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Investigations of Human Contour Perception:

Psychophysics and Visual Evoked Potentials

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of
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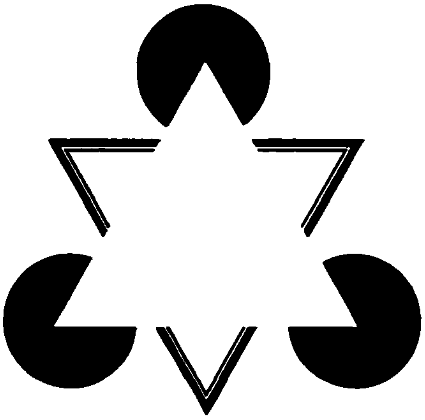

The task of the real intellectual consists of analyzing illusions in order to discover their causes. *Arthur Miller*

We must select the illusion which appeals to our temperament, and embrace it with passion, if we want to be happy. *Cyril Connolly*

Wokka-wokka-wokka-wokka... *Pac-Man*

In memory of my grandmother Sylvia, who so badly wanted to attend college at a time when many families could only afford to educate their boys;
who, throughout her life, never missed an opportunity to learn something new;
and who wanted to give her family the chances she never had.

Grandma, this one is most definitely for you.

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ABSTRACT

Two studies were performed to investigate the temporal dynamics of shape discrimination using real (RC) and illusory (IC) surfaces. A psychophysical study employed backward masking to elucidate the microgenesis of the illusory percept as subjects performed the "thin/fat" task introduced by Ringach and Shapley (*Vision Research*, 1996). Although an IC could mask another IC at latencies of ~275-600ms post-stimulus onset, an RC did not produce masking at this stage even if its contrast subjectively resembled that of the IC. Furthermore, RCs could not be masked by either ICs or RCs in an analogous experiment. The masking between ICs appeared to be size-invariant. In a second study, visual evoked potentials (VEPs) were measured as subjects performed the shape discrimination task for ICs, RCs, and no contours (NCs). Contour-dependent modulations of the VEP were observed at the N1 (~164ms) and the N_{cl} (~286ms), over occipital and lateral occipital electrode sites. The N1 and the N_{cl} both demonstrated responsiveness to performance accuracy, implying that a correlation with behavior can be seen even at VEP modulations reflecting relatively early stages of processing. These results, which suggest major differences between the temporal dynamics of IC and RC perception, are consistent with a multi-stage model of IC processing in which occipital and lateral occipital cortex play fundamental roles.

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ILLUSORY CONTOURS: INTRODUCTION

Illusory contours (ICs) present a truly puzzling perceptual phenomenon which has baffled physiologists and psychologists for at least the last century (Schumann, 1987). After decades of debate, the questions of how they are formed and why we should be able to perceive them remain without satisfactory answer. Illusory contours occur when ghostlike boundaries and surfaces are perceived to traverse a homogeneous region of visual space (see Fig. 1 for examples). Their appearance is generally prompted by carefully aligned figural elements, known as inducers, which may take the form of lines, "pac-men" (Iwatani, 1980), or other shapes that appear against an otherwise homogeneous field. If the background is white, with dark inducers, observers report that the resulting illusory figure appears brighter than its background; similarly, with light inducers against a dark background, the figure seems to be a heightened shade of black.

Many authors have reviewed the history of illusory contours (Bachmann, 1978; Dresp, 1997; Lesher, 1994; Petry & Meyer, 1987; Purghé & Coren, 1992) in an attempt to arrive at an explanation of their existence. However, no one theory has thus far been able to unite the plentiful physiological, psychophysical, and phenomenological data into a cohesive whole. Several types of models have been proposed to explain various features of the illusion.

Gestalt Theories

The Gestaltists were responsible for revitalizing popular interest in illusory contours (Kanizsa, 1955; Kanizsa, 1976) within the last half-century. According to the principles of Gestalt psychology, information is automatically organized into configurations that promote certain standards of "figural goodness". The configuration is more important than the characteristics of the individual elements ("the whole is greater than the sum of its parts"). For example, we tend to make sense out of complex visual arrays by grouping together things that are similar in appearance to result in a regular percept. The Gestalt principle of closure, which operates to organize visual information into closed regions of space, is commonly invoked as justification for illusory contour perception. Rather than perceiving four irregular, unrelated, and incomplete circles, our visual systems "choose" a more elegant solution that results in the percept of an illusory square occluding four circles. While Gestalt theory makes certain assumptions about optimal configurations for perception, it does not necessarily advocate any one particular physiological model to implement these organizational tenets (Meyer & Petry, 1987).

Cognitive Theories

Proponents of top-down theories of illusory contour formation generally prefer the terms "cognitive contours" or "subjective contours" to describe the phenomenon. They maintain that the illusion results from cognitive influences on lower-level visual processes, usually involving some form of hypothesis-testing

(Coren, 1983; Parks, 1995; Rock, 1987) or other unconscious reasoning. The hypotheses arise to account for unusual stimulus configurations; in essence, the brain generates the contour to solve the "problem" of an intractable stimulus display by relating it to past visual experience. The interpolation of an illusory contour might result from cues that commonly co-occur with the occlusion of one surface by another. Untroubled by the absence of the actual boundary which would explain the presence of the cues, the visual system simply fills it in (Day, 1987). Evidence for such models includes the observation that replacing the pac-men with irregular, jagged shapes tends to obliterate contour perception despite presence of the same inducing edges; an occluding surface is no longer "needed" to explain the figural irregularities. Conversely, the more edge cues that are added to the figure (i.e., suggesting depth, occlusion, or transparency), the stronger the illusion tends to be.

Physiological Theories

While cognitive theories account for many of the phenomena associated with illusory contour perception, they are often pitted against bottom-up models that propound low-level neural origins for the illusion. An early physiological explanation targeted the perceived brightness of the figures, suggesting that simultaneous brightness contrast initiated the process. In recent years, this idea has served as a straw man for theorists of all persuasions who generally agree that supra-retinal mechanisms must be involved. Spatial-filtering models (Ginsburg, 1987), which suppose the Fourier-like decomposition of the visual image through frequency-tuned channels, suggest that illusory contours do exist physically in low-to-middle-bandpass channels. Physiological responses to illusory stimuli have been recorded in the early visual areas of owls (Nieder & Wagner, 1999), monkeys (Grosof, Shapley, & Hawken, 1993; Lee & Nguyen, 2001; Peterhans & von der Heydt, 1989; Peterhans & von der Heydt, 1993; Peterhans, von der Heydt, & Baumgartner, 1986; Ramsden, Hung, & Roe, 2001; von der Heydt & Peterhans, 1989; von der Heydt, Peterhans, & Baumgartner, 1984), and, with the recent advent of functional neuroimaging, humans (ffytche & Zeki, 1996; Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998; Hirsch et al., 1995; Larsson et al., 1999; Mendola, Dale, Fischl, Liu, & Tootell, 1999a; Seghier et al., 1999). Initial interpretations of the non-human primate data strongly favored the involvement of areas V1 and V2 in IC genesis, suggesting a primarily bottom-up model; the more recent studies, however, have demonstrated that V2 activation appears to precede that observed in V1 (Lee & Nguyen, 2001), in support of a top-down processing scheme. Indeed, the observation of activity in hierarchically early visual regions does not necessarily imply that it is the *temporally earliest* visual response to ICs. Murray et al. (2001b) noted electrophysiological correlates of the earliest identifiable differences between IC and no contour (NC) activation in humans over regions of lateral occipital scalp. These results are in accordance with findings from functional neuroimaging studies, which have generally supported the involvement of crudely retinotopic, intermediate-level mechanisms of visual processing in IC perception (ffytche & Zeki, 1996; Hirsch et al., 1995; Larsson et al., 1999; Mendola et al., 1999a).

Computational Theories

Many computational models for illusory shape formation were designed to dovetail with evidence from studies that implicate low-level visual areas in boundary completion. Grossberg and colleagues (i.e., Francis & Grossberg, 1996; Francis, Grossberg, & Mingolla, 1994; Grossberg, 1998; Grossberg, Mingolla, & Ross, 1997) have developed elaborate neural-network theories to account for segmentation in a variety of scenarios, including illusory boundary formation. These models include the parallel operations of a contrast-blind boundary contour system (BCS), which detects real and illusory edges through the interactive responses of end-stopped cells, and a feature contour system, which propagates brightness and color information within closed boundaries.

Simpler models were proposed by von der Heydt and colleagues (Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989), who hypothesized that illusory contour responses detected in area V2 of macaque result from the activity of parallel groups of V1 cells. In this model, the V2 neurons receive excitatory input from large receptive fields at the same orientation as the illusory contour (the "edge-detecting input"), as well as from groups of smaller, orthogonal, end-stopped cells along the illusory edge (the "grouping input"). This model is similar to that of Grossberg and colleagues in that it involves the collaboration of end-stopped neurons from disjunct portions of the retinal image, which are combined in a manner similar to that which Grossberg proposed for the BCS. However, the models disagree about such key features as the orientation of induced line segments at line terminators and the dissemination of brightness information. (See Peterhans & von der Heydt, 1989 for discussion.)

Other researchers (Ullman, 1976) have introduced neural network models that involve small, locally-connected cells. After several iterations, these networks reach an equilibrated solution that leads to the creation of the illusion. Ringach and Shapley (1996) have pointed out that a combination of these two approaches (receptive field and local network) may ultimately be the most viable.

MOTIVATIONS FOR THE STUDY OF ILLUSORY CONTOURS

Despite the vast literature that exists on the topic of illusory contours, there is remarkably little consensus regarding the origin of this enigmatic phenomenon. As is so often the case in science, early investigators have been staunchly divisionist in their approach to a theory of contour perception while more recent diplomats have attempted to unify the seemingly disparate viewpoints. The top-down/bottom-up debate rages on, though it has become obvious that solid evidence exists on both sides. Clearly, higher cognitive processes have an influence on lower visual regions; conversely, lower visual regions have networks of neurons with sufficient computational power to manufacture boundaries where no luminance border exists. A possible compromise resides in a feedback-driven model of visual perception in which information from many stages converges upon the same group of intermediate-level neurons.

The Role of Illusory Contours in Understanding of Conventional Perception

The mere existence of any illusion generally signals a shortcut or "loophole" in neural processing which is important for the facilitation of some aspect of everyday perception. The appearance of the illusion is a byproduct of our normal perceptual processes. Thus, a careful study of how the illusion is produced may lead us to important discoveries about the inner workings of human vision which operate virtually seamlessly in cases of conventional retinal stimulation.

Kellman and Shipley (1991), as well as Dresp (1997), have speculated about the ways in which illusory contour formation might be useful to a visual system operating outside the laboratory. They proposed that the same mechanisms also play a role in the perception of non-illusory objects, viewed under conditions of poor lighting or camouflage. Many authors (i.e., Corballis, Fendrich, Shapley, & Gazzaniga, 1999; Davi, Pinna, & Sambin, 1992; Greene & Brown, 2000; Lesher, 1994; Ringach & Shapley, 1996; Yin, Kellman, & Shipley, 1997) have discussed the relation between illusory contours and amodal completion, a phenomenon in which one surface is interpolated behind another such that the inducers are seen as "windows" onto the figure (Michotte, Thines, & Crabbe, 1964). These situations are examples of segmentation, the process by which the brain assigns different parts of the ambiguous two-dimensional retinal image to three-dimensional objects that overlap in depth. Such phenomena are often thought to account for our perception of continuous objects despite partial occlusion by other objects (Sekuler & Palmer, 1992). Occlusion is an extremely common visual event; we are constantly interpolating pieces of objects behind other objects to perceive integrated wholes. This observation suggests a relationship between the completion we commonly experience in natural visual scenes and the illusory (amodal or modal) completion that can be induced in the laboratory.

Clinical Relevance of the Study of Illusory Contours

On a larger theoretical scale, understanding of any neural process will undoubtedly help to unravel the functional organization of the brain at other levels. The methodology used to understand normal perception often can be applied to the study of neurological or psychiatric pathology. By employing techniques such as functional imaging, electroencephalography, or certain types of psychophysics, all of which are commonly used to facilitate clinical diagnoses, one can capture baseline activity of normal cognitive processes. Once these baselines are understood, similar experiments can be repeated with clinical populations thought to have functional deficits in certain visual pathways. For example, functional neuroimaging has clarified the motion pathway deficits in individuals with dyslexia (Eden et al., 1996), while backward masking can be used to identify those with or at risk for a diagnosis of schizophrenia (Green, Nuechterlein, Breitmeyer, & Mintz, 1999; Slaghuis & Bakker, 1995). Closure processes, in particular, seem to be impaired in schizophrenia; the perceptual impairment correlates highly with negative symptoms (Doniger, Silipo, Rabinowicz, Snodgrass, & Javitt, 2001b; Doniger, Foxe, Murray, Higgins, & Javitt, in press). Knowledge of this kind may be useful in making differential diagnoses or in screening members of a high-risk population.

Cases of impaired illusory contour perception have been described in the neuropsychological literature (Corballis et al., 1999; Sajda & Finkel, 1995; Wasserstein, 1981; Wasserstein, Zappulla, Rosen, Gerstman, & Rock, 1987). In such cases, clinical practice and basic research can inform each other about the perceptual mechanisms needed to experience illusory contours and other related phenomena. While the clinical data may suggest double dissociations between subprocesses of cognition and perception, the scientific findings may lead to the development of new assessment techniques or even rehabilitation strategies that would be useful to patients recovering from certain neurological conditions.

Incidentally, psychologists and neurologists are not the only clinicians who would be well served by familiarity with illusory contours. They frequently crop up in X-rays and MRIs, confounding the unwary radiologist who does not recognize the cues to illusory boundary formation (Daffner, 1989).

RELATIONS BETWEEN ILLUSORY CONTOURS AND REAL CONTOURS

If the visual system creates illusory contours through a perceptual process that also underlies real contour perception, then logically both types of stimuli must proceed through at least partially overlapping channels. Numerous psychophysical studies point to a common mechanism for both real and illusory edges. For example, there are interactions between real and illusory lines in a task of vernier acuity (Greene & Brown, 1997) and in versions of famous perceptual phenomena such as the Poggendorff (Beckett, 1989; Beckett, 1990) and Bourdon (Walker & Shank, 1988a) illusions. Studies have been made of common aftereffects (Paradiso, Shimojo, & Nakayama, 1989; Smith & Over, 1976; Smith & Over, 1977; Smith & Over, 1979) involving tilt and orientation masking; results were always comparable for real and illusory contours. Other researchers have found evidence of binocular rivalry between real and illusory shapes (Bradley, 1982). Neuropsychological studies (Vuilleumier & Landis, 1998; Vuilleumier, Valenza, & Landis, 2001) have shown that line or shape bisection performance is similar for real and illusory contours, as compared with gap bisection when illusory contours are not present. In these cases, it appears that the brain treats illusory figures as though they were real.

Physiological evidence for shared processing of luminance- and subjectively- defined contours is slightly more controversial. Recordings from the secondary visual cortex of macaque, collected by von der Heydt and his associates (Peterhans & von der Heydt, 1989; Peterhans & von der Heydt, 1993; Peterhans et al., 1986; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984), point to orientation-tuned cells which respond to both real and illusory lines (though not necessarily tuned to the same orientation for each). In humans, Larsson and colleagues (1999) found that ICs alter the correlation between activity in V1 and V2, as compared to the RC response.

Although no direct electrophysiological recordings have thus far been made in human brain, the last decade has seen the publication of multiple neuroimaging studies in which activation related to real and illusory contours has been compared. Hirsch et al. (1995) noted extrastriate areas uniquely involved in the passive viewing of illusory shapes, using functional magnetic resonance imaging (fMRI) of the occipital lobe. The right hemisphere was preferentially activated in comparison with the left. Like many other investigations of real-illusory relationships, however, Hirsch used "real contours" which were black outlines against a white background. Since the corresponding illusory figure generally bears closer resemblance to a solid occluding surface, a "coloring-book"-style shape might be an inappropriate comparison. A positron emission tomography (PET) study by ffytche and Zeki (1996) shared this constraint. The PET results indicated significant levels of activity only in extrastriate regions that were presumed to be V2. Larsson and colleagues (1999) performed an updated PET study in which observers had to make active form discriminations about real and illusory contours.

Larsson and colleagues reported extensive overlap between areas activated by both types of figure; however, ICs produced unique activation in higher visual areas such as the right fusiform gyrus. The ratio between V2 and V1 activity was also different for ICs relative to RCs. Most recently, Mendola and co-workers (1999a) used fMRI with a rigorous visual-field-mapping procedure to compare homogeneously defined luminance shapes (gray occluding squares) with Kanizsa squares and stereo-defined figures. While there was sizable overlap between the bilateral areas activated by Kanizsa and luminance-defined squares, degree of activation was again found to differ. Illusory shapes generated stronger activity in higher-level, non-retinotopic or crudely retinotopic regions such as V3A, V4v, V7, V8, and other, lateral occipital areas. Furthermore, illusory- and stereo- defined squares had extremely similar patterns of activation. These results indicate that common mechanisms may underlie the segmentation of figures in depth.

Other functional imaging studies further support a partial relationship between brain regions subserving illusory contour and real object perception. In all of the aforementioned neuroimaging reports, the IC-sensitive regions overlap with an area we now know to be the Lateral Occipital Complex, or LOC. First described by Malach et al. (1995), this lateral-ventral region of cortex sits just behind MT/V5 and has been selectively implicated in cue-invariant object perception (Grill-Spector et al., 1999; Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998a; Grill-Spector et al., 1998b). The LOC, thought to be homologous with monkey inferotemporal cortex or IT (Tanaka, 1997), is also believed to have size-invariant and position-invariant receptive fields (see Grill-Spector et al., 1999). In other recent work by Doniger et al. (2000) using high-density electroencephalography, signals from a population of neurons near LO were recorded in response to a task involving the identification and closure of incomplete objects. New data suggest that this region may exhibit the earliest cortical response to ICs as compared with NC controls (Murray et al., in press). These studies collectively support a connection between the substrate of visual object recognition in LOC and the regions involved in closure of incomplete objects, such as ICs.

Neurophysiological activity seen in conjunction with the presentation of illusory contours is an important clue to how such images are processed, but it should not be confused with a complete account of their existence. Unless there is information about the function of neurons within active brain regions, vision researchers are still at a loss to list the steps involved in seeing an illusory contour or to put them in chronological order. Other techniques must be invoked which boast much finer temporal resolution than what is seen in the typical functional imaging study. Electroencephalography (EEG) has been put to some use in this capacity (Brandeis & Lehmann, 1989; Brandeis, Jin, Lehmann, & Mueller, 1985; Murray et al., in press; Sugawara & Morotomi, 1991; Tallon, Bertrand, Bouchet, & Pernier, 1995; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). In order to analyze the functional subprocesses which culminate in the perception of an illusory contour, some researchers have employed visual masking (Gellatly, 1980;

Muise, LeBlanc, Blanchard, & de Warnaffe, 1993; Parks, 1994; Reynolds, 1981; Weisstein & Matthews, 1974).

MASKING

Visual masking is an experimental method that permits the researcher to dissect the processes that culminate in perception. This dissection is accomplished by manipulating the relative spatial and temporal properties of the stimulus of interest (the target) and of another stimulus that interferes with target perception (the mask). The approach in which a mask is presented prior to the target is known as forward masking; if the mask follows the target, it is called backward masking. In either case, the experimenter generally studies the subject's ability to perceive the target while various properties of the target-mask relationship are altered. It is common to systematically vary the duration elapsing between the target and the mask (often called the Stimulus Onset Asynchrony, or SOA), and to study the efficacy with which the mask disrupts target perception as a function of this SOA. Here, primarily backward masking (Weisstein, 1966) will be considered.

Two general classes of masking function have been described by Kolers (1962); they are illustrated in Figure 2. The Type A backward masking function is monotonic, such that for short SOAs the mask maximally degrades target perception. Type A functions are also symmetric around SOA = 0; the effect of the mask is a function of the absolute value of the SOA such that the distance between target and mask results in the same degree of impairment regardless of whether masking is forward or backward. The Type B masking function, often described as a U-shaped curve, is associated with backward masking and peaks at a particular SOA.

The mechanism by which a backward mask is able to "catch up with" and thus affect the perception of the target is rather ill-understood. One model which has been proposed to handle this and other problems of masking was described by Breitmeyer (1984). Central to this model is the concept that information passes through the visual system simultaneously in two parallel yet very different channels. Neurons of the *sustained* channel characteristically have small receptive fields, endowing them with sensitivity to fine detail at high spatial frequencies. At the same time, the temporal resolution of these cells is rather coarse. They generally exhibit long response latencies, respond preferentially to sustained stimuli, and conduct signals slowly along their axons. Color opponency and fine orientation tuning are also typical. The *transient* channel has characteristics that allow it to provide information about sudden stimulus appearances and rapid changes in location (motion). These neurons respond quickly to the onset (and sometimes to the offset) of a stimulus. They are sensitive at high temporal frequencies and low spatial frequencies relative to the components of the sustained channel. Physiologically, these complementary types of visual information are somewhat segregated at all levels of the visual system from retina to cortex (Merigan & Maunsell, 1993).

Breitmeyer's model (Breitmeyer, 1984; Breitmeyer & Ganz, 1976) assumes that both the target and the mask activate neurons in both sustained and transient channels. Within a channel, inhibition can occur via the antagonistic center/surround organization of cellular receptive fields; this allows masking between spatially adjacent stimuli (known as metacontrast masking when the target precedes the mask). Masking can also occur by reciprocal inhibition between the two channels. Finally, spatially overlapping stimuli might activate the same population of neurons within a channel. The result of this shared activation could be integration across images of stimulus and mask, such that the individual properties of either are lost.

According to Breitmeyer, backward masking can occur when the sustained response to a target is inhibited by the transient response to a subsequent mask. Because the latency of the transient response is so short, and that of the sustained response is so long, it is theoretically possible that the transient response to the mask temporally coincides with the sustained response to the target. The duration of the SOA determines which target spatial frequencies will be masked most strongly, as higher spatial frequencies (which may recruit more sustained-channel processes) are thought to have longer processing latencies.

In this model, backward masking also results when two temporally discrete stimuli activate a sustained mechanism that integrates over a relatively large temporal window. This type of masking, seen with the shortest SOAs, leads to a Type A (monotonic) masking function.

Michaels and Turvey (1979) proposed a model of central masking which dovetails at the cognitive level with Breitmeyer's (1984) work. Three stages in processing are described: 1) a preiconic stage; 2) iconic memory, a kind of short-term buffer for unprocessed visual information (Neisser, 1967); and 3) an attention-mediated "read-out" process that connects visual information from the iconic stage with higher cognitive levels. Masking at the initial stage occurs when there is an integration of target and mask at the iconic level, which results in a Type A masking function. Integration is thought to occur primarily when the target and mask are presented in close temporal proximity. In the second stage, termed "transient-on-sustained inhibition", transient responses to the mask inhibit sustained target responses at the preiconic level. In this way, target information is blocked from the iconic stage. Breitmeyer and Ganz (1976) suggest that different spatial frequency channels convey their information to the iconic stage at different temporal latencies, with the highest frequencies having the longest latencies and spending the most time in iconic memory. The transient component of the mask, which contains mostly low frequencies, interferes with progressively higher target spatial frequencies the later it is presented. Although this type of "interference masking" is seen when somewhat longer SOAs between target and mask are utilized, it should be noted that the level of disruption is actually earlier in the processing stream (i.e., the mask transient component interferes with the target sustained component prior to the iconic level). A Type B function describes this form of interference masking. Finally, at the third stage, the "read out" process which transfers information out of iconic memory to semantic and other cognitive mechanisms is susceptible to an attentional disruption from the mask.

It is crucial to understand the processing level at which a mask affects a target; once this has been established, the experimenter can halt the chain of processing events at that level and thereby gain access to the temporary state of the system at that point. Masking thus provides a way to "peek inside the box", effectively querying the system about a static point in a dynamic sequence of events. This renders it a powerful tool for accessing information processing at any of the aforementioned stages, which provides clinical utility for apprehending pathological processes in certain neuropsychiatric conditions through behavioral methodology. Work by Slaghuis and Bakker (1995) and Green et al. (1999) has revealed abnormalities of Type A (precognitive) backward masking in patients with schizophrenia, while other work (Bachmann et al., 1998) has revealed abnormalities in masking associated with Parkinson's Disease. In a similar manner, masking has been used to understand more thoroughly the stages underlying a number of visual phenomena. It seems logical, if one is trying to understand the temporal sequence of events leading to illusory contour perception, to apply masking as a way to access the output of a particular processing stage. Such an approach has been applied to the microgenesis of illusory contour perception.

