; $t(1,47) = -3.18, p < 0.003$, two-tailed).

A repeated-measure ANOVA performed on Experiment 2 correct “familiar” versus “novel” classification RTs yielded a significant main effect of Block ($F[3, 75] = 23.46, p < 0.001, \epsilon = 0.60$); overall RTs significantly decreased across blocks (Block 1 = 641 ± 25 ms to Block 4 = 534 ± 16 ms; $p < 0.004$). A main effect of Silhouette Type was also significant ($F[1, 25] = 9.61, p < 0.005$); as in Experiment 1, Experiment 2 participants were faster to categorize familiar (564 ± 21 ms) than novel silhouettes (590 ± 19 ms). The Block × Silhouette Type interaction was not significant ($F[3, 75] = 0.55, p > 0.57, \epsilon = 0.63$).

RTs to correctly categorize experimental vs. control silhouettes as “novel” were compared in a second two-way ANOVA. The ANOVA showed a significant main effect of Block ($F[3, 75] = 12.65, p < 0.001, \epsilon = 0.58$); correct “novel” RTs for both experimental and control silhouettes decreased across block (Block 1 = 650 ± 26 ms to Block 4 = 550 ± 17 ms; $p < 0.004$). A main effect of Silhouette Type was also significant ($F[1, 25] = 6.80, p < 0.015$), but the Block × Silhouette Type interaction was not significant ($F[3, 75] = 0.49, p > 0.69, \epsilon = 0.84$). As in Experiment 1, participants were faster to accurately categorize experimental silhouettes (583 ± 19 ms) than control stimuli (596 ± 19 ms) as “novel.” Once again, this result indicates that the presence of a familiar configuration on the outside of the experimental silhouettes did not produce response interference. The question of why participants were faster to categorize experimental silhouettes as “novel” than control silhouettes as “novel” is intriguing but is beyond the scope of the present experiments.

**Electrophysiology—Experiments 1 and 2**

Figure 3 shows the grand-average ERP responses (computed from trials retained via the long EOG rejection interval criterion; see Methods section) for Experiments 1 and 2. Both experiments produced typical P1, N1, and P2/P3 responses. The P1 and N1 responses reflect early processing of the silhouettes alone, while the P2/P3 response reflects late silhouette processing plus early processing of the mask. Of note is the prominent N1 response in Experiment 1 that is reduced or absent in Experiment 2. In addition, the P1 scalp topographies appeared to differ somewhat between the two experiments (see below for further discussion).

The statistical cluster analysis comparing early (0–200 ms) ERP responses for the critical experimental and control novel silhouettes revealed significant experimental vs. control differences in the early phase of the ERP.
Experiment 1 (Figure 4A) demonstrated significantly greater ERPs for experimental vs. control conditions from approximately 109 ms to 142 ms over 15 midline and posterior sites. Experiment 2 (Figure 4B) demonstrated significantly greater ERPs for experimental vs. control conditions from approximately 106 ms to 156 ms over 9 midline and right-hemisphere posterior locations. (Recall that the montage for Experiment 2 had fewer posterior electrodes.) The omnibus permutation t-tests performed over early phase ERP amplitudes collapsed across statistically significant cluster points (see Methods section) confirmed that the ERP responses over the indicated time ranges and electrode locations were greater for experimental than control conditions for both experiments (Experiment 1 Omnibus past experience effect = 1.52 μV ± 0.29 μV, t(1, 22) = 2.07, t_cutoff = 2.07, p < 0.005, two-tailed; Experiment 2 Omnibus past experience effect = 0.76 μV ± 0.20 μV, t(1, 25) = 3.69, t_cutoff = 2.05, p < 0.008, two-tailed). In contrast to the early ERP responses, the late ERP statistical cluster analysis (200–600 ms, not shown) revealed no statistically significant differences for either experiment, and thus no follow-up omnibus testing was performed.