BACKWARD MASKING AND MODELS OF BOUNDARY COMPLETION

Reynolds (1981) applied a backward masking technique to the study of illusory contour microgenesis. He theorized that the inducing pattern is perceived prior to the IC surface; he also thought that subsequent stages of processing represented the output of various hypothesis-testing stages. Reynolds presented Kanizsa-type triangles for a duration of 50msec. After various SOAs, he presented a patterned mask consisting of 3 random-noise discs in place of the inducers. Observers were asked to discriminate between a straight-sided triangle, a curved triangle, or no triangle at all. In some stimulus displays, the triangle was intercepted by a brick-wall pattern that was logically incompatible with the depth information that would correspond with a perceived illusory triangle. By varying SOA between triangle and mask, Reynolds found that IC perception could take place by 100msec but that the percept disintegrated 50-100msec later when the brick overlay was present. He concluded that top-down processes were operational at these relatively late durations, consistent with a hypothesis-testing model of IC perception. He assumed that he was collecting output from several processing stages, each one of which represented the most logical hypothesis at that time. However, there were several potential confounds inherent in his experimental design. Reynolds failed to measure reports of IC perception at long SOAs *without* the presence of the brick overlay, rendering its relevance to the loss of the IC percept at late durations somewhat questionable. Further, as Parks (1994) later pointed out, by varying blank duration rather than stimulus presentation time, Reynolds was merely manipulating how long subjects needed to hold the inducing pattern in their iconic memory. Not surprisingly, at longer durations, the illusion would disappear because the icon of the inducers would be forgotten. While in a later study Parks (1995) did demonstrate some top-down influences on IC perception at SOAs of approximately a half-second, these findings alone do not necessarily advocate a purely top-down model. For example, a bottom-up model of IC perception that can be attentionally modified at later stages would also be consistent with Parks' findings.

Ringach and Shapley (1996) introduced a new, objective task to approach the problem of illusory boundary completion. The "thin/fat" task requires observers to discriminate between two classes of illusory shape, which differ from each other only in the magnitude of a single parameter. While previous studies of illusory contour strength relied upon subjective ratings or simple "presence/absence" reports, the new task allows the measurement of a psychometric function that precisely describes an observer's ability to perceive the contour.

Ringach and Shapley proposed a two-stage model of boundary completion, in which local features are detected prior to a stage of global integration. This proposal is supported by earlier reports (Muise et al., 1993) that perception of the inducers precedes awareness of the illusory surface. Ringach and Shapley used backward masking to estimate the temporal dynamics of each of the two stages.

Using a mask containing local orientation information, they found that the initial stage is completed within 117 msec of stimulus onset. This phase was thought to represent local processing of the inducers. Adding a second mask, another illusory figure, interfered with processing at intermask durations of 140-200 msec (SOAs of 307-367 msec). Ringach and Shapley concluded that such long periods of integration time suggest that boundary interpolation is an iterative process, requiring crosstalk among multiple mechanisms. They also noted that Sekuler & Palmer (1992) found that objects can be perceptually completed in 100-200 msec, which seems comparable with their own result. This study represents an improvement over previous attempts to mask illusory contours (Gellatly, 1980; Muise et al., 1993; Parks, 1994; Reynolds, 1981; Weisstein & Matthews, 1974), in that many only introduced masking at one stage of processing and did not use an objective task to measure performance.

The notion of a boundary completion system that subsumes at least two processing stages is logical, given our knowledge of cortical physiology. Early stages in visual processing are specialized for the detection of local features, while later stages are associated with larger receptive fields and presumably more abstract image features (i.e., faces, object primitives). However, a two-stage model is certainly not the only interpretation of the aforementioned result (see, e.g., Bar et al., 2001). In fact, work from the neuropsychological literature (Riddoch & Humphreys, 1987) and from the field of computational vision (Marr, 1982) suggests that multiple stages intervene between local orientation detection and the full-fledged activation of an object's representation. Boundary completion, surface segmentation, object identification, and categorical recognition are likely candidates for such stages. While Ringach & Shapley's results are intriguing, they leave certain issues open to interpretation. One very important issue is that of which stage(s) in the hierarchy of visual processing their second mask is actually disrupting.

The precise timing in the Ringach & Shapley experiment was as follows: First, a Kanizsa figure was presented for 117msec. The subject was later required to make a judgment about the shape of this figure. Next, a mask containing local orientation information was flashed on-screen for 50msec. The third interval contained a blank screen, whose duration was varied systematically. Finally, the second mask appeared for 300 msec. The second mask was also a Kanizsa figure, in this case a square. Following presentation of all images in a given trial, the subject was asked to report on the shape of the first figure.

In considering the details of the above procedure, several items are worthy of note. First, the Kanizsa square remained on the screen long enough to ensure that local processing was completed, according to an earlier experiment. Therefore, one may safely assume that no further local processing is *required* in order to perform the task. Since an iterative process is postulated, however, it is logical to present the first (local) mask anyhow; this ensures that no further local stimulus information will enter the system, and makes it unlikely that local processing of the stimulus will continue.

Next, although Ringach and Shapley posit that the second, boundary completion stage requires 140-200 msec to complete, they base this estimate solely on the intermask duration that results in a threshold elevation. However, 140-200 msec should be regarded as a *minimum* for the length of this stage, since there is no way to know from their experiment whether Stage II receives valid input prior to the end of Stage I[1]. Furthermore, they are excluding the duration of the local mask from their estimate. Finally, since the global mask is also an illusory contour, it seems reasonable to factor in some period of time (less than 117msec) in order for the local processing of the mask to complete. The combined time for any interaction of the two stages during the viewing of the stimulus, and any local processing time for the second mask itself, must always total 117msec. Thus, the revised estimate of the time taken by "Stage II" is thus ~307-367msec. More recent studies by Imber et al. (2000) suggest that masking may be seen at intermask durations up to 400 msec, which would increase the original estimate by an additional 200 msec.

It is hard to imagine, given such a lengthy estimate of processing time, that the posited "Stage II" consists of merely one step in the chain of object-recognition events. There are several possible alternatives. For example, if Stage II is the level at which boundary completion takes place, it may still iteratively interact with higher (and possibly lower) stages before reaching an equilibrium state that is

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[1] This situation might occur if, for example, the 117 msec includes time for both Stage I to complete and for an iterative interaction between Stages I and II. Perhaps there is a short time during which

interpreted as a "final answer". Until equilibrium is attained, the subject's percept may be more easily perturbed by the mask, which competes with the input from higher stages.

Another plausible scenario is that "Stage II" (boundary completion) is completed well before the presentation of the second mask, and that the mask interrupts something beyond this step. In this case, we would expect that the interference would involve a visual-cognitive process such as surface representation, shape categorization, or perhaps conscious decision-making. A third possibility is some combination of the two—the mask could interfere with boundary completion at the purported Stage II as well as the cognitive representation at a higher, yet concurrent, stage of processing.

It is worthwhile to ask how the results of this experiment bear upon the theories of masking discussed previously. Given the extremely long durations between stimulus and mask, integration of the two stimuli into one percept (i.e., Type A masking) is unlikely to be the cause of degraded performance. Some remaining possibilities are: 1) The transient response to the illusory square mask interferes with the sustained component of the target illusory shape, prior to storage in iconic memory. 2) The target shape proceeds to iconic memory, but the mask creates a distraction which prevents the target from ever being "scanned out" to higher areas (i.e., a more "attentional" explanation). No distinction between these

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Stages I and II proceed in parallel.

possibilities is currently possible. One might suppose that "iconic memory" refers to the stage at which the illusory shape representation is constructed. If this is so, what stage of processing must the *mask* have reached in order to disrupt this icon? Need the mask have undergone "local processing" itself, or is the low-pass transient response sufficient to prevent transfer of the sustained target response into the iconic stage? A myriad of possibilities exists, but there are not yet enough data to draw a clear conclusion.

Ringach and Shapley (1996) have made a valuable contribution to the study of illusory contour microgenesis with their introduction of an objective task that measures illusory boundary strength. The number of studies that have adopted this methodology since its introduction testifies to the void in the field which was filled by this task (e.g., Gazzaniga, 2000; Gegenfurtner, Brown, & Rieger, 1997; Gold, Murray, Bennett, & Sekuler, 2000; Greene & Brown, 2000; Imber et al., 2000; Liinasuo, Rovamo, & Kojo, 1997; Rubin, Nakayama, & Shapley, 1996; Victor et al., 2000). Further, the authors have demonstrated a clever means of accessing various stages of this operation through the use of differing types of backward masks. What is not yet known is at what location(s) in the brain these stages occur; what leads up to them, and what are the processes involved? How do these processes relate to "normal" object perception? Once the procedure is more thoroughly understood, it can be more fully adapted for the investigation of numerous questions regarding the formation of illusory contours.

HIGH-DENSITY ELECTROENCEPHALOGRAPHY

Although psychophysical methods such as masking can provide some temporal information about neural processes, the nature of this information is dependent upon observations of a subject's behavior. While a mask may disrupt some of the processes that culminate in perception, it cannot prevent all subsequent processes that might be reflected in the actions of the observer. Therefore, post-perceptual mechanisms such as cognition, memory, and response formulation may all be affecting an observer's report when it is taken at the end of a given trial. A means of directly measuring neural processes as they occur, prior to the "output" stage, would be optimal. Event-related potentials, or ERP, represent one method of gathering such information (Luck & Girelli, 1998; Vaughan & Arezzo, 1988). ERP can be recorded non-invasively and with real-time precision (at the msec scale), by placing an electrode array on the scalp and recording voltage differences that occur between individual electrodes and a reference electrode placed in a relatively neutral anatomical region. These voltage differences, or potentials, represent the post-synaptic activity of large neuronal populations. Depending upon the position and orientation of the active cortical region, the voltage measured at the scalp will vary in amplitude and distribution. The resistivity of the meninges and skull leads to a smearing at the scalp of potentials originating in different brain areas. However, there are methods which can help to recover some of the spatial information about neural generators that originate scalp potentials (see e.g. Luck & Girelli, 1998; Perrin, Bertrand, & Pernier, 1987; Vaughan & Arezzo, 1988).

Because there are numerous artifacts that can be confounded with the EEG signal, it is generally necessary to time-lock the measurement of ERP to the presentation of a stimulus or some other event. It then becomes a fairly simple matter to average the waveforms from a number of identical trials, which reduces the ERP to its essential componentry. ERP are often described in terms of a series of peaks and valleys, whose amplitudes depend upon signal strength and generator location and whose polarities are determined by generator location with respect to the reference electrode. Positive peaks are usually referred to as "P" plus their ordinal place in the componentry, while negative valleys are "N" plus their ordinal position. Therefore, "P1" is the first positive component while "N3" is the third negative component. Occasionally, components will be discussed with reference to their latency; for example, P300 is the positive component at 300msec post-event. By comparing the amplitude and latency of each component evoked by different stimuli, one can hope to identify common or disparate mechanisms associated with their respective processing.

ERP have previously been applied to the study of illusory contours (Brandeis & Lehmann, 1989; Herrmann & Bosch, 2001; Herrmann & Mecklinger, 2000; Herrmann, Mecklinger, & Pfeifer, 1999; Korshunova, 1998; Korshunova, 1999; Murray et al., in press; Sugawara & Morotomi, 1991; Tallon et al., 1995; Tallon-Baudry et al., 1996). One early study showed that ICs modulated the scalp topography at latencies (170-380msec) similar to the effects of attention (Brandeis & Lehmann, 1989). More recently, studies have found differential activity related to IC processing over lateral occipital electrodes (e.g., Herrmann et al., 1999; Korshunova, 1999; Murray et al., in press; Sugawara & Morotomi, 1991; Tallon et al., 1995; Tallon-Baudry et al., 1996). The earliest low-frequency differences have been reported at the N1 component at ~140-180msec post-stimulus onset, although at times the effect can be delayed until ~200-275msec when processing is more effortful (Murray et al., in press). Other studies have examined high-frequency (gamma-band) activation in response to illusory contours (e.g., Herrmann et al., 1999; Tallon et al., 1995; Tallon-Baudry et al., 1996). This activity, usually seen at relatively late durations (>200msec), can include occipito-temporal electrode sites but is sometimes seen over anterior scalp as well. While the gamma-range activity has been ascribed to feature-binding processes (e.g., Tallon et al., 1995), Murray and colleagues (in press) note that lower-frequency differences between contour types precede the high-frequency oscillations and suggest a possible role for these oscillations in an attentional or other high-level process.

To date, none of the earlier ERP studies have made use of a challenging task; the possibility therefore remains that ICs engage more attentional resources than do their NC counterparts (which could account for some of the differences seen in the ERP). Although some have attempted to compare ICs and RCs using ERP, no other researchers have used a solid gray surface as a comparison to the IC. The high temporal resolution of the evoked potential method is optimal for a comparison between illusory, real, and no-contours, especially in the context of a difficult task (i.e., the thin/fat task described above). Such a study would further help to flesh out the processes that have been identified in psychophysical masking studies, and to tie them to object recognition processes in lateral occipital cortex.

RATIONALE FOR THE PRESENT STUDIES

A major goal of the first study is to compare real contours and illusory contours in their ability to interfere with a task (Ringach & Shapley, 1996) that is believed to require boundary completion and/or surface formation. The original masking effect (in which an illusory square masked perception of thin/fat shapes) was demonstrated on only two experienced subjects; I propose to replicate this result in a larger population. My colleagues and I subsequently aimed to expand the result to include a comparison of real and illusory shapes. Most explanations of illusory figures posit a common mechanism for the perception of illusory surfaces and of real surfaces in degraded conditions. If this is entirely so, then a real surface might also be expected to mask an illusory shape. While previous studies have purported to address this issue, their characterization of a "real shape" was usually merely an outline rather than a homogeneous surface. Use of a surface is more consistent with the properties of occlusion and "objectness" generated in the illusory case, and would be expected to produce the most similar effect.

If, however, the real surface does not produce masking in this instance, one cannot necessarily conclude that there is *no* common processing. If the late-stage mask does not truly interrupt boundary completion, but prevents some other process from occurring, then a real contour might not necessarily be expected to interact with the illusion. Therefore, a second goal, which will improve our understanding of the real-illusory interactions we propose to explore, is a more thorough characterization of the late-stage masking described by Ringach and Shapley (1996). Whether the mask interrupts early boundary completion as opposed to a higher-level representation of the stimulus is unclear. Properties of the second mask such as contrast, surface type, and size are therefore manipulated to gain more information about the scope of the masking. If the illusory mask is still effective despite variations in low-level attributes, an intermediate or high-level process is implicated. Whether this process plays a role in boundary completion, or in some later, cognitive process, also remains to be determined.

The goal of the second study is to connect performance on this psychophysical task with an electrophysiological measure of visual closure. It would be instructive to record EEG signals from human brain regions which have been implicated in object perception (Doniger et al., 2000; Grill-Spector et al., 1998b; Malach et al., 1995) and illusory contour perception (ffytche & Zeki, 1996; Imber, 1999; Larsson et al., 1999; Mendola et al., 1999a; Murray et al., in press) while the thin/fat task is performed, to find a neural correlate of the stages at which masking is effective. If the latency of the electroencephalographic trace is comparable to the latency of peak masking, then we have the means to link the second processing stage proposed by Ringach & Shapley (1996) to a discrete neural region. Furthermore, we can investigate the neural signatures of the thin/fat task when observers are judging real, illusory, or no-contour stimuli. This study will yield a direct comparison of the processing timecourses affiliated with each contour type, further helping to explain the masking results. The inclusion of the task will increase participant engagement and allow us to manipulate difficulty and monitor accuracy. In combination with previous findings in the literature, our results will promote the understanding of the processes of object recognition and illusory shape formation.

FIGURES

FIGURE 1.1: SOME EXAMPLES OF ILLUSORY CONTOURS.

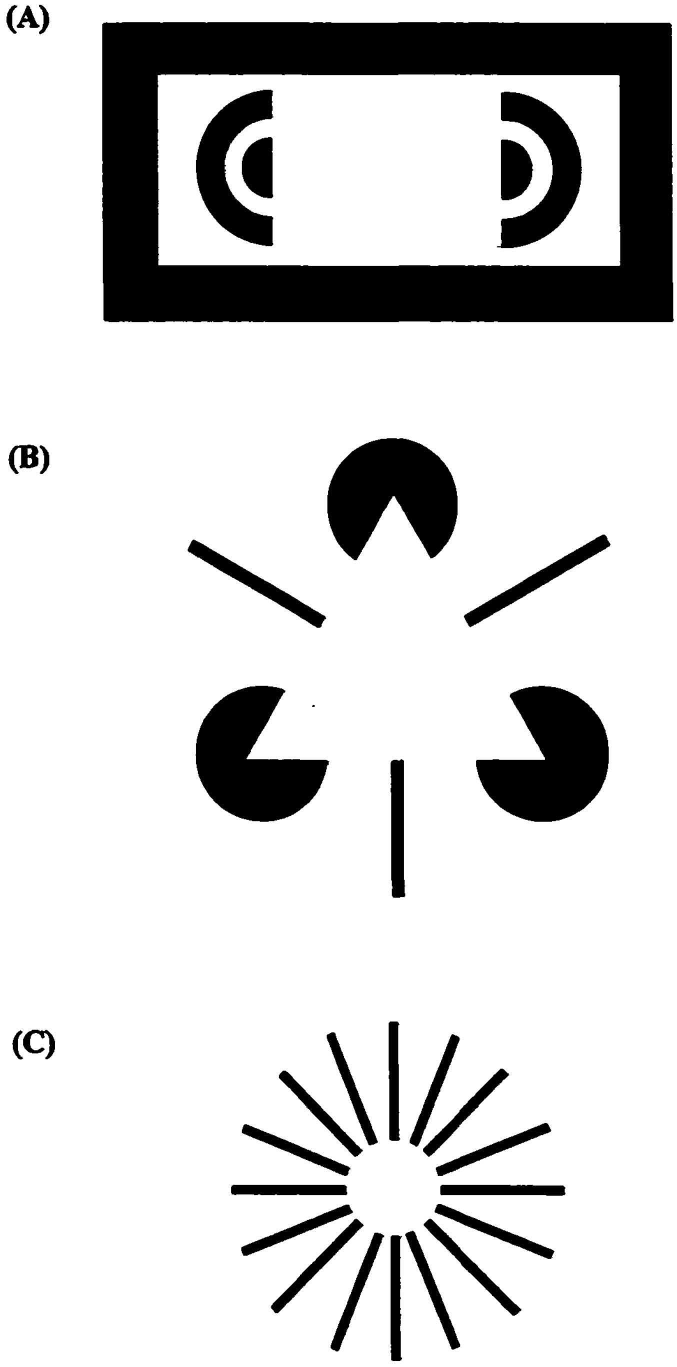
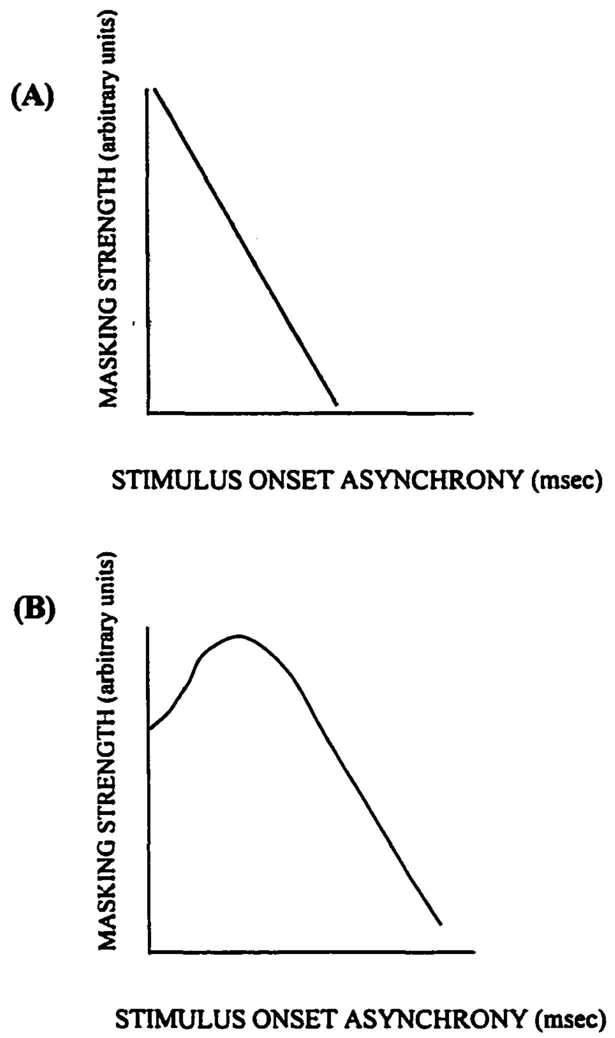


FIGURE 1.2: MASKING FUNCTIONS.



Paper I:

Discrepancies in microgenesis of real and illusory contour perception revealed by backward masking

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ABSTRACT

Illusory contours (ICs) are thought to be a by-product of processes involved in the perception of real objects under degraded conditions. Here, we investigate the relationship between real and illusory contour microgenesis using a shape discrimination task and backward masking paradigm first described by Ringach and Shapley (1996). Although we replicate their finding that ICs can mask other ICs at very late (in the vicinity of 300msec) SOAs, we find that real contours (RCs) are not similarly effective. This result holds for RCs at perceptually salient contrasts, as well as RCs with contrast lowered to match the apparent contrast of the illusory surface. We also find that RCs are not masked at this late stage, either by ICs or by other RCs. Finally, we demonstrate that the masking seen between ICs is size-invariant in nature. We interpret these data in support of an iterative model of IC processing, in which surface representation occurs at intermediate levels of the visual hierarchy.

INTRODUCTION

Neuroscientists have long tried to understand the normal processes of the brain by studying what is abnormal or unusual. In attempts to dissect the complex computations that result in visual recognition of objects, researchers have studied a perceptual illusion known as the illusory contour (Kanizsa, 1955; Kanizsa, 1976; Petry & Meyer, 1987; Schumann, 1987), or IC. This phenomenon, illustrated in Figure 1, results when observers perceive a surface occluding a set of carefully aligned inducing elements (inducers, or pac-men) over an otherwise homogeneous background. It is thought that illusory contours are byproducts of routines (or automatic processes) in the neural mechanisms responsible for segmentation. These routines are believed to underlie perception of real objects in the visual world, particularly in degraded visual conditions such as poor contrast between object and background, low luminance levels, or the occlusion of one object by another (Kellman & Shipley, 1991).

If the visual system creates illusory contours through a perceptual process that also underlies real contour perception, then logically both types of stimuli must proceed through at least partially overlapping channels. Numerous psychophysical studies point to a common mechanism for both real and illusory edges. For example, there are interactions between real and illusory lines in a task of vernier acuity (Greene & Brown, 1997) and in versions of famous perceptual phenomena such as the Poggendorff (Beckett, 1989; Beckett, 1990) and Bourdon (Walker &

Shank, 1988a) illusions. Studies have been made of common aftereffects (Paradiso et al., 1989; Smith & Over, 1976; Smith & Over, 1977; Smith & Over, 1979) involving tilt and orientation masking; results were always comparable for real and illusory contours. Other researchers have found evidence of binocular rivalry between real and illusory shapes (Bradley, 1982). In these cases, it appears that the brain treats illusory figures as though they were real.

In order to analyze the subprocesses that culminate in the perception of an illusory contour, researchers have employed visual masking techniques (Gellatly, 1980; Muise et al., 1993; Parks, 1994; Reynolds, 1981; Ringach & Shapley, 1996; Weisstein & Matthews, 1974) in which the processing of a target shape is interrupted by the presentation of a second figure. Masking is thought to enable the investigator to halt the stream of visual processes, and to query the system about its current state at the time of the disruption. Such paradigms can be useful for elucidating the temporal evolution of the illusory percept.