Figure 5 shows experimental and control early phase waveforms collapsed across all electrodes demonstrating statistically significant between-condition differences for Experiment 1 (Figure 5A) and Experiment 2 (Figure 5B). In Experiment 1, significant experimental vs. control differences occurred just after the peak of the early P1 ERP response during the falling phase of this component. In Experiment 2, the significant experimental vs. control differences occurred before, during, and after the P1 peak. Figure 5 also displays ERP scalp topographies for each experiment collapsed across the temporal intervals containing statistically significant between-condition differences. The mean scalp topography over these intervals differed between experiments. In Experiment 1, the P1 response was centered over medial occipital and parietal scalp sites; in Experiment 2, the P1 was distributed over medial and lateral occipital sites. There was some topographical agreement between the two experiments in that the difference-wave scalp topographies of both experiments exhibited significant experimental vs. control differences over midline and right-hemisphere locations.

A notable difference between the two experiments is the presence of a large N1 response and a qualitative between-condition N1 difference in Experiment 1 that was minimal in Experiment 2. The statistical cluster plots did not indicate that the apparent Experiment 1 between-condition N1 difference was significant, however. One possible explanation for this N1 discrepancy between Experiments 1 and 2 may be due to topographical distortions arising from the use of a linked-ear EEG recording reference during Experiment 1 that are not present in Experiment 2 where such a recording reference was not used (see Discussion section).

Finally, Figure 6 shows the Experiment 2 CSD topographies collapsed across early phase time points containing statistically significant between-condition differences. The CSD foci for Experiment 2 experimental and control conditions are consistent with bilateral occipital-temporal generators, while the CSD difference topography suggests greater ERP generator activity for experimental vs. control conditions in right-hemisphere temporal-parietal-occipital cortical locations.

In summary, in both Experiments 1 and 2, a larger early ERP response was observed for experimental silhouettes
Given that the experimental and control silhouettes were carefully matched on stimulus features known to be relevant to figure–ground perception (as well as a variety of other stimulus features), it appears that the early ERP responses already vary with access to object memories, or with competition induced by such access, or both.

**Discussion**

**An early influence of past experience on shape assignment**

The present study investigated when in the course of figure–ground perception past experience, in the form of access to pre-existing shape representations, might influence shape assignment. This question was addressed by comparing ERP responses evoked for two types of novel silhouettes—experimental silhouettes that suggested a portion of a familiar shape on the groundside of their borders and control silhouettes that sketched novel objects on both the figure side and the groundside of their borders—under conditions where participants were

Figure 5. Grand-average ERPs and scalp topographies for experimental (black line) and control (red line) conditions in (A) Experiment 1 and (B) Experiment 2. ERP waveforms/topographies are collapsed, respectively, across electrodes (indicated by black dots) and stated time intervals (indicated via horizontal black lines) demonstrating statistically significant between-condition differences. Light/dark colors indicate $t$ values.

Figure 6. Experiment 2 CSD topographic maps for early phase (top) experimental, (middle) control, and (bottom) experimental–control conditions. Light/dark colors indicate $\mu V$ current density values. The CSD foci for experimental and control conditions are consistent with bilateral occipital-temporal generators; the CSD difference foci indicates a greater response for experimental vs. control conditions over right hemisphere locations, consistent with the ERP difference topography.

(with familiar shapes suggested on the outside) than for control silhouettes (with no familiar shapes suggested on the outside). Given that the experimental and control silhouettes were carefully matched on stimulus features known to be relevant to figure–ground perception (as well as a variety of other stimulus features), it appears that the early ERP responses already vary with access to object memories, or with competition induced by such access, or both.
unaware of the differences between them: they perceived the inside of both types of silhouettes as figures and they were equally accurate in classifying figures of both types as "novel." The main finding of this study was that in both Experiments 1 and 2, larger amplitude ERPs were observed for experimental vs. control silhouettes within an early temporal window (approximately 106–156 ms after stimulus onset) over right-hemisphere posterior scalp locations. These differences overlapped within a time range (140–160 ms) during which processing is believed to be related to initial edge segmentation in humans (Caputo & Casco, 1999; Heinen et al., 2005; see also Neri & Levi, 2007). Hence, the ERP differences in our experiments are most likely related to the presence of a familiar configuration along the outside of the edges of experimental silhouettes but not control silhouettes. These early differences suggest that familiar configurations suggested along an edge are accessed early in the course of figure–ground perception, when edges are initially being segmented and assigned to an adjacent region.