Reynolds (1981) applied a backward masking technique to the study of illusory contour microgenesis. He theorized that the inducing pattern is perceived prior to the IC surface; he also thought that subsequent stages of processing represented the output of various hypothesis-testing stages. Reynolds presented Kanizsa-type triangles for a duration of 50msec. After various stimulus onset asynchronies (SOAs, the duration between onset of the target and onset of the mask), he presented a patterned mask consisting of 3 random-noise discs in place of the inducers. Observers were asked to discriminate between a straight-sided triangle, a curved triangle, or no triangle at all. In some stimulus displays, the triangle was intercepted by a brick-wall pattern that was logically incompatible with the depth information that would correspond with a perceived illusory triangle. By varying SOA between triangle and mask, Reynolds found that IC perception could take place by 100msec but that the percept disintegrated 50-100msec later when the brick overlay was present. He concluded that top-down processes were responsible for the disappearance of the illusory surface at these relatively late durations, consistent with a hypothesis-testing model of IC perception. However, there were several potential confounds inherent in his experimental design which could have erroneously biased his results towards a top-down interpretation (see Parks, 1994; Parks, 1995 for discussion).

Ringach and Shapley (1996) devised a shape discrimination task that allows an objective measurement of the strength of IC perception. They employed this task in a variety of experiments to probe several characteristics of boundary completion. In experiments which used a backward masking paradigm (Weisstein, 1966), they double-masked illusory targets to investigate the temporal evolution of IC perception. The first mask contained local orientation information meant to confound the extraction of low-level features from the stimulus array (i.e., line terminators and edges affiliated with the inducers). This mask proved effective until SOAs of ~117msec following stimulus onset. A second mask, which consisted of another illusory surface, was thought to disrupt global shape integration and impaired performance at latencies of ~140-200msec after the presentation of Mask 1. A no-contour (NC) control, with all inducers facing outwards, failed to mask the illusory shape at this latency. Based on their findings, Ringach and Shapley conjectured the existence of at least two discrete stages in the processing of ICs. In the first stage, local luminance features are detected; in the second, the illusory boundary is interpolated into a global percept of a shape. They proposed an iterative model of boundary completion, which could be implemented at numerous possible levels in the hierarchy of visual processing.

The purpose of the present study was to investigate the relationship between real and illusory contour processing, by characterizing more fully the second processing stage initially described by Ringach & Shapley (1996). In addition, we sought markers that would link this stage in the microgenesis of IC perception with anatomical and physiological correlates of object perception phenomena described elsewhere in the literature. To that end, we employed the shape discrimination task and backward masking paradigm described by Ringach and Shapley (1996). We measured participants' thresholds for the amount of curvature needed to discriminate between thin and fat illusory shapes, while we manipulated the properties of a late-stage mask. The late mask could be either an IC or a surface defined homogeneously by a luminance decrement (a real contour, or RC). We explored the effect of surface contrast on shape discrimination by employing RC masks at two different contrast values: perceptually salient, and low contrast (to resemble the IC). Further, we used a cross-masking technique to test the ability of illusory masks to interfere with perception of RC targets. Finally, we studied the sensitivity of this stage of masking to low-level stimulus properties. Our findings support the localization of IC completion at intermediate stages of the visual processing stream, with a time course which differs greatly from that of RC perception.

GENERAL METHODS

Observers

All observers had normal or corrected-to-normal vision, and were naïve as to the purposes of the experiment. Prior to their acceptance into this study, observers completed one or more training/screening sessions (adapted from Rubin, Nakayama, & Shapley, 1997) to ensure their ability to perform the task properly and consistently. The initial session generally comprised six blocks of trials, where Block 1 and Block 2 contained fairly easy practice trials designed to familiarize the subject with the task. In Block 3, the subject made a more difficult discrimination. Blocks 4 and 5 were identical, and each contained a mixture of difficult and easy trials. Finally, Block 6 was identical to Block 3. Rubin et al. (1997) showed that this procedure leads to an abrupt, stimulus-specific form of perceptual learning. Significant improvement from Block 3 to Block 6 was a criterion of acceptance into this study; specifically, subjects whose thresholds exceeded 3.0 degrees on Block 6 or who performed the task in an erratic manner were not retained. Across all four of our experiments, approximately half of individuals who participated in the screening met these inclusion criteria. All participants were compensated for their participation, either with payment or with credit hours that filled a course requirement.

Stimuli

A Silicon Graphics Indigo II computer generated all stimuli and presented them on a 343 mm x 274 mm screen (resolution of 1280 x 1024 pixels). The refresh rate was 72 Hz, and the mean luminance was 16.7 cd/m^2. Participants sat in a darkened chamber, where they viewed stimuli binocularly at a distance of 60 cm from the screen.

Illusory shapes were Kanizsa squares or distorted versions of Kanizsa squares. They consisted of four "pacman" inducers aligned to produce the illusion of a square occluding four disks. The corners of the square were located at the center of each inducer, such that the length of the square's side equaled the distance between inducer centers. Real shapes were identical to the analogous illusory shapes except that their surfaces were colored uniformly to make the location of the shape explicit. See Figure 1 (B,C) for examples.

The inducers and local masks were always brighter than the background at +30% contrast (such that they appeared white against a field of gray, with a luminance of 21.7 cd/m^2). When real squares were presented, the inducers were at +30% contrast while the real surface appeared dark gray. In most cases, real surfaces were presented at a contrast of -15% (luminance = 14.2 cd/m^2). For Experiment 2, however, the real surface appeared only slightly darker than the background at a contrast of -3% (16.2 cd/m^2). Unless otherwise noted, all square figures subtended ~15.6° of visual angle (and hence were bounded at an eccentricity of 7.8°). The inducers subtended approximately 2°, yielding a support ratio of $\mu = 0.25$ (i.e., 25 % of each side of the square was "supported" by the presence of the inducers, while 75% was illusory).

Procedure

The task for this experiment was first described by Ringach & Shapley (1996). Subjects discriminated between two types of shapes, called "thin" or "fat" (see Figure 1). To generate a test shape, the inducing elements of a Kanizsa square were rotated by an angle of α degrees. The top-left and bottom-right inducers were rotated by $+\alpha$, and the top-right and bottom-left inducers were rotated by $-\alpha$, such that a positive angle denotes counterclockwise rotation. The angle of rotation for the upper-left-hand inducer is taken, by convention, as the α for a particular stimulus. Inspection of Figure 1(A) reveals that shapes having a positive value of α appear to have pinched-in sides and an outward-bulging top and bottom (called "thin"), while shapes with a negative α bulge outwards at the sides but inwards at the top and bottom ("fat"). It should be noted that the terms "thin" and "fat" were not used with participants. For each subject and condition, five values of $\pm\alpha$ were presented (yielding 10 stimulus levels). Each stimulus level was shown 20 times in block-randomized order using the method of constant stimuli. In the resulting psychometric functions, based on 200 trials each, the angle of inducer rotation α was the independent variable while the dependent variable was the fraction of trials in which subjects classified the shapes as "thin". Because a within-subjects design was used, multiple psychometric functions were measured for each subject in a counterbalanced order. Subjects fixated on a small black diamond throughout the experiment, located at the center of the figure, and were given audible feedback in the form of a computer beep for each correct response.

Analysis

For each experiment, thresholds were computed both for individual observers and for averaged observers based on pooling of the raw data. Psychometric functions for individual observers were fitted to sigmoidal curves of the form $y = ([1 + \tanh(B(x-A))]/2)$, such that the slope B and the bias A were free parameters. The abscissa was the rotation angle α and the ordinate was the fraction of stimuli the subject reported as "thin" at that value of α. The threshold was defined as the α at which 81.6% of the stimuli were classified as "thin". Bootstrap simulation (Efron & Tibshirani, 1993) was employed to determine the statistical reliability of the estimated parameters. One thousand simulated experiments were performed for each psychometric function fit, weighted by the subject's actual performance at each stimulus level. Thus, 1000 new sigmoid functions were fit to the simulated data and 1000 new estimates of threshold and bias were computed. The mean and standard deviation of the resulting distribution of parameters were then calculated to estimate the bias and variance of the original psychometric function fit. Thresholds are reported ±1 standard deviation of the bootstrap distribution. For "pooled" data, raw data from individual subjects (% "thin" for each stimulus level) were averaged across all subjects within an experimental condition and the resulting curve was fit to a sigmoidal function as before. This procedure allowed us to again obtain threshold, bias, and standard deviation information for each experimental condition. Unless otherwise noted, figures depict pooled data.

Experiment 1: Backward Masking of Illusory Shapes with Real and Illusory Squares

The first goal in this series of experiments was to replicate in a larger sample Ringach & Shapley's (1996) finding that illusory squares are an effective late-stage mask for illusory thin/fat shapes, and furthermore to determine whether real squares are similarly effective.

Method

Observers

Seven naïve observers participated in this experiment. Each observer was required to attend and pass a training/screening session as described above. Data for this experiment were collected in three subsequent sessions of 30-45 minutes each.

Procedure

The events composing each trial are depicted in Figure 1(B,C). To initiate a trial, the subject pressed a button on the computer mouse. This produced a fixation mark, which remained on the screen throughout the duration of the trial. The first stimulus in the sequence was the illusory figure, which could either be thin ($\alpha>0$) or fat ($\alpha<0$). It remained on the screen for 83 msec, and was followed by a blank screen (mean luminance, with the fixation point) for 42 msec. Next, a "local" mask consisting of four pinwheel shapes was shown for 56 msec. Each pinwheel shared an identical radius, position, and contrast with the inducer previously occupying its location. The local mask, rotated randomly from trial to trial, contained orientation information that, according to Ringach & Shapley's (1996) model, served to limit the local processing time for the illusory stimulus to under 125 msec. A second blank was then presented, for a variable duration (Γ msec). Finally, a late-stage mask comprised of a square ($\alpha=0$) plus inducers was presented for 306 msec. The square could be either real or illusory. At this point in the trial, the fixation mark disappeared and subjects pressed a button to indicate whether the first shape appeared to be thin or fat. Within each block of trials, α and Γ were varied but mask condition (real or illusory) was constant. Block order was alternated such that all odd blocks contained only illusory square masks and all even blocks contained only real square masks. Each observer contributed data for both mask conditions and for each of five Γ durations, yielding a total of 10 psychometric functions per observer.

Results

Pooled thresholds, computed by fitting threshold curves to the averaged raw data of all seven participants, appear in Figure 2. The masking function obtained when Mask 2 was an IC square is in agreement with data reported previously (Imber et al., 2000; Ringach & Shapley, 1996). The IC mask causes an elevation in discrimination threshold that peaks at intermask durations of ~100 msec. When Mask 2 is an RC, however, no masking is seen. Significant differences between IC and RC thresholds are observed at all points prior to $\Gamma = 403$ msec. A baseline threshold value was obtained from the last block of the training session, in which trials included only three frames—a stimulus, blank screen with fixation, and pinwheels mask. The reader should note that in subsequent experiments (Experiments 3 and 4), we also remeasured the baseline threshold after the completion of the study. Because for most subjects some degree of additional learning was evident in those experiments, it is likely that the baseline estimate depicted in Figure 1 is somewhat higher than the "true" value.

Discussion

Ringach and Shapley (1996) proposed that the pinwheels mask (Mask 1) interferes with local processing of the pacman inducers, while the square mask (Mask 2) disrupts boundary completion processes for the illusory surface. Here, we find evidence suggesting that RCs are not able to interfere with IC completion at latencies similar to those at which an IC mask is effective. There are a host of possible reasons for this finding. It could be that different populations of neurons are involved in IC and RC shape completion. Another possibility is that the time course of IC and RC processing is drastically different, such that the stimulus and mask do not interact temporally at these relatively long masking latencies (with SOAs of ~280-350 msec). A third alternative is that the second mask disrupts a process upstream from boundary completion, such as visual categorization or shape recognition, which may be the product of disparate neural mechanisms for ICs and RCs. However, before these questions can be addressed, there remains the possibility that low-level stimulus properties are preventing the RCs from serving as a strong mask. This question was investigated in Experiment 2.

Experiment 2: Backward Masking of Illusory Shapes with Low-Contrast Real Squares

Observers reported that the real square appeared "so much darker" and thus "perceptually different" from the illusory shapes of Experiment 1. We thus considered the possibility that a contrast-sensitive mechanism was behind the masking effect. Alternatively, perhaps the relatively high contrast of the gray square made it seem irrelevant and thus easily ignored. In Experiment 2, we tested the possibility that the RC would be a more effective mask if its perceived contrast more closely resembled that of the IC. The contrast of the RC mask was decreased to the smallest just-noticeable-difference above detection threshold that was resolvable by the limitations of the stimulus delivery system.

Method

Observers

Two individuals, who participated in Experiments 1 and 3 respectively, also served as participants for this control experiment.

Procedure

The experimental procedure was identical to that of Experiment 1, except that Mask 2 was a pale gray RC presented at -3% contrast to the background.

Results

Observers reported that a pale real square bore a strong phenomenological resemblance to an illusory contour, even though the shape was still perceived as a real surface. However, the individual masking functions shown in Figure 3 suggest that a pale real square is not able to mask an illusory shape. For observer EP, significant differences between masking conditions are observed at $\Gamma = 97, 125, 137$, and 403 msec; for observer GE, significant differences are evident at $\Gamma = 167$ and 403 msec.

Discussion

These data are consistent with pilot data presented earlier (Imber et al., 2000), which similarly suggested that drastically decreasing the contrast of a gray surface does not improve its ability to mask an illusory shape. Observers seem not to be merely ignoring the RC due to a gross qualitative difference from the IC. A mechanism relying on perceived contrast can likely be discounted as well.

The results of Experiments 1 and 2 imply that there is a fundamental divergence in the processing of ICs and RCs within the context of the thin/fat task. This difference could reflect spatial segregation of processing resources, incongruities in time course of processing, or some combination of the two. Another vital issue is the point in the microgenesis of the task at which the IC mask causes its disruption. Possible candidates are boundary completion, shape closure, object representation, or shape categorization. In the latter case, one might argue that the participants are never asked to make shape judgments about the RC class of stimuli. Therefore, they may seem irrelevant to the decision process. To control for this, and to explore the interaction between real and illusory shapes further, a new experiment was devised in which a 2 x 2 design allowed both RCs and ICs to function as stimulus and mask.

Experiment 3: Cross-Masking Between Real and Illusory Shapes

To this point, only ICs have served as a target for the thin/fat discrimination. It would be useful to know if the task can be made similarly challenging using RCs as thin/fat targets. By connecting the points tangent to the inducer "mouths" with an arc, we made RC versions of the thin/fat stimuli. With a 2 x 2 design, we were therefore able to compare RCs and ICs in terms of their ability to mask and be masked.

Method

Observers

A new set of 6 observers were recruited, and divided into two groups. For this experiment, two training sessions were required for each observer. One group of observers completed the standard six-block training session as described previously. The other group completed a similar training session, except that they first learned to make the thin/fat discrimination using real instead of illusory shapes. In the second session of the experiment, observers trained in the alternate contour condition. This allowed us to control for the order in which subjects were exposed to the different contour classes.

Stimuli

The structure of trials in this experiment followed that used in Experiments 1 and 2. A thin or fat target stimulus was presented in the first of five frames. The target could be illusory, as before, or a real surface, at −15% contrast compared to the background so that it appeared dark gray. The second frame was again a blank screen with fixation point. It was evident, however, that an alternative to the pinwheels was needed in place of the first mask when the target was a real shape. The new mask must contain sufficient information to obscure local edge information about the curvature of the surface. Accordingly, we created a real surface whose sides were defined by a sinusoidal function (see Fig. 4(A) for example). This surface was used as Mask 1 only when the target was a real shape; if the target was illusory, the pinwheels were used as before. Each side of the new figure varied randomly in phase across trials. The amplitude of the sinusoidal edges and contrast of the surface were adjusted to produce a similar level of performance for shape discrimination in the absence of the second mask, for both IC and RC targets (i.e., in the training sessions). As before, the fourth frame was a blank screen which varied in duration across trials, and the fifth frame was a square that could be either real or illusory in nature.

Procedure

Each subject participated in a total of six sessions. The first two were training sessions, as described above. In all subsequent sessions, there were four conditions that allowed for all possible combinations of real and illusory targets and masks. Trials within a block all belonged to the same condition, as before, but again varied as to intermask duration (Γ) and angle of inducer rotation (α). Each block consisted of 100 trials; a subject completed 40 blocks for a total of 4000 trials and the measurement of twenty psychometric functions (5 levels of Γ x 4 combinations of stimulus and mask). Block order was counterbalanced across conditions. After the final session of the experiment, observers repeated the last block of the training sessions for RCs and ICs. These measurements enabled us to determine whether further learning had taken place over the course of the experiment.

Results

Figure 4(B) illustrates the dependence of threshold upon Γ duration. In general, thresholds were highest for IC targets masked by IC squares. The masking function peaked at ~100 msec. Once again, as in our previous experiments, RCs yielded a flat masking function and thus proved to be ineffective masks for ICs. When the RC was the target stimulus, thresholds were overall slightly lower (by ~0.5-1°). Neither RC nor IC masks elevated thresholds for RC target discrimination at any of the latencies we tested. Masking, therefore, was elicited only when both target and mask were illusory. As before, we measured thresholds in the absence of the second mask, both before and after the experiment. Subjects showed similar performance for IC and RC targets. This performance did not significantly improve over time, although there was a trend towards lower post-experiment thresholds for RCs. Estimates of the baseline threshold pooled across time (before *vs.* after the experiment) are also indicated for IC and RC shapes (gray symbols on graph). For IC shapes masked by IC squares, thresholds were elevated above baseline at all Γs tested. For IC shapes masked by RC squares, thresholds were slightly elevated relative to baseline only at Γ = 125 msec. For RC targets, no elevations above baseline were observed whether masks were real or illusory.

Discussion

The results of Experiment 3 generally replicate those reported in Experiments 1 and 2. One noticeable difference is the higher overall magnitude of IC thresholds. A possible explanation of this phenomenon resides in an artifact of our threshold calculation procedure. If a subject performs at chance or close to chance level, a sigmoid function is an extremely poor fit (to what is essentially a flat horizontal line). This results in greatly inflated and even nonsensical threshold estimates (since the inducers will no longer enclose an illusory shape after excessive rotation). Some subjects reported a binary distinction between performing the task confidently on some trials *vs.* having no idea which stimulus was presented on others. This pattern of guessing, primarily seen when both stimulus and mask were illusory, could account for the increased thresholds in this group of subjects.

It is well known that visual objects can mask other visual objects at shorter latencies (see, e.g., Breitmeyer, 1984). In pilot studies, we found that the "local mask" (Fig. 4(A)) was extremely effective in raising thresholds for RCs when presented at short SOAs (<100ms; data not shown). At the masking latencies used here, however, real contours appear to be immune to interference from a real or illusory mask. It is very likely that the processes involved in making the shape discrimination for the real contours are more rapid in course than those involved in the same task for ICs. However, the nature of the processes occurring at these long latencies (i.e., ~280-350 msec) remains to be elucidated.

Experiment 4: Cross-masking Between Illusory Shapes of Different Sizes

At latencies of ~280-400 ms, processes occur which are integral to the task of illusory shape discrimination. The mechanisms involved appear not to be active when the target is an RC. Where these processes occur in the hierarchy of the visual system, however, remains unclear. If the masking interferes with a process occurring in early visual areas, then it is likely to be driven by the physical properties of the stimulus such as retinal size. If the masking is affecting later stages of processing, such as stages in which the surface is represented or the discrimination judgment is made, then the way observers cognitively categorize or represent the stimulus might be more important to masking efficacy than its low-level physical properties. One way to approach this question is to see if smaller illusory shapes can mask larger ones, and vice-versa. If they can, it would suggest that something specific to IC perception, rather than the physical extent of the stimulus, motivates the masking. If they cannot, it might suggest that the masking is affecting lower-level processes that simply differ among real and illusory shapes.

Method

Observers

A new group of ten observers participated in this experiment. Observers were trained in the thin/fat task over the course of two sessions, as in Experiment 3. One group of observers completed the standard six-block training session with Kanizsa targets as described previously. The other group completed a similar training session, except that the ICs were of smaller size (70%) than those seen by the first group. In the second session of the experiment, observers switched to train with the other shape size.

Procedure

This experiment was in design analogous to Experiment 3, which compared cross-masking ability for ICs and RCs. Instead of contour type, however, what varied across conditions was the size of the illusory shape used as Mask 2. The large shapes used in previous conditions (side length=15.6°; inducer radius=2.0°)

were paired with smaller IC shapes that were 70% the size of the originals (side length=11°; inducer radius=1.4°), making them just small enough so as to avoid physical overlap with the larger ICs. The support ratio of $\mu=0.25$ was maintained in both conditions. Mask 1 was always the pinwheel pattern, adjusted to match the size of its antecedent target stimulus. This again led to a 2 x 2 design, with four combinations of the stimulus and the second mask (large masked by large, large masked by small, small masked by large, and small masked by small), five durations of Γ, 40 blocks of trials, and 20 resultant psychometric functions per observer. Block order was randomized and counterbalanced. Again, thresholds from the training sessions were re-measured after the completion of the experiment to test for additional perceptual learning.

Results

Prior to beginning the experimental blocks, thresholds were comparable for large and small Kanizsa shapes. However, subjects tended to find the smaller shapes somewhat easier. Following the experiment, some improvement in perception of both stimuli but especially the small ICs became evident, indicating that subjects continued to learn over the course of the study (see Fig. 5). Once again, pooled baselines were calculated which were averaged across time. Thresholds were somewhat elevated above respective baselines for all experimental conditions (with the exception of large ICs masked by small ICs at 97 msec), indicating that ICs of different size are capable of masking each other at these long SOAs.

Discussion

There are several previous reports of size invariance in IC processing, including psychophysical findings (Kojo, Liinasuo, & Rovamo, 1993; Ringach & Shapley, 1996; Shipley & Kellman, 1992) and physiological demonstrations of insensitivity to size in IC-activated cortical regions (Mendola et al., 1999a). Our study contributes evidence of size invariance by the latency of the second mask, implying that the mechanisms involved at this level are situated beyond retinotopic regions of visual cortex.

General Discussion

The results of our experiments provide some useful information about the timing and locus of the processing stage that a late-presented illusory mask effectively disrupts. In agreement with Ringach and Shapley (1996), we find that the peak of the masking function generally occurs ~280ms following stimulus onset. This latency is in close accord with that reported for a negative electrical potential associated with the closure and recognition of incomplete objects (Doniger et al., 2000). Doniger and colleagues recorded event-related potentials in human subjects who viewed and attempted to identify fragmented line drawings of objects. They found a bilateral component of the evoked waveform which attained maximal amplitude with successful closure of the figure; the component, which they termed the N_{cl}, onset at ~232msec and peaked at ~290msec over the lateral occipital scalp. A component with similar temporal and spatial properties has been reported during detection of other coherent, meaningful objects (Vanni, Revonsuo, Saarinen, & Hari, 1996; see also Murray et al., in press). Functional neuroimaging studies have implicated regions of the LOC in object recognition (Malach et al., 1995) and in IC processing as well (ffytche & Zeki, 1996; Hirsch et al., 1995; Larsson et al., 1999; Mendola, submitted; Mendola et al., 1999a; Murray et al., in press). This area, like its ostensible simian homologue, inferotemporal cortex (see, i.e., Tanaka, 1997), is thought to contain neurons with size-invariant receptive fields (Grill-Spector et al., 1998b; Malach et al., 1995; Tootell, Mendola, Hadjikhani, Liu, & Dale, 1998) which therefore respond in a size-invariant manner to ICs (Mendola et al., 1999a). Taken together with the temporal coincidence between the N_{cl} and the peak of the masking function described here, our finding of size-invariance could endorse a connection between the processes disrupted by the late illusory mask and the generators of the N_{cl} in lateral occipital cortex.

The fact that an illusory mask is required for successful disruption of IC processing at this stage suggests that the masking is driven by mechanisms not shared by processing of real shapes. The divergence could, in principle, be spatial, temporal, or both. That is, separate populations of neurons could be active in perception of ICs and RCs; the RCs could be processed at a different time scale; or perhaps segregated neural mechanisms are involved at disparate times. Several psychophysical studies find evidence for interactions and similarities between real and illusory contour perception (e.g., Fahle & Palm, 1991; Gegenfurtner et al., 1997; Ringach & Shapley, 1996; Vuilleumier et al., 2001; Walker & Shank, 1988a; Weisstein & Matthews, 1974). Physiological studies, however, have found some differences in the relative strengths with which RCs and ICs activate the same cortical areas (Larsson et al., 1999; Mendola et al., 1999a), and in the properties of neurons responding to each contour type within an area (e.g., Ramsden et al., 2001; von der Heydt & Peterhans, 1989). Regions of the LOC do seem to be more weakly activated by RCs than by ICs (Larsson et al., 1999; Mendola et al., 1999a). One plausible explanation for the observed differences between IC and RC processing is that complete RCs might require fewer resources and thus be processed more rapidly than their illusory counterparts. The LOC activation taking place at the latency of N_{cl} has been linked to an effortful, pre-semantic level of object completion and recognition (Doniger et al., 2001a; Murray et al., in press), possibly involving surface representation (Mendola et al., 1999a; Nakayama & Shimojo, 1992; Sajda & Finkel, 1995). If copious resources are required for observers to complete and discriminate classes of illusory surfaces, a mask that appears at this critical time period is likely to disrupt the task. Likewise, if RCs do not require such an investment of resources, they may generate a smaller and quicker response that is therefore not prone to masking at late durations. In support of this idea is our finding that RCs are not effectively masked by other RCs at these relatively long latencies. Of course, real contours can mask other real contours at much shorter durations (Breitmeyer, 1984; Weisstein, 1966).