The early ERP effects may reflect fast early access to pre-existing shape memory representations prior to shape assignment, or the competition that ensues following implicit access to these memories (see Peterson, 1994, 1999, 2003). In either case, the present results favor the suggestion that familiar configurations accessed early in shape assignment reside in intermediate levels of the visual hierarchy of shape representations (Peterson, 2003), below the level at which figure assignment has already occurred (Baylis & Driver, 2001). There is some evidence that the later phases of the P1 ERP component (the temporal locus of the present past experience effect) reflects activity in the human equivalent of macaque V4v (Di Russo et al., 2002). In addition, the ERP and CSD scalp distributions observed in Experiments 1 and 2, although somewhat inconsistent with each other (see Electrophysiology—Experiments 1 and 2 section and further discussion below), are consistent with a locus for these past experience effects over right-hemisphere occipital–parietal scalp regions. These scalp regions are adjacent to extrastriate and lateral occipital (LOC) cortex, the latter of which is believed to be the human homologues of macaque IT cortex (Kobatake & Tanaka, 1994; Sary, Vogels, & Orban, 1993). Additional neuroimaging research is needed to determine the precise cortical locale of the present past experience effects.

These early ERP differences cannot reflect differences in perceived figural outcome, inasmuch as the insides of both experimental and control silhouettes were perceived as the shaped figures, and were classified as novel shapes equally accurately. It is also unlikely that these differences reflect low-level stimulus properties to which such early ERP responses are sensitive (VanRullen & Thorpe, 2001), as these stimuli were explicitly matched in terms of stimulus factors (see Appendix A). Furthermore, it is not the case that the early ERP findings merely reflect differences in categorization difficulty between the two stimulus types, as RTs revealed no evidence that it was more difficult to classify experimental than control novel silhouettes.

Might these early ERP differences reflect a case of repetition priming (in which behavioral responses are typically faster on additional presentations of a stimulus relative to the first presentation) or repetition suppression (in which brain responses are reduced with repeated exposure to a stimulus)? The experimental and control stimuli were repeated throughout the study, but they were repeated equally (see Procedure section). Response differences between our experimental and control stimuli did not vary across the 4 blocks of each experiment (see Behavior section). Thus the present findings are not due to differential repetition of experimental and control stimuli during the experiment. Might the ERP results measure differential repetition suppression/enhancement for experimental versus control stimuli? We think not because repetition suppression is typically observed for familiar shapes, whereas repetition enhancement has been observed for novel stimuli. Inasmuch as there was a familiar shape suggested on the outside of the experimental, but not the control stimuli, on this account, one would expect responses for the experimental stimuli to be reduced compared to the control stimuli; instead they were enhanced. Finally repetition suppression typically manifests as a reduction in late (>200 ms) ERP responses for repeated vs. novel stimuli (Hertz, Porjesz, Begleiter, & Chorlisan, 1994; Zhang, Begleiter, Porjesz, Wang, & Litke, 1995), whereas the critical differences in the present study were evident in early responses (<156 ms).

Even if it could be clearly established that the present ERP effects are related to repetition priming, the present finding stands apart from typical repetition priming results. Our stimuli were designed such that the familiar configurations suggested on the outside of the experimental stimuli would be accessed over a visual region that would lose the cross-edge competition and thus would be perceived as a shapeless ground. This is different from typical studies of repetition priming in which familiar configurations are accessed over regions that win the cross-edge competition and are seen as shaped figures.

The special nature of our stimuli also illustrates the difference between our study and previous human electrophysiological studies of object, face, and scene recognition that control for low-level stimulus differences (Linkenkaer-Hansen et al., 1998; Rousselet, Mace, Thorpe, & Fabre-Thorpe, 2007; Schendan & Kutas, 2003; Thierry et al., 2007; VanRullen & Thorpe, 2001). In these studies, participants either passively viewed or made an explicit judgment regarding familiar figures. Across studies, recognition-related ERP differences emerged over posterior scalp locations from approximately 50–150 ms, an interval that overlaps with the time range of the present familiarity-dependent ERP differences. These
findings provide further support for the idea that early visual processing stages may be modulated by past experience with visual stimuli.

Other EEG, MEG, and/or fMRI studies have revealed a larger response over lateral occipital regions at approximately 100 ms post-stimulus onset when illusory contours are present (Murray et al., 2006, 2002). This is in the same temporal window where edge effects are observed in figure–ground studies, including the present study. This similarity provides convergent evidence that the past experience effects observed here are related to early contour processing. Although the present silhouette stimuli always possessed contrast borders, a previous study (Peterson & Gibson, 1994b) showed that illusory contours support effects of past experience just as contrast borders do. Studies of visual closure processes underlying contour completion have found brain responses reflecting visual closure to occur later in time at approximately 170 ms with an additional response at 230 ms–330 ms (Doniger et al., 2000, 2001). We did not observe any past experience effects late in processing, possibly because the masking stimuli presented immediately after the silhouettes obscured later effects. (Recall that masking stimuli were used to prevent changes in the cross-edge balance of cues that may result in the conscious perception of the familiar shapes along the outsides of the experimental silhouettes.)

Finally, we should note that the data reported in this paper were acquired from Non-Seer participants who were unaware of the familiar shapes sketched along the outsides of the experimental silhouettes. We only analyzed Non-Seers so as to avoid confounding any effects of past experience with effects related to conscious recognition of the familiar shapes (see Post-experiment questioning section). In addition, pragmatic concerns limited examination of Seer participants, as the number of Seers in this study was low (Experiment 1: \( N = 11 \); Experiment 2: \( N = 7 \)) and thus there was not enough statistical power to afford a proper analysis. Given the observed ratio of Seers to Non-Seers obtained via the present design (approximately 2:5), two to three times as many participants would be required in order to obtain a Seer sample size of sufficient statistical power. It should also be noted that post-experimental questioning indicated that Seers saw only a small subset of the shapes suggested on the groundsides of the silhouettes, further precluding a robust contrast between Seers and Non-Seers. Hence the question of what differences, if any, characterize Non-Seers from Seer participants, although interesting, is beyond the scope of the present study and awaits future research.

**Differences between Experiments 1 and 2**

Although the findings of Experiments 1 and 2 were generally similar, there were three differences between the ERP responses of the two experiments that need to be addressed. First, the period of significant between-condition differences was smaller for Experiment 1 (33 ms interval) than for Experiment 2 (50 ms interval); see Figure 4. Second, the scalp and temporal distributions of this effect were somewhat different between the two experiments, with the Experiment 1 past experience effect manifest over a larger subset of electrodes and a narrower time range than the past experience effect observed in Experiment 2 (see Figure 5). Third, there were qualitative between-condition differences between the N1 ERPs, with a large N1 and qualitative between-condition N1 differences for Experiment 1 that were not present in Experiment 2 (see Figure 5).

These topographical and qualitative differences between Experiments 1 and 2 may be due to the use of a linked-ear EEG reference during the data recording of Experiment 1. This choice of reference is non-optimal in that it can create a low-resistance shunt between the two scalp hemispheres that can distort the scalp distribution of ERP components (Nunez & Srinivasan, 2006). Distortions induced by this reference are not necessarily resolved by transformation to an FPZ reference, as was done here (see ERP data analysis section). This possibility was one motivation for the undertaking of Experiment 2, which employed a recording reference scheme that was not subject to this problem (see ERP data acquisition section). Although the occurrence of such EEG reference-induced electrical shunting appears to be unlikely under most circumstances (Miller et al., 1991), it remains possible that the spatial configuration of neural sources active during the early time range was such that it would induce a degree of topographical distortion of the ERPs during Experiment 1.

In addition, the observed between-experiment differences may be due to subtle differences in electrode placement, as two different EEG cap systems (Neuroscan and BioSemi; see ERP data acquisition section) were employed across the two experiments, although both employ extended 10–20 system locations. Finally, population differences may account for some of the between-experiment differences; the existence of such population differences is suggested by the fact that Experiment 1 participants were significantly faster overall to perform the shape discrimination task than were Experiment 2 participants (see Table 1).

Given these concerns, the more reliable pattern of ERP findings of this study are likely to be those of Experiment 2, although we should emphasize that both experiments demonstrated similar early phase between-condition ERP differences. We should note, however, that the possible issues with regard to the reference scheme of Experiment 1 most likely do not affect the main conclusions regarding the timing of past experience influences on shape assignment, as we observed comparable onset times of between-condition differences across experiments (Experiment 1: 113 ms; Experiment 2: 106 ms).
Evidence for competition?