Lateral occipital cortex is known to be active in a host of object recognition processes, including the perception of complete objects (Bar et al., 2001; Grill-Spector et al., 1999; Grill-Spector et al., 1998a; Grill-Spector et al., 1998b; Ishai, Ungerleider, Martin, & Haxby, 2000; Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995). Indeed, lateral occipital activation has been recorded in humans at latencies below 200 msec (see, e.g., Murray et al., in press; Allison et al., 1994; Doniger et al., 2001a; Tanaka & Curran, 2001). Our present understanding of object recognition is highly concordant with a multi-stage model (e.g., Grossberg et al., 1997; Ullman, 1995), which could entail multiple volleys of information through the lateral occipital region. We conjecture that the LOC does respond to images of complete real objects during an earlier volley of activity; perhaps fewer iterations through LOC are required for RC processing, accounting for the overall weaker response obtained in neuroimaging studies. In contrast, if the object is visually incomplete, such as a fragmented image or an illusory contour, it may recruit additional processing resources or pass through an anatomical region multiple times. Such additional activation could generate the stronger signals seen in the processing of incomplete figures, and could eventually result in output of comparable salience to complete real shapes. Whether the same or different populations of neurons are involved for different contour types, including real contours, illusory contours, or degraded versions of real contours, remains a topic for future study. The functional-MR adaptation technique such as that suggested by Grill-Spector et al. (1999) represents one possible approach to this question.

In summary, we find evidence that illusory shapes are processed along a different spatiotemporal trajectory from complete real shapes. The neural mechanisms involved in contour closure and recognition appear to be size-invariant, and are most easily disrupted by another illusory mask at peak durations ~280msec after stimulus onset. Our findings are consistent with a multistage, recursive model of visual processing, with illusory shape completion and recognition occurring in the bilateral lateral occipital cortex at the latency of the N_{cl}.

Figure Captions

Figure 1. (A) At right, the thin/fat discrimination task. The names "thin" and "fat" were not explicitly used with observers, who were shown exemplars of each category as a basis for their decision. At left, α represents the degrees rotation of the top left inducer. (After Ringach & Shapley, 1996.) (B) The sequence of events within a trial, Experiment 1, for an Illusory Contour (IC) mask. Each trial was composed of five frames: stimulus, fixation point, "pinwheels" (local orientation) mask, fixation point, and illusory square mask. The IC stimuli shown here are not drawn to scale; in our experiment, the support ratio (between the inducer diameter and the illusory square side) was only 25%. The duration of each frame in msec is shown in the lower left-hand corner. The duration of the fourth frame, Γ, was varied across trials. (C) Sequence of events for trials in which Mask 2 was a real square.

Figure 2. Illusory contours are masked by illusory squares but not by real squares. When the second mask is an IC, thresholds are elevated for relatively short values of Γ. No such elevations are seen for real masks. A baseline threshold, shown at right, was computed from the last block of the training session in which the second mask was absent. Thresholds shown were calculated for a "pooled observer" (see text).

Figure 3. Data for two individual observers who participated in Experiment 2. When Mask 2 is a very pale RC, with perceived brightness similar to that of the illusory shape, it still proves an ineffective mask in comparison with the Kanizsa square.

Figure 4. (A) The local mask used when the discrimination target was a real contour. Note that in the experiment, the mask was presented with pale inducers on a gray background, with surface at –9% contrast to the ground. The edges are defined by 3 cycles of a sinusoid, with the phase of each side independently and randomly jittered from trial to trial. (B) Pooled thresholds as a function of the duration between Mask 1 and Mask 2. No cross-masking between illusory and real contours is seen at these latencies. At extreme right, pooled thresholds from the last block of the training session, measured prior to (hexagonal markers) and following (triangular markers) the experimental blocks. Only Mask 1 was used in these trials. There is no evidence of significant difference between RC and IC thresholds or between pre-and post-experimental sessions. Gray symbols indicate pooled baseline thresholds collapsed across time of measurement.

Figure 5. Pooled thresholds for Experiment 4, illustrating cross-masking between ICs of different sizes (subtending 15.6° and 11° respectively). At extreme right of graph, data from the last block of the training session, collected just prior to and just following completion of the experiment, indicate some improvement in threshold which is most prominent for the smaller shapes. Once again, gray symbols indicate pooled baseline thresholds collapsed across time of measurement.

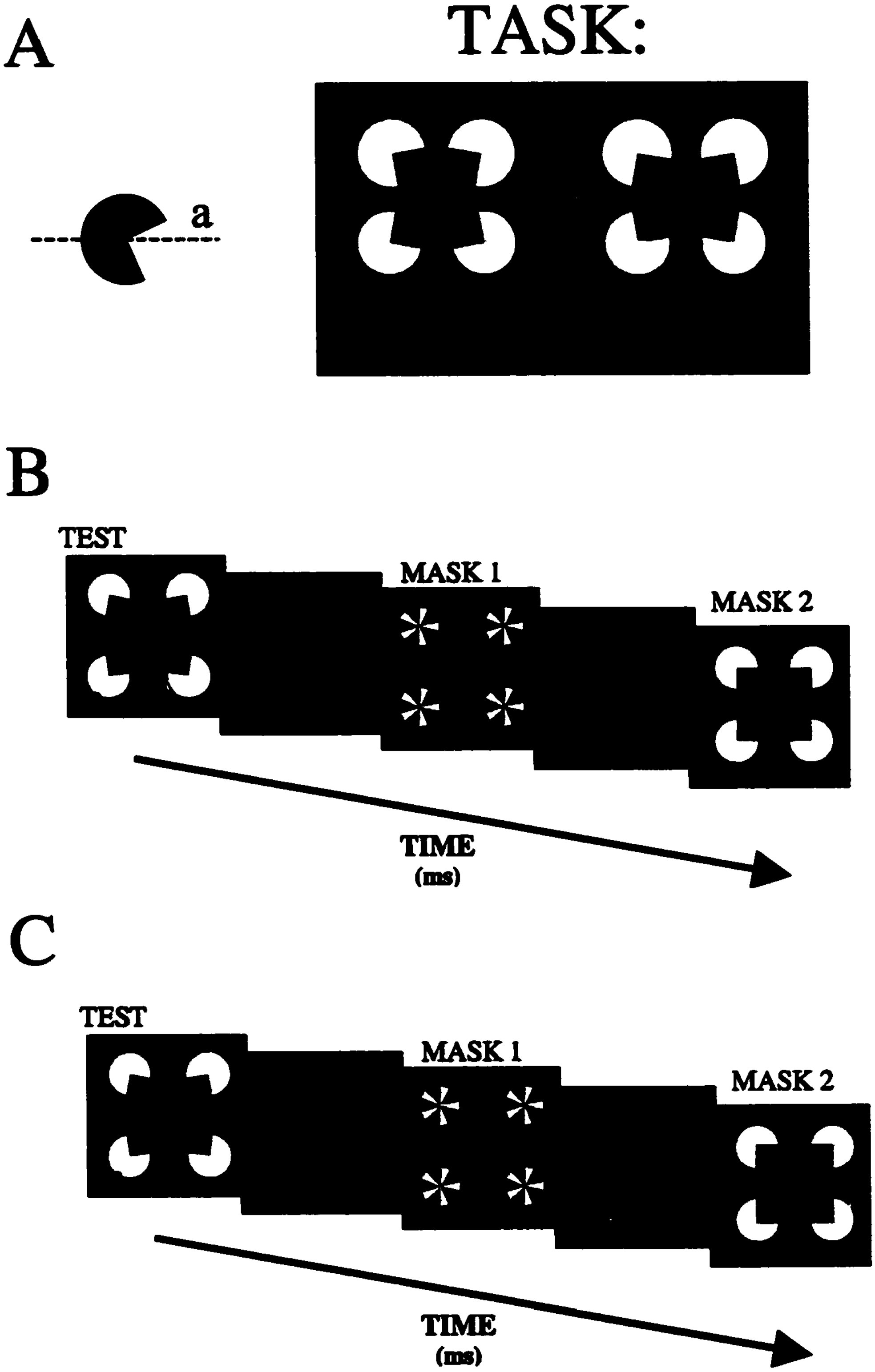

Figure 2.1

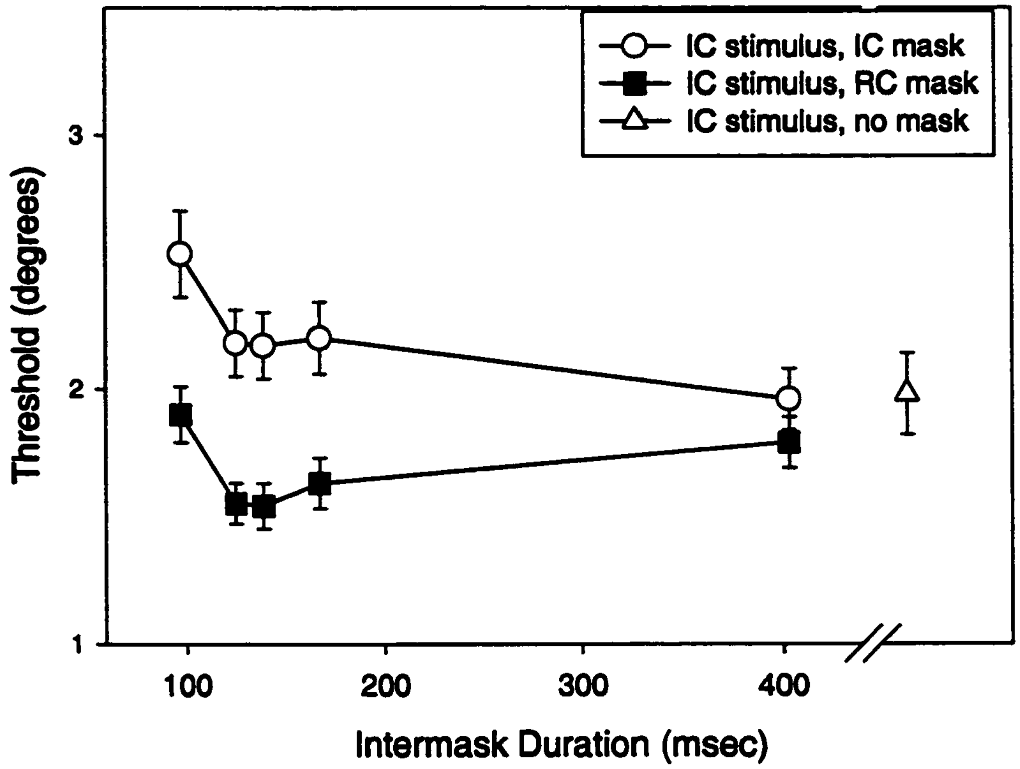
IC stimulus, IC mask
IC stimulus, RC mask
IC stimulus, no mask
Threshold (degrees)
1
2
3
100
200
300
400
Intermask Duration (msec)

Figure 2.2

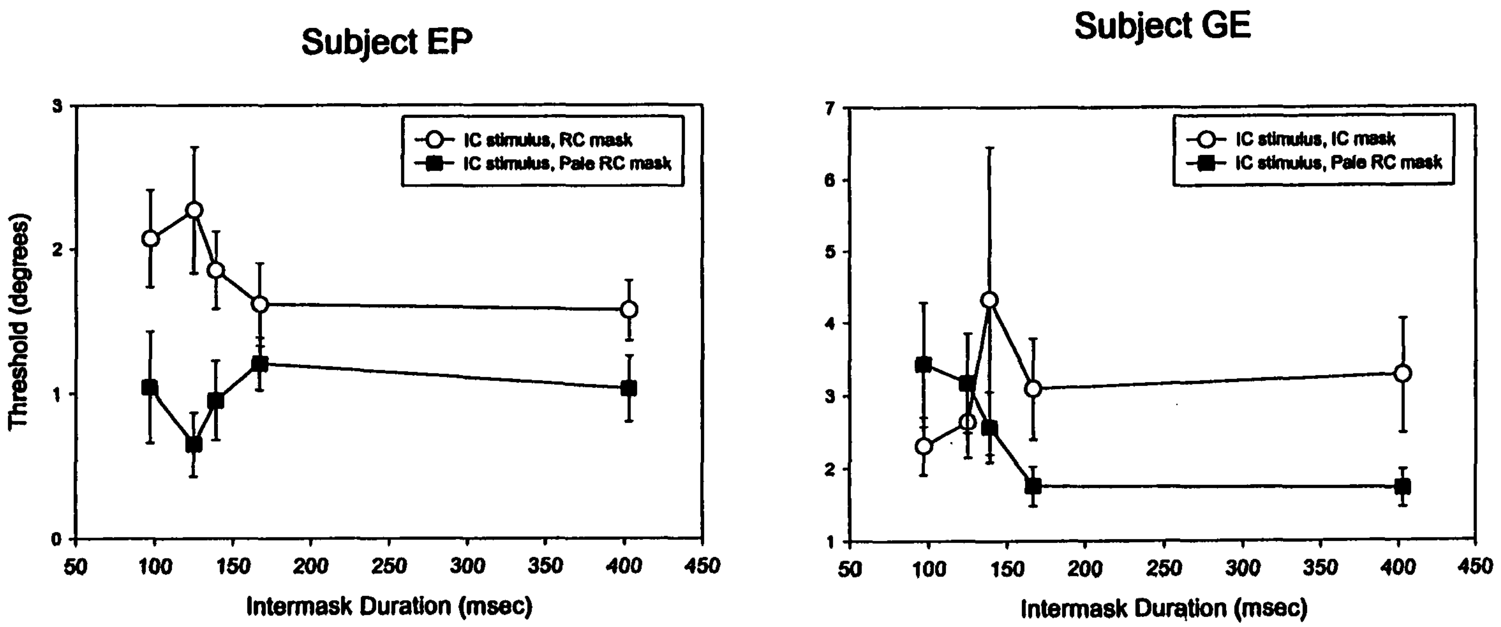
Subject EP
Threshold (degrees)
0
1
2
3
50
100
150
200
250
300
350
400
450
Intermask Duration (msec)
IC stimulus, RC mask
IC stimulus, Pale RC mask
Subject GE
1
2
3
4
5
6
7
50
100
150
200
250
300
350
400
450
Intermask Duration (msec)
IC stimulus, IC mask
IC stimulus, Pale RC mask

Figure 2.3

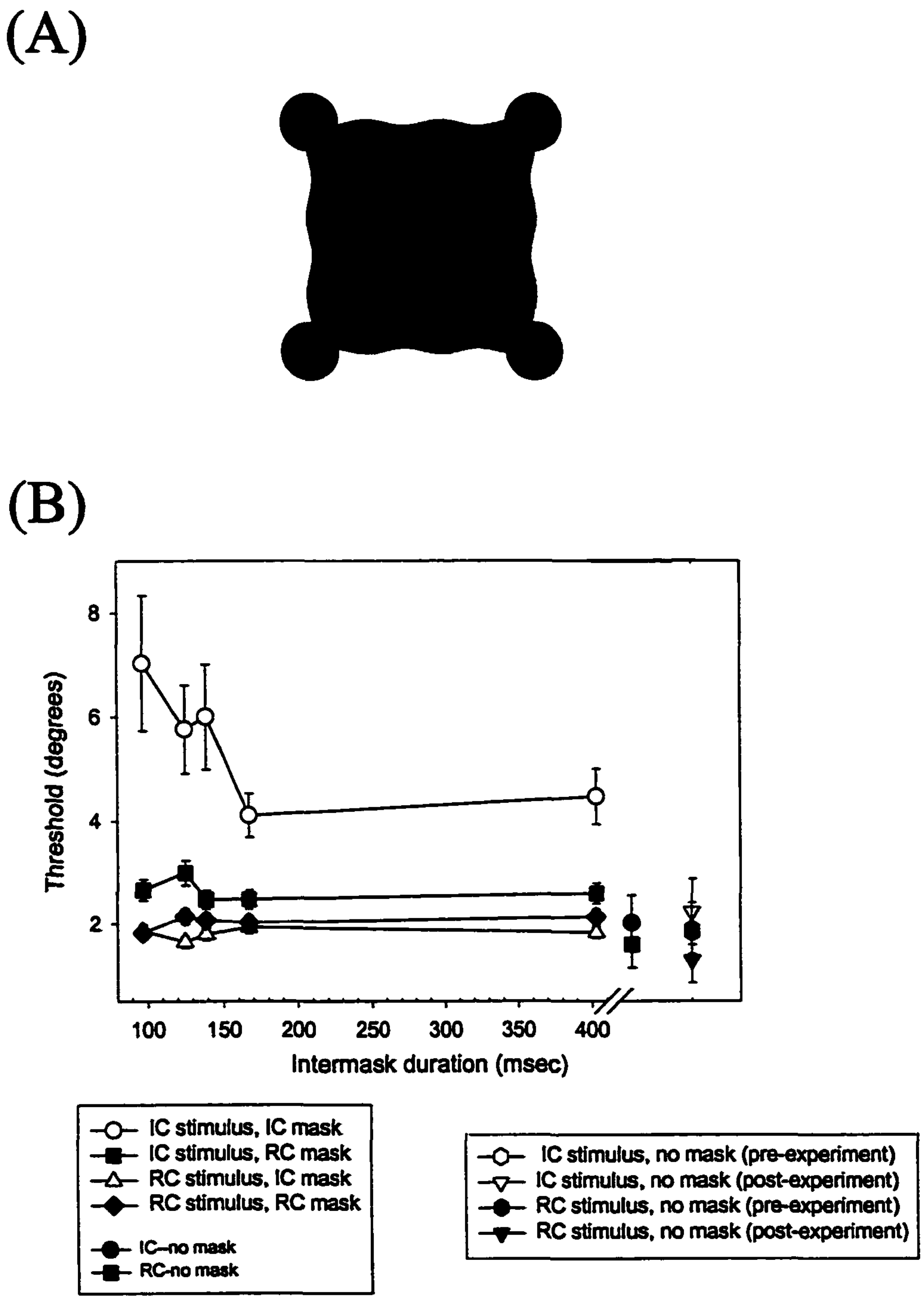
(A)
(B)
8
6
4
2
Threshold (degrees)
100
150
200
250
300
350
400
Intermask duration (msec)
IC stimulus, IC mask
IC stimulus, RC mask
RC stimulus, IC mask
RC stimulus, RC mask
IC–no mask
RC-no mask
IC stimulus, no mask (pre-experiment)
IC stimulus, no mask (post-experiment)
RC stimulus, no mask (pre-experiment)
RC stimulus, no mask (post-experiment)

Figure 2.4

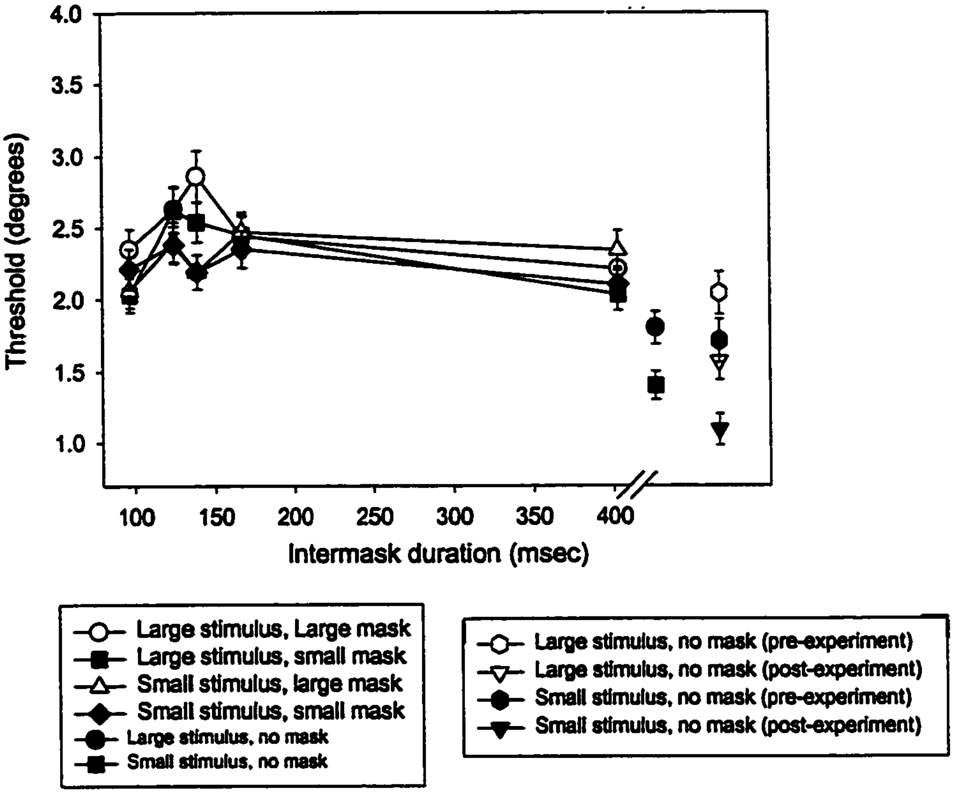
Threshold (degrees)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
100
150
200
250
300
350
400
Intermask duration (msec)
Large stimulus, Large mask
Large stimulus, small mask
Small stimulus, large mask
Small stimulus, small mask
Large stimulus, no mask
Small stimulus, no mask
Large stimulus, no mask (pre-experiment)
Large stimulus, no mask (post-experiment)
Small stimulus, no mask (pre-experiment)
Small stimulus, no mask (post-experiment)

Figure 2.5

paper 2:

Performance Accuracy Correlates with Early Modulations of Visual Evoked Potentials to Illusory Contours

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Abstract

We used high-density, 128-channel visual evoked potentials (VEPs) to study differences in processing of real (RC), illusory (IC), and no-contour (NC) stimuli in the context of an active discrimination task that was performed across all contour types. Collection of behavioral data enabled us to relate performance with observed physiology. Modulations to contour type were observed over electrodes in bilateral occipital and lateral occipital scalp, at the N1 (~164msec post-stimulus onset), at the N_{cl} (~286msec), and at longer (~400msec) latencies. At the N1, the largest responses were evoked by ICs, followed by NCs and lastly by solid gray RCs. In trials when subjects responded incorrectly, the differential effect of ICs at the N1 and N_{cl} was greatly diminished. We interpret these findings in terms of a multistage model of object recognition, dependent on reentrant connections to and multiple phases of activity through posterior cortex.

Introduction

Object perception is a robust phenomenon that withstands degraded visual conditions, including poor lighting, scotoma, and the partial occlusion of one object by another. Due to the two-dimensional nature of the retinal projection, such impediments will produce object images with discontinuous boundaries. The cerebral mechanisms involved with 'filling in' this incomplete information have been a focus of investigation by vision scientists for over a century (see Kanizsa, 1976; Mendola, submitted; Pessoa, Thompson, & Noe, 1998; Schumann, 1987). Illusory contours (ICs; see Figure 1), stimuli which have traditionally been used to investigate closure and completion processes, are percepts of a ghostly surface spanning regions of homogenous luminance. Because these illusions result from the alignment of 'real' (luminance-defined) inducing shapes, they are thought to tap processes similar to those that fill in degraded contours and forms in natural viewing conditions. Indeed, numerous psychophysical studies (e.g. Beckett, 1989; Beckett, 1990; Beckett & Hurajt, 1988; Bradley, 1982; Greene & Brown, 1997; Paradiso et al., 1989; Smith & Over, 1976; Smith & Over, 1977; Smith & Over, 1979) have demonstrated perceptual similarities between ICs and 'real' contours (RCs) in the effects of several popular illusions. However, the extent to which ICs and RCs engage the same underlying neurophysiological mechanisms remains to be established.

Comparisons of IC- and RC- related activity have been made at various anatomical levels of the visual hierarchy. While intracranial studies of animals have shown some evidence for IC sensitivity in early areas such as V1 (e.g., Grosof et al., 1993; Lee & Nguyen, 2001; Sheth, Sharma, Rao, & Sur, 1996; see also Ramsden, Hung, and Roe, 2001) and V2 (e.g. Lee & Nguyen, 2001; Peterhans & von der Heydt, 1989; Sheth et al., 1996; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984), responses to RCs in these areas were both larger (e.g. Lee & Nguyen, 2001; Nieder & Wagner, 1999; Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989) and, in some laminae, earlier (Lee & Nguyen, 2001). While functional neuroimaging studies in humans have demonstrated similar patterns in these lower-tier areas, they have conversely reported that higher-tier regions and particularly the lateral occipital complex (LOC; Malach et al., 1995) yield larger responses to IC than to RC stimuli (e.g. Larsson et al., 1999; Mendola et al., 1999c). The LOC, a network of brain regions that has exhibited sensitivity to real object features in numerous studies (e.g. Grill-Spector et al., 1998a; Grill-Spector et al., 1998b; Kourtzi & Kanwisher, 2000; Kourtzi & Kanwisher, 2001; Malach et al., 1995; Moscovitch, Kapur, Kohler, & Houle, 1995), is considered to be the homologue of macaque inferotemporal (IT) cortex (see e.g. Tanaka, 1997 for review). Many researchers have suggested that lateral occipital regions are involved in IC processing (Huxlin & Merigan, 1998; Huxlin, Saunders, Marchionini, Pham, & Merigan, 2000; Larsson et al., 1999; Mendola et al., 1999b; see also Wasserstein, Zappulla, Rosen, & Gerstman, 1984). A recent study utilizing both visual evoked potentials (VEP) and functional magnetic resonance imaging (fMRI) concluded that the differential response to IC presence versus absence (the *'IC effect'*) is first seen at ~90ms post-stimulus onset in signals emanating from the LOC (Murray et al., in press).

While earlier studies have conjectured about the localization of IC and RC processing, little is presently understood about the relative time-evolution of each. Studies that rely upon blood flow, necessarily constrained by the poor temporal resolution of the hemodynamic response, lose valuable information about the relative timing of responses to IC *versus* RC stimuli. Time-integrated measurement, therefore, cannot resolve either when responses to ICs and RCs differ or where such differences are first achieved. Regarding the latter, for example, it may be the case that responses in a given area are initially identical for both stimulus types and only differ at later time points. Thus, the relative time course of IC and RC processing remains unresolved. One goal of the present study was to address this question using the high temporal resolution of high-density VEPs.

A second aim was to study the correlation between VEP modulations and performance accuracy. Earlier work (e.g., Ritter, Simson, Vaughan, & Friedman, 1979; Ritter, Simson, Vaughan, & Macht, 1982) has suggested that at least two stages of electrophysiological activity can be distinguished during perceptual discrimination tasks. The earlier stage has been linked with automatic perceptual processing, and is enhanced and delayed when target perception is degraded through the use of a backward mask (Ritter et al., 1982). The later stage is thought to be dependent on the first stage and differs as a function of discrimination task.

More recently, correlates of these stages have been reported in studies of visual closure and object recognition (Doniger et al., 2000; Doniger et al., 2001; Doniger et al., in press; Murray et al., in press). The N1, a negative deflection of the VEP occurring ~170ms post-stimulus onset, appears to reflect automatic perceptual processes (i.e., Doniger et al., 2001a; Murray et al., in press). The N_{cl} ("negative potential due to closure"), at ~290ms post-stimulus onset, may index a more effortful mode of object recognition (Doniger et al., 2000; Doniger et al., 2001a; see also Murray et al., in press). We were interested in further delineating the roles of these potentials in terms of boundary completion and shape discrimination. To accomplish this aim, we had subjects perform a discrimination task using real, illusory, and no contour stimuli at two levels of difficulty. We collected performance data, which allowed us to determine the earliest modulation of the VEP that was correlated with response accuracy.

While evoked potentials to ICs have been studied previously (i.e., Brandeis & Lehmann, 1989; Brandeis et al., 1985; Herrmann et al., 1999; Korshunova, 1999; Murray et al., in press; Sugawara & Morotomi, 1991; Tallon et al., 1995; Tallon-Baudry et al., 1996), our study differs from prior reports in several critical ways. To date, most VEP studies of IC perception have not included an RC comparison. Those which have done so (i.e., Tallon-Baudry et al., 1996) have used an outline figure rather than a solid shape. In the present study we used a solid form for the RC stimulus, since the illusory "contour" is thought to be perceived as a surface, rather than merely an outline (Petry & Meyer, 1987). The solid surface is more perceptually salient than the outline, and provides depth and occlusion cues that are more analogous to those perceived in the illusory case. Moreover, those investigators who have observed response modulations to IC vs. (outlined) RC stimuli (Tallon-Baudry et al., 1996) have emphasized response differences within the high-frequency gamma band (~30-60Hz), rather than on the earliest broad-band VEP modulation. Our study focused on the low-frequency components of the VEP. Furthermore, other experiments have employed tasks in which it could be argued that attention was at least partially confounded with stimulus condition. Here, we employed the "thin/fat" discrimination task, introduced by Ringach & Shapley (1996), which can be performed for ICs, NCs, and RCs alike. This task actively engages the subject on each trial, promoting attention and motivation across stimulus types. Manipulating the task difficulty enabled us to study its effect on VEP responses believed to be associated with closure and discrimination processes: at what stage does task difficulty modulate evoked potentials? Because we also collected data about performance accuracy, we were able to compare VEP responses to the same stimulus when the subject responds correctly vs. incorrectly. An incorrect response may reflect a failure to "close" the IC properly, or a failure at the shape discrimination level of the task. We were thus able to track the earliest discrepancies between responses ultimately yielding correct and incorrect judgments.

Our analyses focused on three time periods: the N1 (~164ms), found by Murray et al. (in press) to be sensitive to IC processing; the N_{cl} (~290ms), which

Doniger et al. (2000) have linked to perceptual closure and identification processes; and an exploratory analysis of late periods (~400ms), to investigate response differences suggested by psychophysical studies of late-stage visual masking found with ICs (Imber et al., 2000; Ringach & Shapley, 1996).

Methods

Subjects

Twelve (9 female) neurologically normal, paid volunteers, aged 19-41 (mean±SD =24.6±7.5) participated. All but one of the subjects were right-handed, as indicated by the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects provided written informed consent, and the Institutional Review Board of the Nathan Kline Institute for Psychiatric Research approved all procedures. All subjects reported normal or corrected-to-normal vision.

Stimuli and Task

Kanizsa-type (Kanizsa, 1976) 'pacman' inducers were presented on a computer monitor (Eizo Flexscan 930; 1280x1024 pixel resolution) located 75cm away from the subject. During all trials, subjects were instructed to fixate a dot located in the center of the screen. There were a total of 12 possible stimulus configurations, yielding a 3 (contour type) x 2 (classification type) x 2 (level of difficulty) within-subjects design. Contour type could be illusory (IC), real (RC), or no-contour (NC). Subjects performed a classification task on ICs, RCs, and NCs, each of which was presented at two levels of difficulty. Illusory shapes were based upon permutations of Kanizsa-type squares whose circular inducers (radius = 1.8° visual angle; distance between centers of inducers = 13°; eccentricity of inducer centers from central fixation = 9.2°) were rotated so as to deform the surface into either a "thin" or "fat" configuration (following Ringach & Shapley, 1996). The upper-left and bottom-right inducers were rotated by α degrees, and the bottom-left and upper-right inducers by $-\alpha$ degrees, such that larger absolute values of α resulted in illusory shapes with more exaggerated perceived curvature. By convention, α refers to the rotation of the top-left inducer. Thus, negative values of α yield shapes that are "fat", while positive values result in "thin" shapes. (See Fig. 1a.) We used α values of ±1° and ±6°, thereby testing subjects at two levels of difficulty (with 1° being the more difficult). Real shapes were identical to the illusory stimuli, except that the shapes' surfaces were explicitly defined by a luminance decrement (see Fig. 1b). Inducers were present in the RC condition so that they appeared as white circles behind the dark gray RC surface. The no-contour condition (NC; Fig. 1c) was identical to the IC condition except that inducers were rotated $180°\pm\alpha$, which resulted in the "mouths" of the pacmen facing outwards to block the induction of an illusory surface. Mean background luminance was 70.5 cd/m^2, while mean luminance of the pacman inducers was 88.7 cd/m^2. In the RC condition, the real surface had a mean luminance of 59.1 cd/m^2. For the IC condition, the support ratio was fixed so that 27% of the illusory boundary was physically apparent due to the presence of the inducers.

A fixation point, presented for 700 ms, preceded each trial. One of the 12 possible stimuli then appeared for 168 ms (Fig. 1d). Following an inter-stimulus interval of 700 ms, subjects were prompted to respond by the presentation of the cue, "L|R"; no accuracy feedback was provided during experimental trials. Subjects made a forced-choice discrimination between two classes of stimuli, $\alpha<0$ vs. $\alpha>0$. Rather than providing subjects with a verbal description of the discrimination task, we showed subjects examples of shapes that would result in a left *vs.* right button-press. At any time during the experiment, subjects could refer to a sheet of paper bearing exemplars of each response type for NCs, ICs, and RCs (see Fig. 1). We instructed subjects not to respond until the prompt appeared, to minimize the effect of motor responses on the sensory VEP. In this manner, subjects also controlled stimulus delivery. A practice block, with accuracy feedback on each trial, preceded the experimental session. The entire experimental session consisted of at least 28 blocks of trials (mean±SD = 32.5±2.8), each block containing 96 stimuli; each of the 12 possible stimuli occurred with equal probability within a block. Subjects were encouraged to take breaks between blocks to maintain high concentration and prevent fatigue. Behavioral data were acquired from 11 of the 12 individuals, although all subjects performed the same task during the acquisitions.

EEG Data acquisition

Continuous EEG was acquired through Neuroscan Synamps from 128 scalp electrodes (~2.4cm inter-electrode spacing; impedances <5kΩ), referenced to nose, band-pass filtered 0.05-100Hz, and digitized at 500Hz (Figure 3, inset). Epochs of continuous EEG (-150ms pre- to 750ms post-stimulus onset) were averaged from each subject separately for each stimulus configuration to compute the visual evoked potential (VEP). Baseline was defined as the 150ms pre-stimulus epoch. Trials with blinks and eye movements were rejected off-line based on HEOG and VEOG. An artifact criterion of ±60μV (n= 10) or ±80μV (n=2) was used at all other scalp sites to reject trials with excessive EMG or other noise transients. The average number of accepted trials per stimulus type (out of 12 types) was 168.6 (±49.0) with the lowest for any subject being 81 and the highest, 248. It is important to note that following our preliminary analyses, which revealed no difference between VEPs to $\alpha<0$ $^{vs.}$ $\alpha>0$ for any contour type, we collapsed the data from both types of classification in order to further increase the signal-to-noise ratio of each subject's data. We then had 6 VEPs per subject with an average sweep count of 337.1±97.8. Statistical analyses as well as topographic mapping for all experiments in this study were performed on broad-band (0.05-100Hz) data, although filtered waveform data (40Hz low-pass; 24dB/octave) are displayed in figures.

Data analysis

Our dependent measures in the electrophysiological data analyses were based on previous studies of illusory contour and perceptual closure processes from our laboratory. We made several predictions about the spatiotemporal dynamics of the neural generators likely to be involved in our task. Converging evidence from studies employing ERP (e.g., Doniger et al., 2000; Murray et al., in press) and fMRI techniques (e.g., Malach et al., 1995; Mendola et al., 1999a; Murray et al., in press) implicate the lateral occipital complex (LOC) in shape and contour recognition. By inspecting group-averaged waveforms that were produced by collapsing across all subjects and conditions, we identified the largest amplitudes of the N1 component at lateral occipital scalp sites, in line with previous results. We chose three, homologous electrode sites over the lateral occipital scalp of each hemisphere (see Figure 3, inset, for locations) for the purposes of further analysis. We defined three temporal windows to capture the major components of interest: the N1, following Murray et al. (in press), who identified IC/NC differences at this time; the N_{cl}, following Doniger et al. (2000), who reported the implication of this region in closure processes; and a late component, at 400ms, based upon psychophysical masking studies that demonstrated differences between IC, NC, and RC processing at this stage (Imber et al., 2000; Ringach & Shapley, 1996). With the aid of the group-averaged waveforms, the temporal features of each component were identified. A window was selected around the peak of each component. For each component, we computed the area under the curve by summing the amplitudes (versus a baseline of 0µV) at each time point and for each subject, computed separately at each of the 6 lateral occipital electrode sites. We averaged the area across the three electrodes within each hemisphere, and this value served as the dependent variable in a three-way, repeated-measures ANOVA. The within-subject factors were hemisphere of electrode location (right *vs.* left), contour type (IC *vs.* NC *vs.* RC), and difficulty (α=1 *vs.* α=6). The results of these three ANOVAs, one per component, are reported below. As with behavioral data, all results reflect Greenhouse-Geisser corrections for sphericity where such adjustments apply. Note that our initial stages of analysis revealed no differences between "thin" and "fat" responses; accordingly, we collapsed across shape in all of the following analyses.

In order to learn more about the temporal activities of intracranial generators related to illusory contour completion, we employed a method recently presented by Murray et al. (in press) and Molholm et al. (in press). This technique provided a means of visualizing the time-evolution of pairwise modulations across multiple electrode sites, which helped us to examine the stability (both in temporal extent and across scalp locations) of VEP differences between experimental conditions of interest. For each electrode and each pairwise comparison (e.g. IC vs. NC), we conducted a series of pointwise paired t-tests between evoked potential amplitudes across all subjects. The first point where these tests satisfied the 0.05 significance criterion for at least the subsequent 11 successive data points (>20ms at 500Hz digitization) was labeled as the onset of a differential effect between these conditions (see also Guthrie & Buchwald, 1991). This onset value was calculated for each of the three pairwise comparisons between contour types (IC, NC, RC) as well as for each of the six electrodes of interest. Onset latencies reported for each hemisphere reflect the average across the three pairwise comparisons and three within-hemisphere electrodes.

The spatiotemporal pattern of these differential effects was visualized by plotting these p-values from 119 of the 128 electrodes in our montage (hereafter referred to as 'statistical cluster plots', or SCPs; see also Murray et al.(in press)). Each plot illustrates one pairwise comparison. The abscissa represents time elapsed relative to stimulus onset. The ordinate represents electrode site, roughly grouped by topographical region and arranged from left to right as one proceeds down the axis. The p-value of each t-test is signified by the color of a data point, for all $p \leq 0.01$ (see Fig. 5 for example).

Results

Behavioral Results

The percentage of correct classifications was recorded for each of the twelve stimulus types, and the resulting values were submitted to a repeated measures, 3 (contour type) x 2 (difficulty level) x 2 (shape, $\alpha > 0 / \alpha < 0$) analysis of variance. All reported statistics reflect Greenhouse-Geisser corrections where data did not satisfy criteria for sphericity.

There was a significant main effect of contour ($F_{(2, 20)}$=33.400, $p<0.0001$), reflecting subjects' superior performance on RC (mean 83.62 ± SE 2.5 percent correct) vs. IC (76.46%±2.9%) vs. NC (55.48%±3.9%) stimuli. Follow-up, planned comparisons (paired samples t-tests) confirmed this graded difference across contour types (IC vs. NC, $t_{(10)}$ = 4.756, $p<0.001$; NC vs. RC, $t_{(10)}$= -7.256, $p<.0001$; IC vs. RC, $t_{(10)}$ = -3.615, $p<0.005$). The main effect of difficulty was also significant ($F_{(1,10)}$ = 93.64, $p<0.0001$), indicating that subjects responded more accurately to $\alpha = \pm 6°$stimuli (81.54%±2.7%) than to $\alpha = \pm 1°$ (62.17%±2.5%). The main effect for shape was not significant ($F_{(1, 10)}$=0.020, p=0.891). Figure 2 displays the overall percentage correct for each combination of contour type and level of difficulty, collapsed across shape (thin/fat, i.e., $\alpha>0/\alpha<0$).

The only significant two-way interaction occurred between contour and level of difficulty ($F_{(2,20)}$=6.55, $p<0.015$), illustrating that difficulty affected performance with ICs (64.17±2.9 percent correct for $\alpha=1$; 88.76%±3.4% for $\alpha=6$) as well as with RCs (70.28%±4.3% percent correct for $\alpha=1$; 96.96%±1.2% for $\alpha=6$), but made no difference when subjects viewed NC stimuli (52.07%±1.3% for $\alpha=1$; 58.89%±6.5% for $\alpha=6$).

Electrophysiological Results

Inspection of the statistical cluster plots (SCPs) reveals two distinct components of the VEP (see, i.e., Fig. 5) prior to 350ms. These modulations appear to correspond with the N1 and N_{cl} components, respectively.

N1 Component

Differences in the N1 component (onset: 137ms at right scalp sites; 136ms at left scalp) were visualized to be maximal over bilateral occipital and parieto-occipital electrode sites (see Fig. 4). The latency window for analysis of the N1 (164±10ms) was determined from visual inspection of the group-averaged VEP collapsed across all conditions, as measured from the 6 electrode sites demonstrating the largest amplitude. These area measures were then submitted to the 3-way repeated measures ANOVA described above. There was a main effect of contour type ($F_{(2,22)}=24.382$, $p<0.0001$). Follow-up, planned comparisons (paired t-tests) revealed that N1 amplitude was graded across the three contour types (IC *vs*. NC, $t_{(11)} = -5.27$, $p<0.0001$; NC *vs*. RC, $t_{(11)} = -4.24$, $p<0.001$); IC *vs*. RC, $t_{(11)} = -5.23$, $p<0.0001$), with the largest N1 amplitude in response to the ICs, followed by the NCs and then RCs (see Figure 3). It is noteworthy that this pattern does not mirror that of task performance. There was also a main effect of hemisphere ($F_{(1,11)} = 13.011$, $p<0.004$), indicating that a larger N1 amplitude was recorded over right hemisphere sites.

N_{cl} Component

The N_{cl} component, which was maximal over occipital and lateral occipital scalp, onset at 256ms in the right–sided sites and 260ms in those on the left. Given the broader nature of this peak in comparison to the N1, we defined a broader window of 286±20ms. The resulting area under the curve was again submitted to an ANOVA. There was a main effect of contour type ($F_{(2,22)}$=24.513, p<.0001; see Fig. 4). As with the N1 component, follow-up planned comparison t-tests indicated a graded difference across all contours (IC vs. NC, $t_{(11)}$ = -3.83, p<0.003; NC vs. RC, $t_{(11)}$ = -3.41, p<0.006; IC vs. RC, $t_{(11)}$ = -6.87, p<0.0001). The largest negative amplitude was seen for ICs, followed by NCs, while the 'N_{cl}' amplitude for RCs was actually of positive polarity. In fact, inspection of the waveforms suggests that no N_{cl} is generated for RCs, which is not surprising. The main effect of hemisphere approached significance ($F_{(1,11)}$=4.660, p<.054), which again reflected our measurement of larger amplitudes over the right-sided scalp. Of the interactions, only the two-way interaction between contour type and hemisphere was significant ($F_{(2,22)}$ = 10.414, p<0.001); although the response was largest over the right scalp for each contour type, the right-left difference for RCs was minimal.

Late Componentry

Given the results of recent masking studies that have hinted at late differences in the processing of illusory, real, and no contours (Imber et al., 2000; Ringach & Shapley, 1996), we decided to explore VEP modulations among conditions at relatively late points in time. In our study, these differences were in fact present over extremely long durations (~350-650ms post-stimulus). Most differences between conditions peaked in the earlier portion of this time range, leading us to focus our analysis on the 400±50ms window. Over this time period, the main effect of contour was again present ($F_{(2,22)}$=30.983, p<.0001; see Fig.4). Follow-up t-tests indicated significant differences between each pair of contour conditions: IC vs. NC ($t_{(11)} = -3.34$, $p<0.007$); NC vs. RC ($t_{(11)} = -3.99$, $p<0.002$); and IC vs. RC ($t_{(11)} = -9.84$, $p<0.0001$). The late potential for the IC was of negative polarity, while both NC and RC yielded positive potentials (for RC, of large amplitude). The main effect of difficulty, while not meeting significance criteria, demonstrated a borderline effect ($F_{(1,11)}=4.36$, $p<.061$) suggestive of greater area under the curve for easy vs. hard stimuli. There was a main effect of side on which electrodes were located, ($F_{(1,11)}=5.87$, $p<.034$), with greater (positive) amplitude as recorded on the left side. All two-way interactions were significant. Of note, contour type modulated difficulty ($F_{(2,22)} = 8.583$, $p<0.005$), in that there was no discernible difference between response to difficult and easy NCs; amplitude increased (became more positive) for both ICs and RCs as stimuli became easier to discriminate (Figure 5). The interactions between contour type and hemisphere ($F_{(2,22)} = 5.973$, $p<.015$), and between difficulty and hemisphere ($F_{(1,11)} = 8.675$, $p<0.013$), were also significant. Finally, the three-way interaction between contour type, difficulty, and hemisphere was significant as well ($F_{(2,22)} = 10.299$, $p<0.001$).

Relation Between Behavior and Electrophysiology

Since we collected both behavioral and electrophysiological data from 11 subjects, we were in a position to compare ERPs associated with correct and incorrect judgments of "thin" vs. "fat". These results should be interpreted with the caveat that they are exploratory in nature. One reason for this caution is the unequal number of sweeps associated with correct (473.1±189.1) vs. incorrect

(180.8±125.4) responses. In particular, since subjects' performance for RCs was so accurate, the difference between sweep count for incorrect trials (98.9±58.7) and sweeps in which subjects made correct judgments (548.1±195.9) was judged to be too great for a meaningful comparison. We therefore elected to focus on the accuracy-related modulation to IC and NC stimuli.

With the above caveats in mind, in Figure 8 we present group-averaged data, sorted by response accuracy, for two contour types (IC and NC). The SCPs (Fig. 8B) illustrate a striking difference in VEP modulations between accurate and inaccurate judgments. When subjects respond correctly, differential activity to IC *vs.* NC stimuli (the '*IC effect*') is seen at the N1, N_{cl}, and late components as before (Fig. 8B, top plot; compare to Fig. 5). When responses are incorrect, however, the magnitude of the *IC effect* is greatly diminished (Fig. 8B, bottom) at all three components. Figure 9 illustrates the comparison between accurate and inaccurate responses within each stimulus type (i.e., correct vs. incorrect responses to ICs). The most robust differences for IC stimuli are seen beginning at the falling phase of the P2, lasting through the N_{cl} and the P3. Accuracy does not appear to differentially modulate VEPs to the NC stimuli (Fig. 9, bottom). These results may be more clearly understood by viewing the representative data shown in Figure 8A, from an electrode located over right lateral occipital scalp. For this electrode site, there are no significant differences between VEPs to correct and incorrect judgments of NC stimuli. For incorrect IC stimuli, however, a small (nonsignificant) decrement is visible at the peak of the N1. This decrease in peak amplitude is large enough to weaken the *IC effect* when responses are inaccurate, because the IC-NC difference is no longer significantly large. This observation accounts for the N1 modulation seen in Figure 8 but absent in Figure 9; the decrement is just large enough to diminish the IC effect but not large enough to differentiate accurate *vs.* inaccurate responses to IC stimuli.

Other spatiotemporal loci

Although precedent led us to focus most of our analyses on posterior regions and at the temporal EP components described above, our statistical cluster plots (SCPs; see Figs. 5, 7-9) enabled us to visualize differential VEP responses throughout scalp and over a wide temporal range. In pairwise comparisons between IC and NC responses (Fig. 5), some frontal and central activity was seen at intermediate times between the N1 and N_{cl} (~300-400ms). There were also robust frontal and central differences between IC and RC EPs lasting from ~350-450ms. Other temporal components of interest were evident at long latencies when responses to hard and easy stimuli within each contour class were considered (Fig. 8). Sustained differences, measurable across the entire scalp, were present for hard vs. easy RCs between ~400-600ms. For hard vs. easy ICs, a shorter, more posterior band of activity was seen between ~500-600ms.

Discussion

Our study employed high-density ERP to investigate the processing of real, illusory, and no-contour stimuli while participants performed a discrimination task.