The theoretical rationale underlying the present study is based on the hypothesis that figure–ground perception entails competition between shapes that might be seen on opposite sides of an edge (Peterson et al., 2000; Peterson & Skow, 2008). According to this hypothesis, at some early point during processing the familiar configuration present along the outer edges of the experimental silhouettes competes with other configural cues present along the inner edges. The winner of the competition is perceived as the figure; the loser is perceived locally as an unshaped ground. Thus, the early ERP differences observed here could reflect either the greater competition across the borders of the experimental versus control silhouettes occasioned by early access to pre-existing memory representations on the outsides of the former but not the latter, or the differential access to object memories that underlies the differential competition.

Is it possible that these early differences reflect the biasing of the cross-edge competition by attention (Kienker et al., 1986; Qiu et al., 2007), which acts to enhance the processing of the cues within the inner region of the experimental silhouettes? The answer appears to be “no,” at least as measured by a target discrimination task. Peterson and Salvagio (2009) asked subjects to discriminate the orientation of a target bar shown on the inside (or the outside) of experimental versus control stimuli. They reasoned that if more attention was drawn to the inside of the experimental silhouettes to resolve the greater cross-edge competition from the familiar configuration on the outside, subject discrimination responses should be faster and/or more accurate for targets shown on the inside of experimental than control stimuli. In contrast to these predictions derived from an attention hypothesis, subject discrimination performance was worse for targets shown on the inside of experimental than control silhouettes. (The same pattern was observed for outside targets.) Thus, at least as measured by an orientation discrimination task, it does not appear to be the case that more attention is drawn to the experimental than the control silhouettes. Therefore, it is unlikely that the early ERP differences we observed measure greater attention to the experimental than control silhouettes.

In contrast to our finding of greater amplitude ERPs for conditions where more rather than less competition was expected, previous studies have found reduced neural activation, as indexed by fMRI or single-unit measures, when there is more competition for visual representation between two (or more) separate objects presented in close proximity (Beck & Kastner, 2005; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Kastner et al., 2001; Kastner & Ungerleider, 2001; Luck, Chelazzi, Hillyard, & Desimone, 1997; Miller, Go chin, & Gross, 1993; Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999; Rolls & Tovee, 1995). The problem with expecting reduced ERP amplitudes to index competition is that a decrease in ERP amplitude could arise from many factors besides a reduction in neural activity, such as a change in the ratio of inhibitory to excitatory cortical processing, a reduction in neural synchrony rather than overall neural activity, and/or a change in the orientation and polarity of the underlying generator(s). Furthermore, competition involving familiar shape may involve conflicts between high- and low-level visual cortex mediated by neural feedback rather than competition between objects within a receptive field. A more sophisticated methodological approach designed to control for many of these factors will be necessary to investigate neural competition using ERP measures. Such an approach was not necessary for the central issue under investigation here, namely elucidating the processing stage at which access to pre-existing shape memories influences shape assignment, whether that influence is through induced competition or some other process.

Conclusions

In conclusion, the present study provides the first neurophysiological evidence for an influence of past experience on the earliest stages of shape assignment and figure–ground processing. In doing so, the present study provides additional support for previous findings that indicate an important role for prior visual experience in the fundamental perception of visual shape (Peterson, 2003; Peterson et al., 2000; Peterson & Gibson, 1994a; Peterson et al., 1991; Vecera & O’Reilly, 1998).

Appendix A

Analysis of stimulus properties

The experimental and control novel silhouettes were equated on a number of low-level stimulus features plus additional image properties known to affect figure–ground perception so as to preclude the possibility that stimulus confounds might contribute to any observed ERP differences between these conditions. Quantifiable measures of luminance, contour length, spatial frequency, and horizontal span (all stimuli had the same vertical height) were computed for the critical control and experimental novel silhouettes and for the filler familiar silhouettes. Luminance and spatial frequency have been shown to influence ERP responses (Goffaux, Gauthier, & Rossion, 2003; Johannes, Munte, Heinze, & Mangun, 1995). 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 artifactual ERP differences. Furthermore, the experimental and control novel stimuli have been previously shown (Peterson & Gibson, 1994a; Peterson & Kim, 2001) to be equated on at least three shape properties known to affect figure–ground segregation (symmetry, enclosure, local convexity). The additional image property of global convexity was also quantified, while the property of relative area was quantified within the analysis of luminance (see below).