The inclusion of this task represents a substantial improvement over previous studies of illusory contours, which often confounded boundary completion with the allocation of attention (i.e., through "oddball" or simple "contour present/absent" paradigms). Because participants performed the same task for all stimulus types, differential effects of attention, motivation, and motor response were minimized. We also varied the difficulty of the task and monitored performance. We found substantial response modulations across contour types, most notably at the N1 and the N_{cl}, as well as at later durations (post-400msec). Stimulus difficulty primarily affected late time points for real and illusory shapes. Finally, we noted a correlation between accuracy of performance and VEP modulations at the N1 as well as the N_{cl}. These results help to explain earlier psychophysical findings, suggesting different timecourses for the processing of complete vs. incomplete objects, and support a multistage model of object recognition that entails multiple phases of activity through posterior cortical regions.

Effects of contour type

We found that the earliest sensitivity to contour type occurs at the N1, with a peak latency of ~164msec. Our finding that IC amplitude is greater than NC amplitude at this component is in agreement with those reported by several others, including the recent study by Murray et al. (in press). Murray and colleagues presented their subjects with IC and NC stimuli and asked subjects to discriminate between 'contour present' and 'contour absent'. Using a high-density ERP paradigm, they found significant differences between IC and NC modulations during the N1 component when stimuli were presented centrally (the '*IC effect*'.) In the present study, we reproduce their 'IC effect' pattern with VEPs, despite the fact that the two studies differ in timing of stimulus presentation, eccentricity, support ratio, and task. The latency of the *IC effect* in our study is somewhat later than Murray et al.'s effect (by ~25msec), which might be due to some or all of the aforementioned differences in design.

Because no source localization techniques were employed in the present study, we cannot assert the precise location of the neural generators responsible for the *IC effect* we observe. In fact, we must limit conclusions about localization to scalp regions at which potential modulations were seen, which may not correspond with the locations of underlying generators due to volume conduction and spatial smearing of signals. Other groups which investigated illusory contour perception have attempted to address this question through the use of various source localization techniques. Murray and colleagues (in press) employed dipole source analysis and functional MRI in an attempt to localize their VEP findings to a specific cortical region. They concluded that lateral occipital cortex (the LOC) was a likely generator site for the VEP modulations they observed. A recent study of IC, NC, and RC processing used global field potentials to estimate generator location (Pegna et al., in press), and also localized their effect to lateral occipital regions. While the data presented in our statistical cluster plots appear consistent with a posterior generator such as LOC, we cannot state with certainty that this is the locus of the differential modulations we see between contour types.

In our study, we found that RCs also evoke a peak at the N1 with similar temporal properties to the IC and NC peaks. Perhaps somewhat surprisingly, however, the N1 amplitude evoked by RCs is smaller than both IC and NC responses. This pattern, although not explicitly reported by the authors, can be seen in Figure 8 of Tallon-Baudry et al. (1996). Tallon-Baudry and colleagues used outline-type RCs, but the N1 differences they found between RCs, NCs, and ICs at the N1 were not significant. The null result was possibly due to a relatively low sweep count. More recently, Pegna and colleagues (in press) found a similar pattern of activation at the N1 in a study which included outline RC stimuli and employed a simple task (identification of contour type). The finding that RCs produce smaller N1 amplitudes is perhaps consistent with neuroimaging data (Larsson et al., 1999; Mendola, Dale, Fischl, Liu, & Tootell, 1999b) which imply a greater response to ICs than RCs in LOC. One alternative explanation would be that separate populations of ventrally-located neurons process RCs, weakening the response recorded at the scalp. The N1 component has been linked to an early stage of processing in lateral occipital regions that entails automatic, perceptual processing of visual stimuli (Allison et al., 1994; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Doniger et al., 2001a).

Electrophysiological differences between contour types reappear at latencies of ~290msec, which corresponds with the timing of a negative potential due to closure (N_{cl}) evoked in previous experiments when observers successfully identified fragmented images of objects which required visual closure (Doniger et al., 2000; Doniger et al., 2001a). This component has been interpreted as a neural correlate of effortful perceptual discrimination and identification (Doniger et al., 2000; Doniger et al., 2001a; Murray et al., in press; Ritter et al., 1979; Ritter et al., 1982). The largest negative deflection we observe at this latency is seen for ICs, followed by NCs. The RC response at this latency has a vastly different morphology. Contour-relevant modulations are also visible at very late potentials, up to 500msec (mainly on the right side) between IC and NC responses and up to 600msec between IC and RC.

Recent psychophysical studies (Imber et al., 2000; Ringach & Shapley, 1996) have used backward masking techniques to explore stages of IC perception. Ringach and Shapley (1996) asked subjects to perform the thin/fat task on IC stimuli in the context of 1) a "local" orientation mask, and 2) a "global" illusory shape mask presented at a later duration. They found that masking the inducers with the local mask caused interference in boundary completion for durations up to ~117msec, while the disruption caused by the global mask lasted an additional ~140-200msec. Their interpretation of these data was a two-stage model of boundary completion, involving extraction of local stimulus features at the earlier time and global shape formation at the later time. Imber and colleagues (Imber et al., 2000) further found that while RCs are not effective masks for ICs at the second stage, other ICs which differed in size did interfere with shape discrimination. They concluded that such size-invariant, contour-specific masking implied that the second stage comprises processes of object representation in intermediate, non-retinotopic regions of the visual hierarchy. The second stage of masking corresponds to ~280msec post-stimulus onset, timing which closely matches the peak latency of N_{cl} reported here and elsewhere (Doniger et al., 2000). These results are concordant with a multistage model of object recognition that involves multiple processing iterations through the LOC (i.e., an early automatic, perceptual and a later effortful stage). In this framework, real and illusory contours are processed by the same region but with differing timecourses. Whether the same neural populations are involved in processing ICs and RCs is a question which merits further study.

Task Difficulty

Differences in response to hard vs. easy stimuli were modulated by contour type. The NC stimuli, which most subjects reported were extremely difficult whether α was 1° or 6°, evoked no appreciable physiological differences. Sustained differences between easy and hard RC stimuli are apparent at latencies of 400-600msec. Curiously, IC stimuli only produce difficulty-related differences at latencies of 500-600msec. It is also interesting that the effects of difficulty appear later in time than those associated with response accuracy. The widespread nature of the VEP modulations to difficulty, in combination with the lateness of the effect, tends to obfuscate suppositions about what process these modulations represent.

Performance and VEP modulations

We monitored subjects' performance by collecting behavioral data simultaneously with recording of VEPs. Our behavioral results, that RCs are easiest to perceive, that ICs are a close second, and that NCs are quite difficult, are in agreement with the report of Ringach and Shapley (1996) for this task. We also found that α does significantly affect performance, thus validating our choice of αs as representing significantly different levels of difficulty.

Because we could examine VEPs correlated with trials yielding correct and incorrect behaviors, we were able to explore the relationship between accuracy and the IC effect. Incorrect responses could be the result of 1) impairment in boundary completion (perceptual), such that the illusory shape is never "filled in"; or 2) difficulty with the shape discrimination task (a failure of the effortful representation or discrimination). These stages might be hypothesized to correlate with the N1 and N_{cl} components of the VEP, as described previously. We observed performance-related modulations at both of these components. The fact that performance is correlated with the VEP at the N1, a relatively early stage, calls into question the automaticity of the IC effect in that it is capable of failure. If the N1 corresponds to boundary completion, then our results could imply that boundary completion does not occur automatically even when properly oriented inducing stimuli are presented to a subject. One possibility is that attentional mechanisms can affect illusory boundary formation even at this early stage. We also note that the N1 does not discriminate between accurate and inaccurate responses to NCs, perhaps because viewing NCs does not recruit mechanisms of boundary completion.

Conclusions

We collected VEP and behavioral data while subjects performed a discrimination task on IC, NC, and RC stimuli. Our task was designed to engage attention across all three stimulus types. We found evidence of different temporal dynamics for real, illusory, and no contour stimuli as measured over lateral occipital scalp. Correlates of performance accuracy were identified at both early and later components for the *IC effect*, calling into question the automatic nature of the early component and the perceptual process it reflects. The phasic nature of the key differences we observe between stimulus types, centered over posterior scalp regions, is consistent with a recursive model of object perception which entails multiple volleys of activation through occipital and lateral occipital areas.

Figure legends

Figure 1. Stimuli and experimental paradigm. All stimuli were defined by the presence of four Kanizsa-type inducers. Participants engaged in a two-alternative-forced-choice task which involved discrimination between $\alpha > 0$ (left column) or $\alpha < 0$ (right column) stimuli, where α refers to the angle of rotation of the top-left inducer. For illustration purposes, the stimuli are shown here as black-on-white, although they appeared white on gray in the experiment (see Methods for details). *a-c.* Sample stimuli are shown from the illusory contour (IC), real contour (RC), and no contour (NC) conditions. *d.* Timeline of a trial. Each stimulus was presented for 168 ms, followed by a blank screen for 700 ms. Participants then saw a "L|R" prompt, signaling them to indicate via a button-press whether the stimulus they had just seen fell into the "$\alpha > 0$" or "$\alpha < 0$" category. Participants were instructed to wait for the prompt before responding and had unlimited time to make their selection. Responses were followed by a fixation point for 700ms before onset of the next trial.

Figure 2. Behavioral results. Percent correct (mean with standard error shown) as a function of difficulty is shown for each of three contour types (illusory, real, or no contours). Data shown have been collapsed across classification types. In general, larger values of α improved performance. This effect was marked for IC (red bars) and RC (blue bars) stimuli, while performance with NC stimuli (green bars)

remained near chance at both difficulty levels tested. All contour types yielded significantly different levels of performance (see text).

Figure 3. VEP morphology. Plots illustrate voltage traces from a lateral occipital electrode in the right hemisphere (displayed at right) and its left-hemisphere homologue, shown as a function of time. The three traces in each plot represent group-averaged data from 12 subjects for each of three conditions: illusory contours (in red), no contours (green), and real contours (blue). The traditional ERP components can be seen, including P1, N1, and P2. At least two later components are prominent: the N_{cl}, similar to that identified by Doniger et al. (2000), and a slow, sustained component which peaks at approximately 400 ms. Inset: The 128-channel electrode montage, displayed on a sample head. The six electrodes included in further statistical analyses are colored in magenta and cyan; traces from the magenta electrodes are shown in this and subsequent figures.

Figure 4. The main effect of contour upon waveform morphology. At left, group-averaged (N=12) event-related potentials (ERPs) from a right lateral occipital electrode site, plotted as a function of time from stimulus onset. Each plot illustrates a pairwise comparison between contour types. Difference waveforms are superimposed in gold. At right, voltage density plots for the three different peak latencies used in our analyses are displayed on the posterior view of a sample head. The voltage plots illustrate topography of the difference waveform. *a.* ICs (red) vs. NCs (green). Difference waveform represents IC response minus NC response. A difference peak can be seen at the N1, which is revealed by voltage density

images to be most intense at left posterior sites. Substantial differences also appear at the N_{cl}, particularly in lateral occipital foci and more intensely in the right hemisphere. A sustained, late-stage difference is noted over bilateral lateral occipital regions. *b.* ICs vs. RCs (blue). Difference waveform represents IC minus RC potential. Three distinct peaks are visible, at the N1, the N_{cl}, and ~370 ms (late potential). After an initially diminished response relative to the IC condition, the RC response reverses in polarity and actually appears to mirror IC response in the opposing direction. Differences center around posterior midline structures, although more pronounced on the right at later times. *c.* RCs vs. NCs. Difference potential represents RC minus NC. Note that general positive direction of difference waveform reflects the direction of the subtraction. The peaks are at similar time points to those noted in *b*, with topography centered over posterior midline and right parietal structures.

Figure 5. Statistical cluster plots (SCPs) indicating spatiotemporal extent of significant differences between experimental conditions. For each electrode, pointwise t-tests were applied in paired comparisons between conditions of interest. For a given electrode, if the p-value met the 0.05 criterion for at least 11 consecutive time points (22ms at our digitization rate of 500Hz), the difference between conditions for that duration was considered statistically significant (after Guthrie & Buchwald, 1991). Plots illustrate differences between conditions at each electrode site (distributed along the y-axis) and over time (x-axis). Color indicates significant p-value for each point in space and time, for $p \leq 0.01$. Electrodes are

distributed by rough topographic region, and proceed from left to right within each area as marked on the graph. Colored electrodes at times before stimulus onset (0ms) provide an indication of Type I errors. For all three comparisons, the greatest differences are seen in posterior regions of scalp for N1, N_{cl}, and late-stage (350-450ms) components.

Figure 6. Interaction between contour type and difficulty. Shown are plots of group-average ERPs from 12 subjects as a function of time, with pairwise comparisons between responses to difficult ($\alpha=1$, brighter line) and easy ($\alpha=6$, darker line) stimuli for each contour type. Difference waveform is depicted in gold. *a.* Responses to easy and hard IC stimuli. The difference peaks at a late time point, ~575ms after stimulus onset. *b.* Responses to easy and hard RC stimuli. Easier stimuli yield a slightly larger (~1.75μV) N1 response. There is also a punctate difference at the N_{cl}, where more difficult stimuli yield a higher (positive) response. A sustained, late-stage difference is present from ~375-600ms. *c.* Responses to easy and hard NC stimuli. No differences are evident between responses to the two conditions. Subjects also showed little behavioral distinction between easy and hard NCs.

Figure 7. Statistical cluster plots illustrating the interaction between difficulty and contour type. At top, the distinction between hard and easy stimuli for ICs is apparent at a late stage (~500-625ms post-stimulus onset) over parietal and occipital scalp. The middle graph illustrates a long epoch of differential response

with onset ~375ms, first noted over right parietal area but evident throughout scalp. Some parieto-occipital electrodes also demonstrate significant difference at the level of the N1. At bottom, no differences are present between responses to hard and easy NC stimuli.

Figure 8. Interaction between accuracy and contour type, for IC and NC stimuli. *a.* Group-averaged waveforms for 11 subjects, sorted by accuracy and contour type, and sampled from a right lateral occipital electrode site. As before, IC responses are indicated in red and NC responses are shown in green. Waveforms associated with "correct" responses appear in bright colors. For ICs, there are significant differences between correct and incorrect responses at the N_{cl} and P3 components (~230-370ms). There are no significant differences between the EPs to correct and incorrect judgments of NCs. Results should be viewed as preliminary, given the disparity between numbers of sweeps to correct vs. incorrect trials (IC correct, 507.4±176.2, vs. IC incorrect, 149.4±79.8; NC correct, 363.8±156.2, vs. NC incorrect, 294.1±133.9). *b.* Statistical cluster plots of differences between ICs and NCs, segregated by accuracy. At top, trials which led to correct responses were averaged across 11 subjects for each contour type. Significant differences between contour types are plotted for correct trials only. The results were comparable to those seen in Fig. 5 (top plot), when accuracy was not considered. At bottom, the comparison between ICs and NCs in trials eliciting

incorrect responses. Note that the N1 effect disappears in this case, and that subsequent differences are focused in posterior right-hemisphere regions.

Figure 9. Statistical cluster plots of differences between evoked potentials to correct and incorrect responses, sorted by contour type. For ICs (top), there are significant differences at the falling phase of the P2 continuing through the P3. The P2 and N_{cl} differences are present primarily over right lateral occipital sites, while differences in the rising phase of the N_{cl} and the P3 may be seen over bilateral parietal and occipital scalp. No significant differences are seen in the NC comparison (bottom), consistent with behavioral data suggesting that larger values of α did not significantly improve subjects' performance.

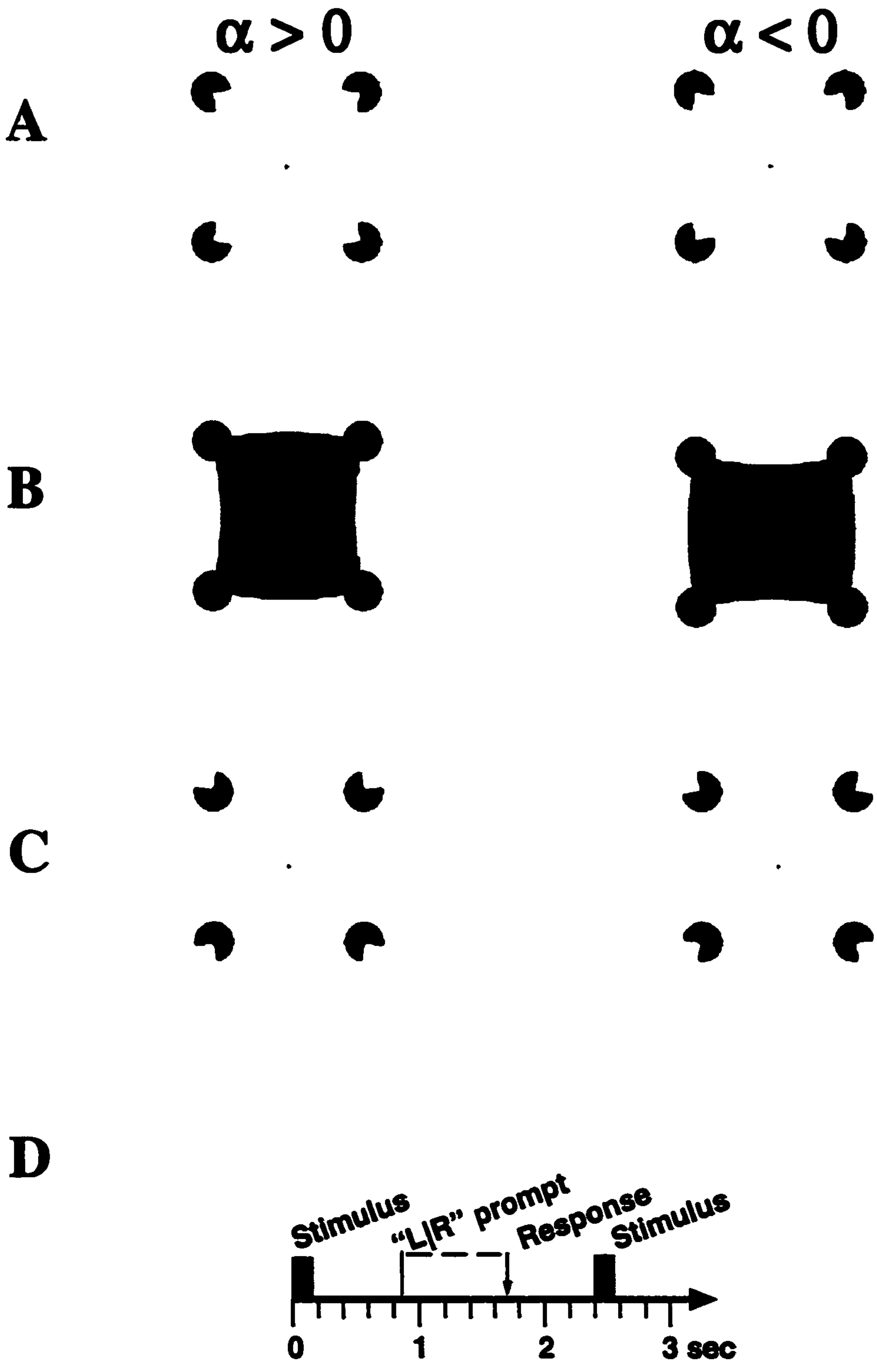

Figure 3.1

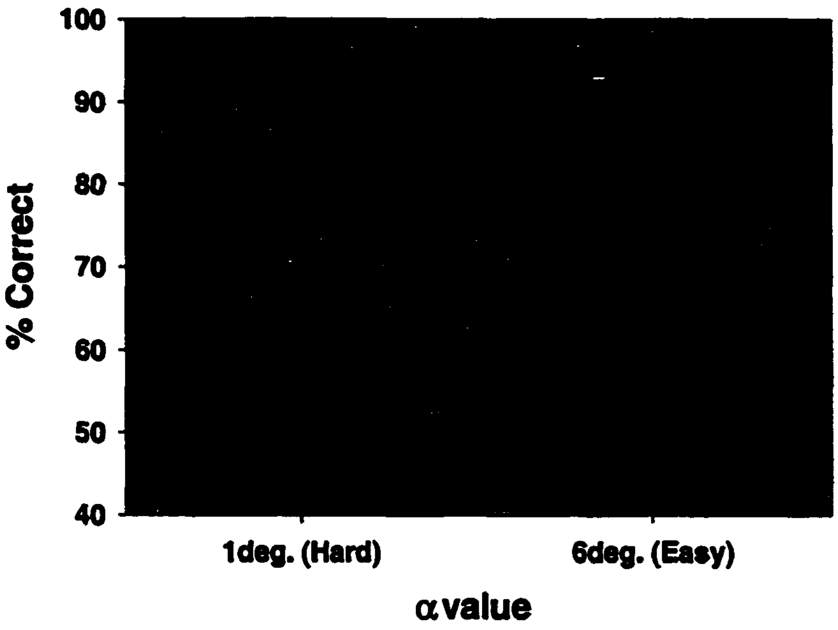

Figure 3.2

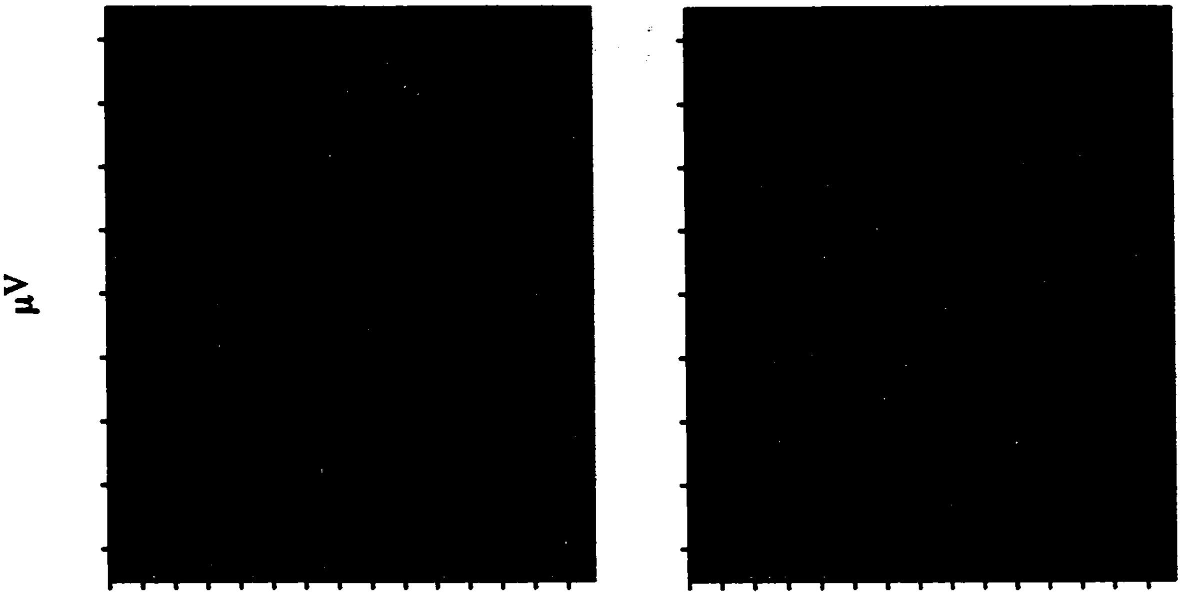

Figure 3.3

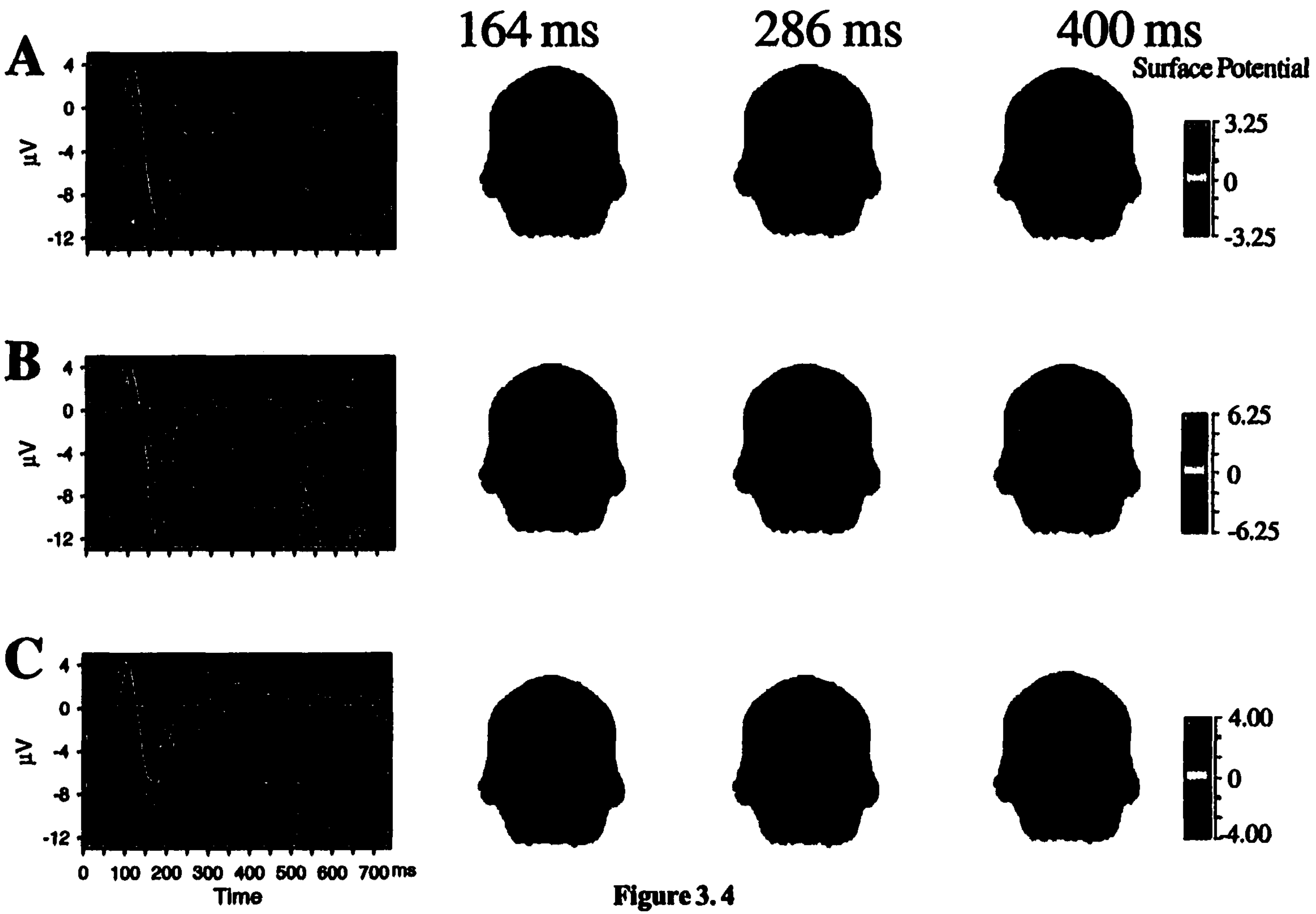
A
B
C
164 ms
286 ms
400 ms
Surface Potential
µV
4
0
-4
-8
-12
0 100 200 300 400 500 600 700 ms
Time
3.25
0
-3.25
6.25
0
-6.25
4.00
0
-4.00