Luminance was computed for each stimulus in terms of the total area (in pixels) of the white center regions of the silhouettes. 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. Note that the quantification of luminance via this method also involves the quantification of the total area of each silhouette.

Spatial frequencies were computed using a previously published method (Trujillo, Peterson, Kaszniak, & Allen, 2005). Two-dimensional Fourier transforms were performed on experimental and control novel silhouettes and the filler familiar silhouettes. 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 frequency and one for vertical frequency.

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).

The configural cue of convexity was assessed by computing the area 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 curvatures along the bounding contour. These area maps were then saved as bitmaps and then analyzed via MATLAB scripts specially written for this purpose (using the bwarea function). Due to the difficulty in defining convex intrusions for some of the filler familiar stimuli, convexity was assessed only for control and experimental novel stimuli.

The values of all stimulus properties were subjected to between-condition two-sample t-tests separately for each property. The primary tests were between control and experimental novel stimuli, which were of central interest in this study; however, tests between the filler familiar stimuli and the critical control and experimental novel stimuli were also performed. The critical control and experimental novel stimuli did not significantly differ from one another in terms of any stimulus properties (all ps > 0.1, two-tailed). The filler familiar stimuli did not differ from the control and experimental novel stimuli on the properties of luminance/area, contour length, or horizontal span (all ps > 0.1, two-tailed). However, the filler familiar stimuli did differ from control and experimental novel stimuli in terms of horizontal spatial frequency (experimental novel vs. familiar: t(1, 39) = 4.41, p < 0.01, two-tailed; control novel vs. familiar: t(1, 39) = 4.01, p < 0.01, two-tailed). For this reason, ERPs were not compared between the filler familiar stimuli and the control and experimental novel stimuli, due to the possibility of artifactual ERP differences arising from the mismatch in spatial frequency.

Appendix B

**Objects suggested on the groundsides of experimental silhouettes**

Set A: Axe, Bell, Bone, Boot, Butterfly, Coffee Pot, Dog, Eagle, Face, Grapes, Hand, House, Hydrant, Lamp, Pig, Palm, Rhino, Train, Women, Wrench.

Set B: Anchor, Bunny, Duck, Elephant, Faucet, Flower, Foot, Guitar, Horn, Jet, Leaf, Mickey Mouse, Owl, Pineapple, Seahorse, Snowman, Sprayer, Teddy Bear, Umbrella, Watering Can.

**Objects depicted by familiar silhouettes**

Apple, Balloon, Bat, Birthday Cake, Boat, Bottle, Bug, Bumblebee, Cactus, Candle and Flame, Castle, Cat, Clover, Crown, Dragonfly, Frog, Goldfish, Graduating Student, Heart, Ice Cream Cone, Jellyfish, Lion, Lizard, Lobster, Missile, Penguin, Racecar, Ram, Screw, Skull, Spade, Spider, Star, Steer, Strawberry, Telephone, Tent, T-shirt, Turtle, Wheel.

**Foil objects listed when determining seers**

Set A: Book, Bowling Pin, Carrot, Chair, Clothes Hanger, Doorknob, Fox, Hammer, Hippo, Kettle, Paintbrush, Pants,
Acknowledgments

This research was supported in part by a US Department of Education Jacob K. Javits Graduate Fellowship and a University of Arizona Institute for Collaborative Biotechnology (BIOS) Graduate Research Award to LTT; National Science Foundation Grants BNS 9906063 and BCS-0418179 to MAP; and Army Grant #W911NF-07-2-0023 to DMS, through the Center for Strategic and Innovative Technologies at the University of Texas at Austin. Experiment 1 was part of a Ph.D. Dissertation submitted by LTT to the University of Arizona.

Commercial relationships: none.
Corresponding author: Logan T. Trujillo.
Email: trujillo@psy.utexas.edu.
Address: Department of Psychology, The University of Texas at Austin, Austin, TX, USA.

References


Kayser, J., & Tenke, C. E. (2006b). Principal components


Qiu, F. T., Sugihara, T., & von der Heydt, R. (2007). Figure–ground mechanisms provide structure for selective
attention. *Nature Neuroscience, 10*, 1492–1499. [PubMed] [Article]