Figure 3. 4

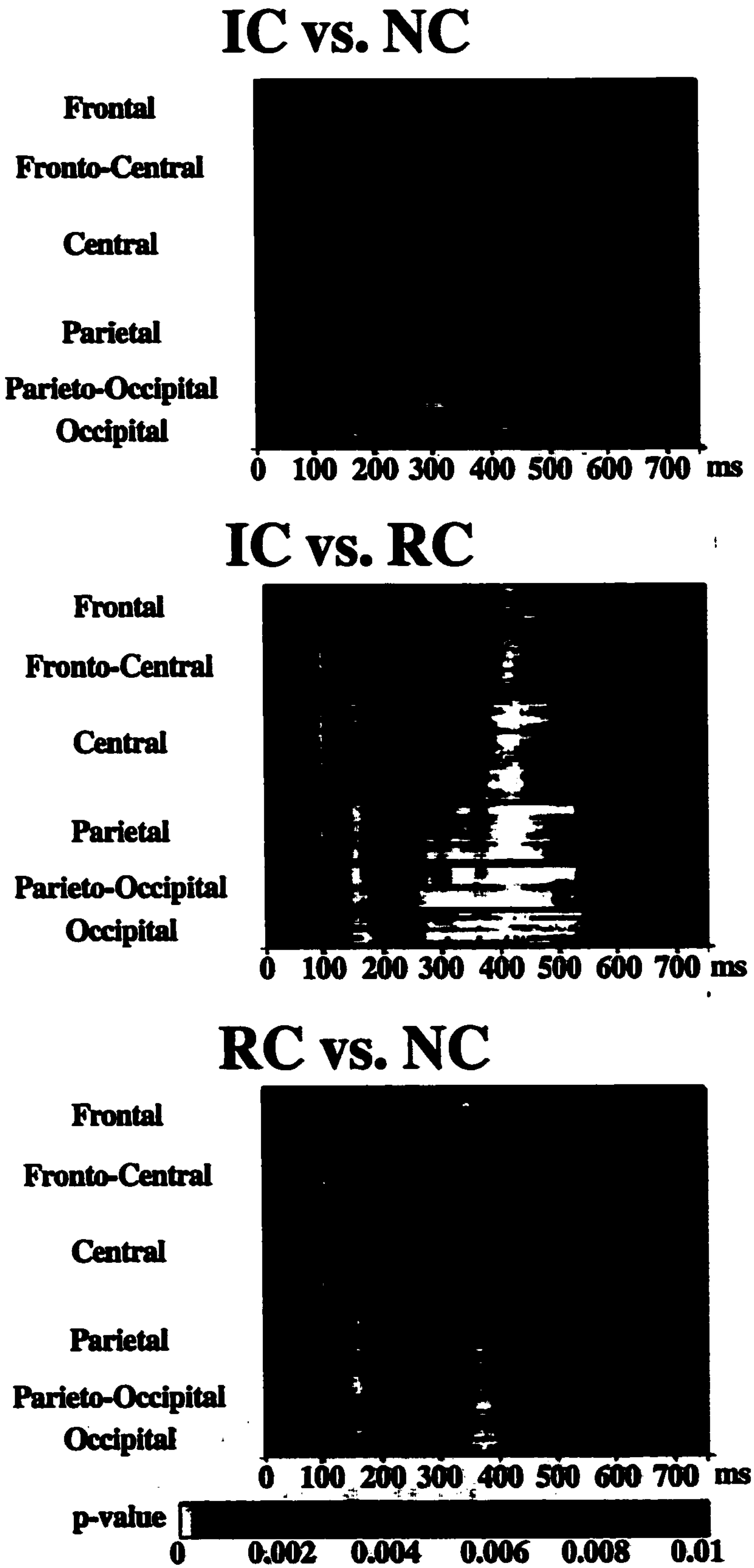
IC vs. NC
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
IC vs. RC
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
RC vs. NC
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
p-value
0 0.002 0.004 0.006 0.008 0.01

Figure 3.5

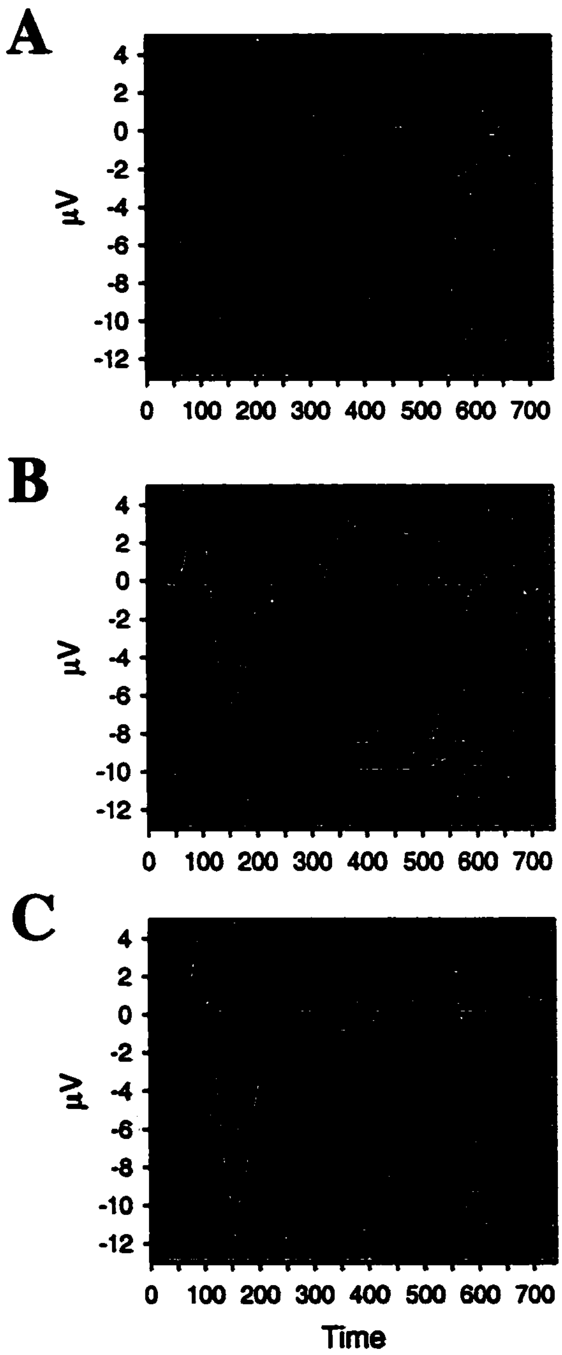

Figure 3.6

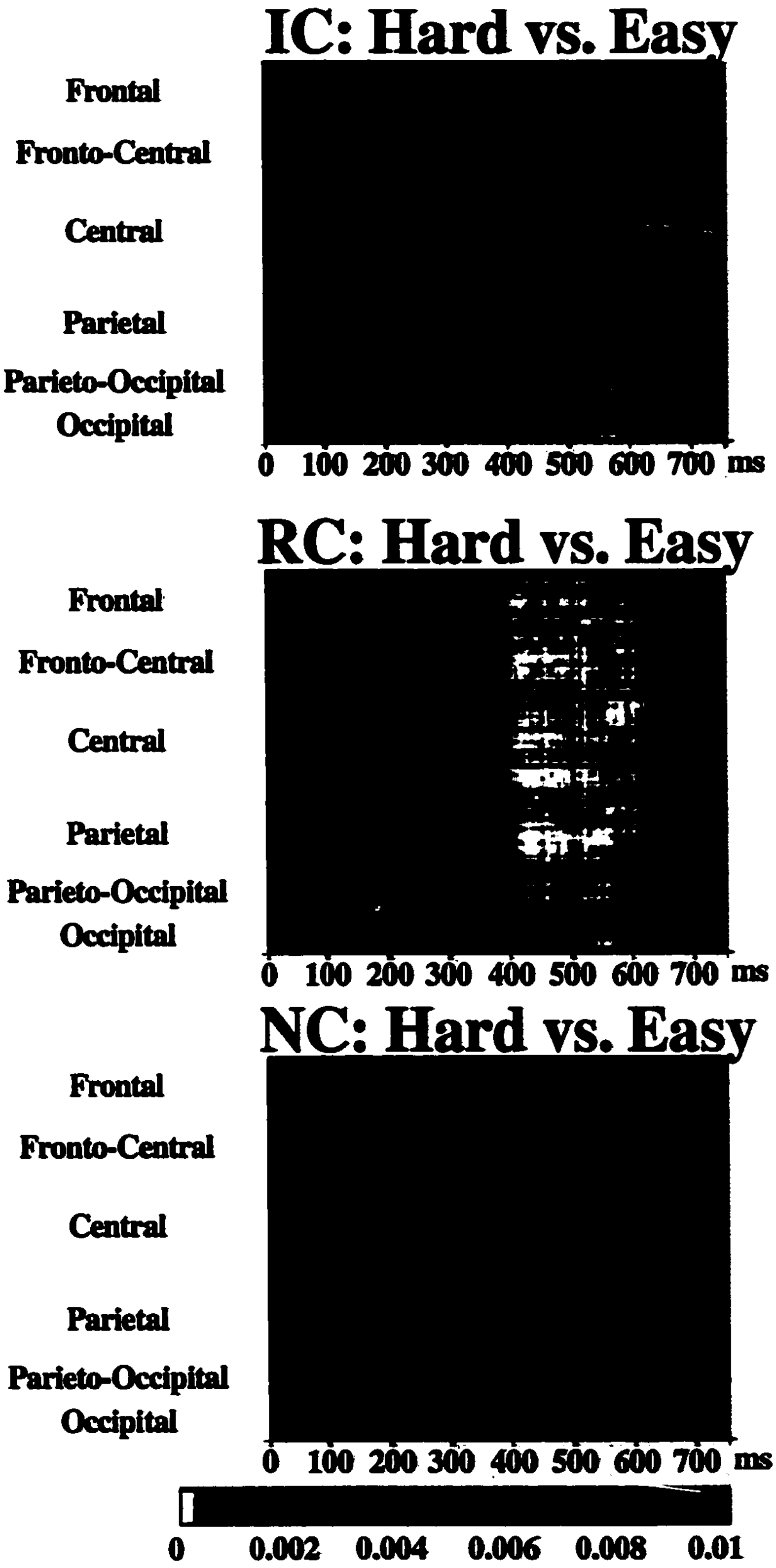
IC: Hard vs. Easy
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
RC: Hard vs. Easy
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
NC: Hard vs. Easy
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
0
0.002
0.004
0.006
0.008
0.01

Figure 3.7

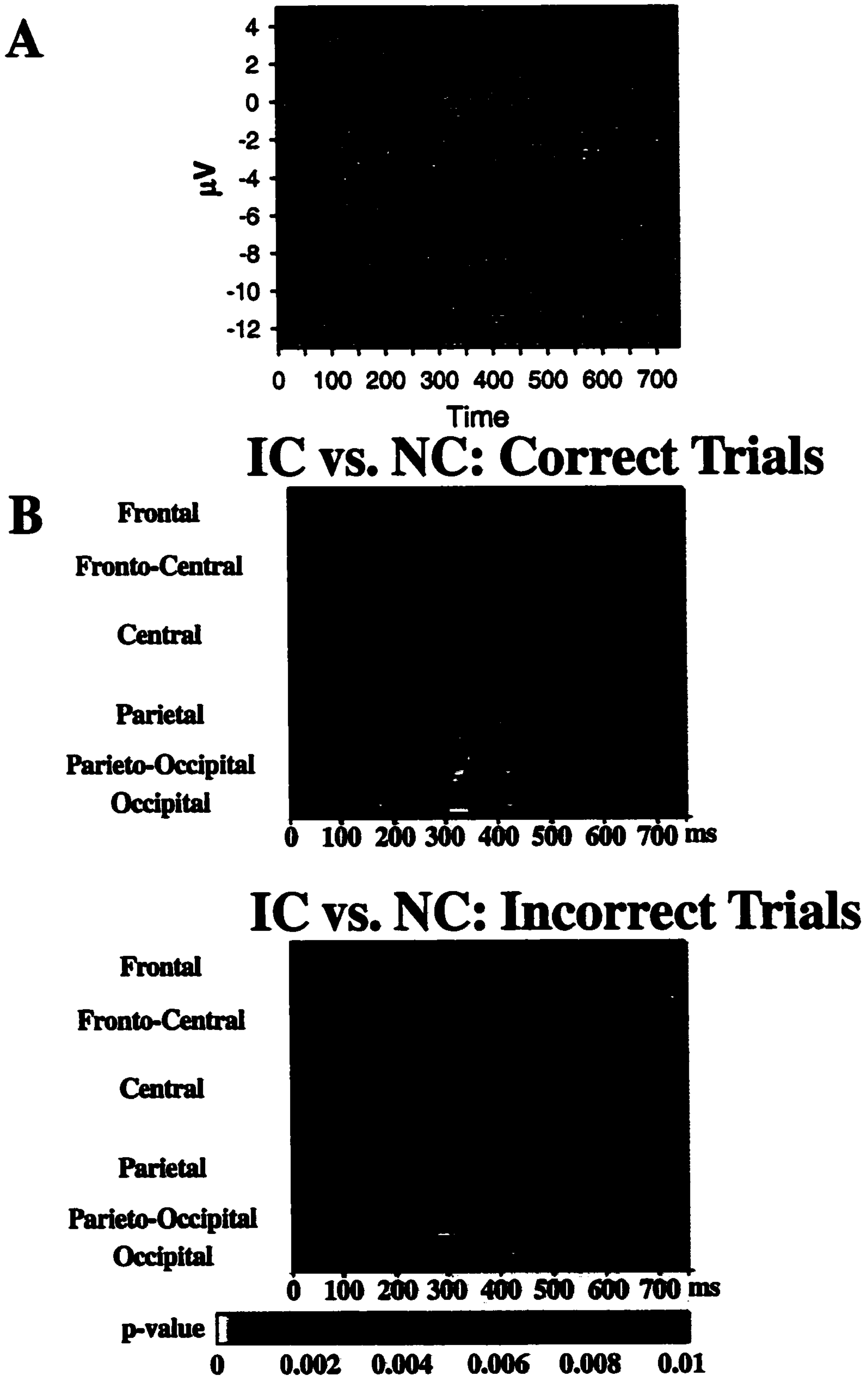
A
4
2
0
-2
-4
-6
-8
-10
-12
μV
0 100 200 300 400 500 600 700
Time
IC vs. NC: Correct Trials
B
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
IC vs. NC: Incorrect Trials
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
p-value
0 0.002 0.004 0.006 0.008 0.01

Figure 3.8

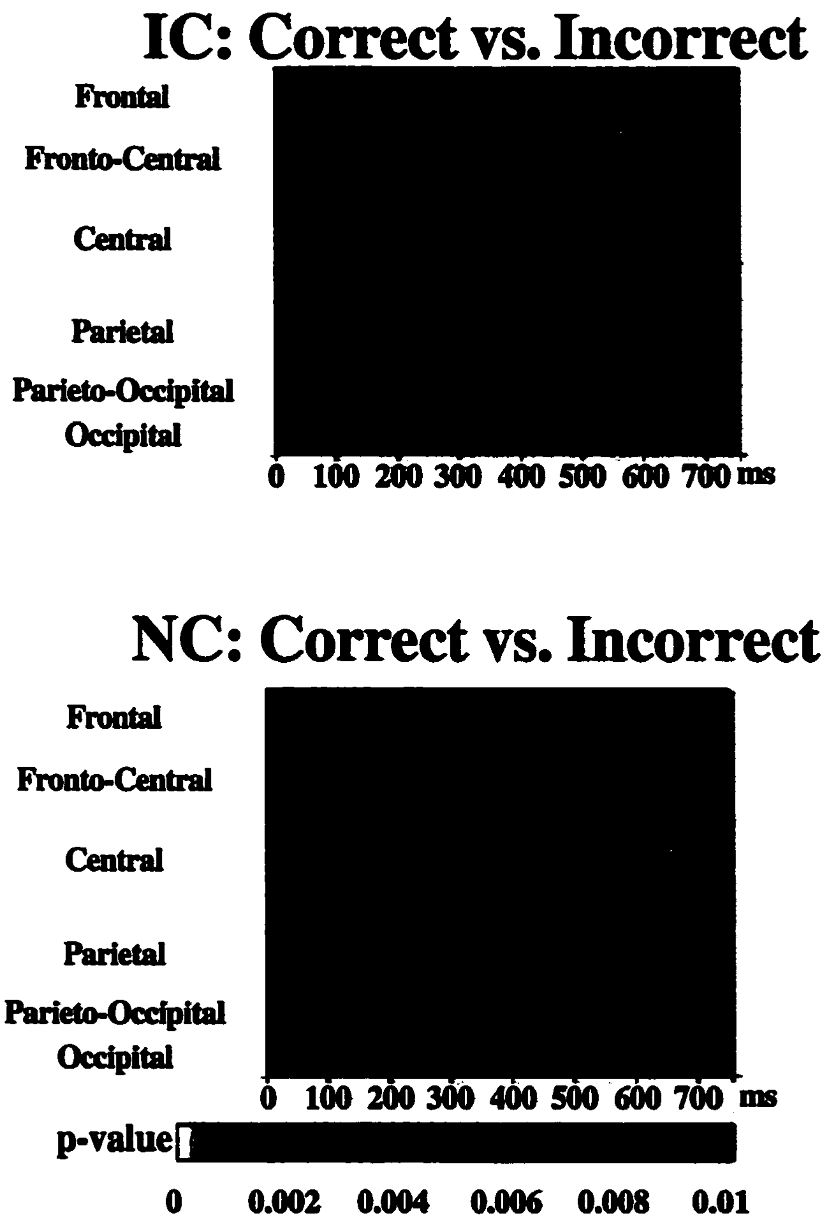
IC: Correct vs. Incorrect
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
NC: Correct vs. Incorrect
Frontal
Fronto-Central
Central
Parietal
Parieto-Occipital
Occipital
0 100 200 300 400 500 600 700 ms
p-value
0 0.002 0.004 0.006 0.008 0.01

Figure 3.9

GENERAL DISCUSSION

A primary purpose of these companion studies was to acquire some insight into the microgenesis of illusory contour perception, and further to relate these findings to the temporal dynamics of real contour perception. In the first study, I employed a psychophysical backward masking paradigm to interfere with the performance of an illusory shape discrimination task (see also Ringach & Shapley, 1996). When both target and mask were illusory shapes, the latency of peak masking occurred at ~275ms post-stimulus onset. This masking was size-invariant. When real contours served as either target or mask, no elevation in thresholds was obtained. We are thus left with at least three questions:

1) What phase of illusory processing have we disrupted with the mask?
2) Where in the visual processing hierarchy does the affected stage take place?
3) Why is this masking apparently dependent upon the illusory nature of both stimulus and mask?

Answers to these questions are somewhat aided by the results of the visual evoked potential (VEP) study, which revealed at least two stages of IC processing during performance of our task. The first stage peaked at ~170ms post-stimulus onset, apparently akin to the '*IC effect*' reported by Murray et al. (in press). Murray and colleagues argued that this stage reflects the first differential response to IC vs. NC stimuli in cortex, and that it originates from lateral occipital regions. Pegna (in press) and our present study further find differences between IC and NC at this stage. This component has been correlated with an automatic, perceptual processing of the visual image (i.e., Allison et al., 1994; Doniger et al., 2001a; Murray et al., in press; Ritter et al., 1982). Because we included the thin/fat task in our ERP study, we were able to investigate the relationship between accuracy on the task and modulations in the evoked potentials. We found that accuracy modulated this early component. This finding suggests that the earlier, 'automatic' stage can actually fail sometimes, and that such failures can be linked to failures in performance. One possible explanation for this pattern is that the earlier stage represents a boundary completion process, which is perhaps less automatic than previously thought (Davis & Driver, 1994; Vuilleumier & Landis, 1998). When the boundaries do not complete properly, subjects may be forced to rely upon the cues provided by the inducer rotation alone. The resulting task appears to be much more difficult and thus yields higher thresholds (and more frequent incorrect responses; see Ringach & Shapley, 1996).

The early stage precedes a second component, at ~286ms post-stimulus onset, which has been linked to effortful sensory discrimination tasks (Ritter et al., 1979; Ritter et al., 1982) including those dependent upon visual closure (Doniger et al., 2001a; Doniger et al., 2000). This component also has been reported to reach its peak amplitude over lateral occipital scalp. We see differential responses to ICs as compared with NCs and RCs at this stage as well. The timing of the second component is clearly very close to the peak of our masking function. These findings, in conjunction with the size invariance of the masking, could be consistent with a lateral occipital origin for the stage interrupted by the masking. But what process is indexed by this stage?

The stage of processing represented by the second ERP component, or N_{cl}, is presently not well understood. As noted previously, this component may be involved in perceptual identifications related to closure (see above). This component is also modulated by accuracy in our visual evoked potentials study. Ringach and Shapley (1996) thought that this stage might represent boundary completion itself. However, in their study, representation of the illusory shape was confounded with the shape discrimination task at these latencies. Furthermore, our psychophysical masking findings point to the involvement of a non-retinotopic, contour-type-dependent mechanism. I therefore propose that the mask is interrupting a shape discrimination process unique to illusory contour perception. This process, which occurs subsequent to boundary completion, perhaps also occurs in lateral occipital areas.

The fact that RCs do not mask ICs at this latency could suggest that different neuronal populations process both contour types. Alternatively, it could imply that RCs are processed more efficiently than ICs and thus are not effective at blocking IC perception when SOAs are so long. The latter hypothesis receives support from our report that neither ICs nor RCs can mask target RC shapes at these latencies. The findings presented here are in accordance with the recent results of Pegna et al. (in press), which suggest that RCs and ICs both activate lateral occipital regions but that RCs are processed with a different (and perhaps faster) electrophysiological signature. The functional neuroimaging literature suggests that ICs and RCs both activate lateral occipital cortex, but that ICs yield stronger signals (Larsson et al., 1999; Mendola et al., 1999a). This result might be obtained in the context of time-averaged analyses, if RCs spend comparatively less processing time in the LOC. Whether same or different neuronal populations within this region are responsible for IC and RC perception remains to be determined; however, it is interesting to note that dissociations between IC and RC shape discrimination have been noted in human (Huxlin & Merigan, 1998) and macaque (Huxlin et al., 2000).

In sum, our findings support a multistage model of IC processing which could entail several phases of activation in lateral occipital regions. The initial stage of IC sensitivity may be a correlate of illusory boundary completion; a later stage may reflect shape discrimination. IC perception may engage more resources than processing of similar RC stimuli, which may occur along a different temporal trajectory and possibly in a different population of neurons.

Future Directions

The present experiments have left several intriguing questions yet unanswered. For example, although it seems that ICs and RCs may both be processed in the LOC, and that the two contour types are processed according to different temporal trajectories, we do not know whether they share similar neuronal populations. One way to approach this question would be to employ the functional Magnetic Resonance (fMR) adaptation approach proposed by Grill-Spector and colleagues (Grill-Spector et al., 1999). In this method, subjects are bombarded with stimuli of a particular class before they are shown images belonging to another class. If response strength for the second group declines as a function of the number of repetitions of the first, the two classes may be presumed to involve overlapping neuronal populations. It would be interesting to note whether ICs and RCs engage disparate neural populations within the LOC, by adapting cortex to one contour type and testing activation strength for the other. This approach could also be employed with amodal completion (AC) stimuli (Michotte et al., 1964), which are thought to be related to ICs.

In the realm of backward masking, we have shown that ICs will mask other ICs at late durations even if the target and mask differ in size. We tested this hypothesis with only two (relatively large) sizes, 11.0° and 15.6° of visual angle respectively. A parametric study of size invariance in this masking effect would be informative. Furthermore, if this type of masking is truly contour-type-dependent and not reliant upon retinotopic mechanisms, one might expect cross-masking between ICs located in different regions of the visual field. It would also be interesting to investigate whether ICs of other subtypes would cross-mask with a Kanizsa figure at these durations. Some suggested stimuli might be Ehrenstein illusions, Kanizsa figures of other geometric shapes, or even higher-order objects requiring visual closure (e.g., Gollin, 1960; Street, 1931). As suggested above, there is a possible relationship between amodally-completed contours and ICs; this, too, could be explored via a cross-masking paradigm.

Finally, the present studies have laid the groundwork for understanding the evoked potentials elicited by ICs, NCs, and RCs. One natural next step might be to extend the masking paradigm to a VEP study, to investigate whether the N_{cl} component to ICs is altered in some way when a mask is presented. Such a study would provide a stronger link between psychophysical and electrophysiological correlates of illusory shape discrimination.

REFERENCES

Allison, T., McCarthy, G., Nobre, A., Puce, A., & Belger, A. (1994). Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cereb Cortex, 4*(5), 544-54.

Bachmann, T. (1978). Cognitive contours: Overview and a preliminary theory. *Tartu Riikliku Uelikooli Toimetised: Trudy po Psikhologii, 474*, 31-59.

Bachmann, T., Asser, T., Sarv, M., Taba, P., Lausvee, E., Poder, E., Kahusk, N., & Reitsnik, T. (1998). Speed of elementary visual recognition operations in Parkinson's disease as measured by the mutual masking method. *J Clin Exp Neuropsychol, 20*(1), 118-34.

Bar, M., Tootell, R. B., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., Rosen, B. R., & Dale, A. M. (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron, 29*(2), 529-35.

Beckett, P. A. (1989). Illusion decrement and transfer of illusion decrement in real- and subjective-contour Poggendorff figures. *Percept Psychophys, 45*(6), 550-6.

Beckett, P. A. (1990). Similar processing of real- and subjective-contour Poggendorff figures by men and women. *Percept Mot Skills, 70*(1), 51-6.

Beckett, P. A., & Hurajt, S. (1988). Real and subjective contour Poggendorff illusions: no differences based on eye color. *Perception, 17*(3), 311-3.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: time course and scalp distribution. *J Cogn Neurosci, 11*(3), 235-60.

Bradley, D. R. (1982). Binocular rivalry of real vs. subjective contours. *Percept Psychophys, 32*(1), 85-7.

Brandeis, D., & Lehmann, D. (1989). Segments of event-related potential map series reveal landscape changes with visual attention and subjective contours. *Electroencephalogr Clin Neurophysiol, 73*(6), 507-19.

Brandeis, D. U., Jin, G. C., Lehmann, D., & Mueller, R. U. (1985). Late EP components related to subjective contour perception and to attention. *Electroencephalography & Clinical Neurophysiology, 61*, 58.

Breitmeyer, B. G. (1984). *Visual Masking: An Integrative Approach*. Oxford: Clarendon Press.

Breitmeyer, B. G., & Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychological Review, 87*, 52-69.

Corballis, P. M., Fendrich, R., Shapley, R. M., & Gazzaniga, M. S. (1999). Illusory contour perception and amodal boundary completion: evidence of a dissociation following callosotomy. *J Cogn Neurosci, 11*(4), 459-466.

Coren, S. (1983). When "filling in" fails. *Behavioral & Brain Sciences, 6*, 661-662.

Daffner, R. H. (1989). Visual illusions in the interpretation of the radiographic image. *Curr Probl Diagn Radiol, 18*(2), 62-87.

Davi, M., Pinna, B., & Sambin, M. (1992). Amodal completion versus induced inhomogeneities in the organization of illusory figures. *Perception, 21*(5), 627-36.

Davis, G., & Driver, J. (1994). Parallel detection of Kanizsa subjective figures in the human visual system. *Nature, 371*(6500), 791-3.

Day, R. H. (1987). Cues for edge and the origin of illusory contours: An alternative approach. In S. Petry & G. E. Meyer (Eds.), *The perception of illusory contours* (pp. 53-61). New York/Berlin: Springer-Verlag.

Doniger, G. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Snodgrass, J. G., & Schroeder, C. E. (2000). Activation timecourse of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes. *J Cogn Neurosci, 12*(4), 615-21.

Doniger, G. M., Foxe, J. J., Schroeder, C. E., Murray, M. M., Higgins, B. A., & Javitt, D. C. (2001a). Visual perceptual learning in human object recognition areas: A repetition priming study using high-density electrical mapping. *Neuroimage, 13*(2), 305-313.

Doniger, G.M., Foxe, J.J., Murray, M.M., Higgins, B.A., Javitt, D.C. (In press). Impaired visual object recognition and ventral/dorsal stream interaction in schizophrenia. *Archives of General Psychiatry*.

Doniger, G. M., Silipo, G., Rabinowicz, E. F., Snodgrass, J. G., & Javitt, D. C. (2001b). Impaired sensory processing as a basis for object-recognition deficits in schizophrenia. *Am J Psychiatry, 158*(11), 1818-26.

Dresp, B. (1997). On "illusory" contours and their functional significance. *Cahiers de Psychologie Cognitive/Current Psychology of Cognition, 16*(4), 489-518.

Eden, G. F., VanMeter, J. W., Rumsey, J. M., Maisog, J. M., Woods, R. P., & Zeffiro, T. A. (1996). Abnormal processing of visual motion in dyslexia revealed by functional brain imaging. *Nature, 382*(6586), 66-9.

Efron, B., & Tibshirani, R. (1993). *An introduction to the bootstrap*. New York: Chapman and Hall.

Fahle, M., & Palm, G. (1991). Perceptual rivalry between illusory and real contours. *Biol Cybern, 66*(1), 1-8.

ffytche, D. H., & Zeki, S. (1996). Brain activity related to the perception of illusory contours. *Neuroimage, 3*(2), 104-8.

Francis, G., & Grossberg, S. (1996). Cortical dynamics of form and motion integration: persistence, apparent motion, and illusory contours. *Vision Res, 36*(1), 149-73.

Francis, G., Grossberg, S., & Mingolla, E. (1994). Cortical dynamics of feature binding and reset: control of visual persistence. *Vision Res, 34*(8), 1089-104.

Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication - Does the corpus callosum enable the human condition? *Brain, 123*, 1293-1326.

Gegenfurtner, K. R., Brown, J. E., & Rieger, J. (1997). Interpolation processes in the perception of real and illusory contours. *Perception, 26*(11), 1445-58.

Gellatly, A. R. (1980). Perception of an illusory triangle with masked inducing figure. *Perception, 9*(5), 599-602.

Ginsburg, A. P. (1987). The relationship between spatial filtering and subjective contours. In S. Petry & G. E. Meyer (Eds.), *The Perception of Illusory Contours* (pp. 126-130). New York/Berlin: Springer-Verlag.

Goebel, R., Khorram-Sefat, D., Muckli, L., Hacker, H., & Singer, W. (1998). The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *Eur J Neurosci, 10*(5), 1563-73.

Gold, J. M., Murray, R. F., Bennett, P. J., & Sekuler, A. B. (2000). Deriving behavioural receptive fields for visually completed contours. *Curr Biol, 10*(11), 663-6.

Gollin, E. S. (1960). Developmental studies of visual recognition of incomplete objects. *Perceptual and Motor Skills, 11*, 289-298.

Green, M. F., Nuechterlein, K. H., Breitmeyer, B., & Mintz, J. (1999). Backward masking in unmedicated schizophrenic patients in psychotic remission: possible reflection of aberrant cortical oscillation. *Am J Psychiatry, 156*(9), 1367-73.

Greene, H. H., & Brown, J. M. (1997). Spatial interactions with real and gap-induced illusory lines in vernier acuity. *Vision Res, 37*(5), 597-604.

Greene, H. H., & Brown, J. M. (2000). Amodal completion and localization. *Vision Research, 40*(4), 383-390.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron, 24*(1), 187-203.

Grill-Spector, K., Kushnir, T., Edelman, S., Itzchak, Y., & Malach, R. (1998a). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron, 21*(1), 191-202.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., & Malach, R. (1998b). A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Hum Brain Mapp. 6*(4), 316-28.

Grosof, D. H., Shapley, R. M., & Hawken, M. J. (1993). Macaque V1 neurons can signal 'illusory' contours. *Nature, 365*(6446), 550-2.

Grossberg, S. (1998). How does the cerebral cortex work? Learning, attention, and grouping by the laminar circuits of visual cortex. *Spatial Vision*.

Grossberg, S., Mingolla, E., & Ross, W. D. (1997). Visual brain and visual perception: how does the cortex do perceptual grouping? *Trends Neurosci, 20*(3), 106-11.

Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiology, 28*(2), 240-4.

Herrmann, C. S., & Bosch, V. (2001). Gestalt perception modulates early visual processing. *Neuroreport, 12*(5), 901-4.

Herrmann, C. S., & Mecklinger, A. (2000). Magnetoencephalographic responses to illusory figures: early evoked gamma is affected by processing of stimulus features. *Int J Psychophysiol, 38*(3), 265-81.

Herrmann, C. S., Mecklinger, A., & Pfeifer, E. (1999). Gamma responses and ERPs in a visual classification task. *Clin Neurophysiol, 110*(4), 636-42.

Hirsch, J., DeLaPaz, R. L., Relkin, N. R., Victor, J., Kim, K., Li, T., Borden, P., Rubin, N., & Shapley, R. (1995). Illusory contours activate specific regions in human visual cortex: evidence from functional magnetic resonance imaging. *Proc Natl Acad Sci U S A, 92*(14), 6469-73.

Huxlin, K. R., & Merigan, W. H. (1998). Deficits in complex visual perception following unilateral temporal lobectomy. *J Cogn Neurosci, 10*(3), 395-407.

Huxlin, K. R., Saunders, R. C., Marchionini, D., Pham, H. A., & Merigan, W. H. (2000). Perceptual deficits after lesions of inferotemporal cortex in macaques. *Cereb Cortex, 10*(7), 671-83.

Imber, M. L. (1999). *fMRI investigation of illusory contours and Street figures: a comparison between two methods of analysis.* Unpublished Master's Thesis, New York University, New York City, NY.

Imber, M. L., Shapley, R., & Rubin, N. (2000). A Kanizsa square is more effective than a real square for masking illusory shapes. *Investigative Ophthalmology and Visual Science, 41*(4), S217.

Ishai, A., Ungerleider, L. G., Martin, A., & Haxby, J. V. (2000). The representation of objects in the human occipital and temporal cortex. *J Cogn Neurosci, 12*(Suppl 2), 35-51.

Iwatani, T. *Pac-Man.* Tokyo: Namco Limited/Midway Mfg.Co.

Kanizsa, G. (1955). Margini. Quasi-percettivi in campi con stimolazione omogenea. *Rivista di Psicologia, 49*, 7-30.

Kanizsa, G. (1976). Subjective contours. *Sci Am, 234*(4), 48-52.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci, 17*(11), 4302-11.

Kellman, P.J., & Shipley, T.F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology, 23,* 141-221.

Kojo, I., Liinasuo, M., & Rovamo, J. (1993). Spatial and temporal properties of illusory figures. *Vision Res, 33*(7), 897-901.

Kolers, P. A. (1962). Intensity and contour effects in visual masking. *Vision Research, 2*, 277-294.

Korshunova, S. G. (1998). [Visual evoked potentials to illusory contours (Kanizsa's square)]. *Zh Vyssh Nerv Deiat Im I P Pavlova, 48*(5), 807-15.

Korshunova, S. G. (1999). Visual evoked potentials induced by illusory outlines (Kanizsa's square). *Neurosci Behav Physiol, 29*(6), 695-701.

Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *J Neurosci, 20*(9), 3310-8.

Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science, 293*(5534), 1506-9.

Larsson, J., Amunts, K., Gulyas, B., Malikovic, A., Zilles, K., & Roland, P. E. (1999). Neuronal correlates of real and illusory contour perception: functional anatomy with PET. *Eur J Neurosci, 11*(11), 4024-36.

Lee, T. S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proc Natl Acad Sci U S A, 98*(4), 1907-11.

Lesher, G. W. (1994). Illusory contours: Toward a neurally based perceptual theory. *Psychonomic Bulletin and Review, 2*(3), 279-325.

Liinasuo, M., Rovamo, J., & Kojo, I. (1997). Effects of spatial configuration and number of fixations on Kanizsa triangle detection. *Invest Ophthalmol Vis Sci, 38*(12), 2554-65.

Luck, S. J., & Girelli, M. (1998). Electrophysiological approaches to the study of selective attention in the human brain. In R. Parasuraman (Ed.), *The Attentive Brain* (pp. 71-93). Cambridge, MA: MIT Press.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci U S A, 92*(18), 8135-9.

Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: W. H. Freeman.

Mendola, J. (submitted). Functional Neuroimaging of contour representation in human visual cortex: Beginning to fill-in the blanks. In P. De Weerd & L. Pessoa (Eds.), *Filling-In: From Perceptual Completion to Skill Learning* : Oxford University Press.

Mendola, J. D., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. (1999a). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *J Neurosci, 19*(19), 8560-72.

Mendola, J. D., Rizzo, J. F., Cosgrove, G. R., Cole, A. J., Black, P., & Corkin, S. (1999b). Visual discrimination after anterior temporal lobectomy in humans. *Neurology, 52*(5), 1028-1037.

Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annu Rev Neurosci, 16*, 369-402.

Meyer, G. E., & Petry, S. (1987). Top-down and bottom-up: The illusory contour as a microcosm of issues in perception. In S. Petry & G. E. Meyer

(Eds.), *The Perception of Illusory Contours* (pp. 3-20). New York/Berlin: Springer-Verlag.

Michaels, C. F., & Turvey, M. T. (1979). Central sources of visual masking: indexing structures supporting seeing at a single, brief glance. *Psychol Res, 41*(1), 2-61.

Michotte, A., Thines, G., & Crabbe, G. (1964). Les complements amodaux des structures perceptives [Amodal complements of perceptual structures], *Studia psychologica* . Louvain, Belgium: Publications Universitaires de Louvain.

Molholm, S., Ritter, W., Murray, M.M., Javitt, D.C., Schroeder, C.E., & Foxe, J.J. (in press). Multisensory auditory-visual interactions during early sensory processing in humans: a high-density electrical mapping study. *Cognitive Brain Research*.

Moscovitch, C., Kapur, S., Kohler, S., & Houle, S. (1995). Distinct neural correlates of visual long-term memory for spatial location and object identity: a positron emission tomography study in humans. *Proc Natl Acad Sci U S A, 92*(9), 3721-5.

Muise, J. G., LeBlanc, R. S., Blanchard, L. C., & de Warnaffe, A. (1993). Discrimination of the shape of the masked inducing figure precedes perception of the illusory triangle. *Perception, 22*(5), 623-8.

Murray, M. M., Wylie, G. R., Higgins, B. A., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (in press). The spatio-temporal dynamics of illusory contour processing: combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging..

Nakayama, K., & Shimojo, S. (1992). Experiencing and perceiving visual surfaces. *Science, 257*(5075), 1357-63.

Neisser, U. (1967). *Cognitive Psychology*. New York: Appleton-Century-Cross.

Nieder, A., & Wagner, H. (1999). Perception and neuronal coding of subjective contours in the owl. *Nat Neurosci, 2*(7), 660-3.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.

Paradiso, M. A., Shimojo, S., & Nakayama, K. (1989). Subjective contours, tilt aftereffects, and visual cortical organization. *Vision Res, 29*(9), 1205-13.

Parks, T. E. (1994). On the microgenesis of illusory figures: a failure to replicate. *Perception, 23*(7), 857-62.

Parks, T. E. (1995). The microgenesis of illusory figures: evidence for visual hypothesis testing. *Perception, 24*(6), 681-4.

Pegna, A. J., Khateb, A., Murray, M. M., Landis, T., & Michel, C. M. (In press). Neural processing of illusory and real contours revealed by high density ERP mapping. *Neuroreport*.

Perrin, F., Bertrand, O., & Pernier, J. (1987). Scalp current density mapping: value and estimation from potential data. *IEEE Trans Biomed Eng, 34*(4), 283-8.

Pessoa, L., Thompson, E., & Noe, A. (1998). Finding out about filling-in: a guide to perceptual completion for visual science and the philosophy of perception. *Behav Brain Sci, 21*(6), 723-48; discussion 748-802.

Peterhans, E., & von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *J Neurosci, 9*(5), 1749-63.

Peterhans, E., & von der Heydt, R. (1993). Functional organization of area V2 in the alert macaque. *Eur J Neurosci, 5*(5), 509-24.

Peterhans, E., von der Heydt, R., & Baumgartner, G. (1986). Neuronal responses to illusory contour stimuli reveal stages of visual cortical processing. In J. D. Pettigrew, K. J. Sanderson, & W. R. Levick (Eds.), *Visual Neuroscience* . Cambridge: Cambridge University Press.

Petry, S., & Meyer, G. E. (1987). *The Perception of Illusory Contours*. New York: Springer-Verlag.

Purghé, F., & Coren, S. (1992). Subjective contours 1900-1990: research trends and bibliography. *Percept Psychophys, 51*(3), 291-304.

Ramsden, B. M., Hung, C. P., & Roe, A. W. (2001). Real and illusory contour processing in area V1 of the primate: a cortical balancing act. *Cereb Cortex, 11*(7), 648-65.

Reynolds, R. I. (1981). Perception of an illusory contour as a function of processing time. *Perception, 10*(1), 107-15.

Riddoch, M. J., & Humphreys, G. W. (1987). A case of integrative visual agnosia. *Brain, 110*(Pt 6), 1431-62.

Ringach, D. L., & Shapley, R. (1996). Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Res, 36*(19), 3037-50.

Ritter, W., Simson, R., Vaughan, H. G., Jr., & Friedman, D. (1979). A brain event related to the making of a sensory discrimination. *Science, 203*(4387), 1358-61.

Ritter, W., Simson, R., Vaughan, H. G., Jr., & Macht, M. (1982). Manipulation of event-related potential manifestations of information processing stages. *Science, 218*(4575), 909-11.

Rock, I. (1987). Cognitive intervention in perceptual processing. In S. Petry & G. E. Meyer (Eds.), *The perception of illusory contours* (pp. 62-70). New York/Berlin: Springer-Verlag.

Rubin, N., Nakayama, K., & Shapley, R. (1996). Enhanced perception of illusory contours in the lower versus upper visual hemifields. *Science, 271*(5249), 651-3.

Rubin, N., Nakayama, K., & Shapley, R. (1997). Abrupt learning and retinal size specificity in illusory-contour perception. *Curr Biol, 7*(7), 461-7.

Sajda, P., & Finkel, L. H. (1995). Intermediate-level visual representations and the construction of surface perception. *Journal of Cognitive Neuroscience, 7*(2), 267-291.

Schumann, F. (1987). Contributions to the analysis of visual perception: First paper. Some observations on the combination of visual impressions into units. In S. Petry & G. E. Meyer (Eds.), *The perception of illusory contours* (pp. 21-34). New York/Berlin: Springer-Verlag.

Seghier, M., Dojat, M., Delon-Martin, C., Rubin, C., Segebarth, C., & Bullier, J. (1999). Moving illusory contours activate primary visual cortex: an fMRI study. *Unpublished manuscript*, 1-21 + figs.

Sekuler, A. B., & Palmer, S. E. (1992). Perception of partly occluded objects: a microgenetic analysis. *Journal of Experimental Psychology: General, 121*(1), 95-111.

Sheth, B. R., Sharma, J., Rao, S. C., & Sur, M. (1996). Orientation maps of subjective contours in visual cortex. *Science, 274*(5295), 2110-5.

Shipley, T. F., & Kellman, P. J. (1992). Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Percept Psychophys, 52*(1), 97-106.

Slaghuis, W. L., & Bakker, V. J. (1995). Forward and backward visual masking of contour by light in positive- and negative-symptom schizophrenia. *Journal of Abnormal Psychology, 104*(1), 41-54.

Smith, A. T., & Over, R. (1976). Color-selective tilt aftereffects with subjective contours. *Perception and Psychophysics, 20*(4), 305-308.

Smith, A. T., & Over, R. (1977). Orientation masking and the tilt illusion with subjective contours. *Perception, 6*, 441-447.

Smith, A. T., & Over, R. (1979). Motion aftereffect with subjective contours. *Perception & Psychophysics, 25*(2), 95-98.

Street, R. F. (1931). *A Gestalt Competion Test*. (Vol. No. 481). New York: Bureau of Publications, Teachers College, Columbia University.

Sugawara, M., & Morotomi, T. (1991). Visual evoked potentials elicited by subjective contour figures. *Scand J Psychol, 32*(4), 352-7.

Tallon, C., Bertrand, O., Bouchet, P., & Pernier, J. (1995). Gamma-range activity evoked by coherent visual stimuli in humans. *Eur J Neurosci, 7*(6), 1285-91.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *J Neurosci, 16*(13), 4240-9.

Tanaka, J. W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychol Sci, 12*(1), 43-7.

Tanaka, K. (1997). Mechanisms of visual object recognition: monkey and human studies. *Curr Opin Neurobiol, 7*(4), 523-9.

Tootell, R. B., Mendola, J. D., Hadjikhani, N. K., Liu, A. K., & Dale, A. M. (1998). The representation of the ipsilateral visual field in human cerebral cortex. *Proc Natl Acad Sci U S A, 95*(3), 818-24.

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science, 247*(4940), 301-6.

Ullman, S. (1976). Filling-in the gaps: the shape of subjective contours and a model for their generation. *Biological Cybernetics, 25*, 1-6.

Ullman, S. (1995). Sequence seeking and counter streams: a computational model for bidirectional information flow in the visual cortex. *Cereb Cortex, 5*(1), 1-11.

Vanni, S., Revonsuo, A., Saarinen, J., & Hari, R. (1996). Visual awareness of objects correlates with activity of right occipital cortex. *Neuroreport, 8*(1), 183-6.

Vaughan, H. G., & Arezzo, J. C. (1988). The neural basis of event-related potentials. In T. W. Piction (Ed.), *Human Event-Related Potentials* (pp. 45-96). Amsterdam: Elsevier.

Victor, J. D., Apkarian, P., Hirsch, J., Conte, M. M., Packard, M., Relkin, N. R., Kim, K. H. S., & Shapley, R. M. (2000). Visual function and brain organization in non-decussating retinal-fugal fibre syndrome. *Cerebral Cortex, 10*(1), 2-22.

von der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *J Neurosci, 9*(5), 1731-48.

von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science, 224*(4654), 1260-2.

Vuilleumier, P., & Landis, T. (1998). Illusory contours and spatial neglect. *Neuroreport, 9*(11), 2481-4.

Vuilleumier, P., Valenza, N., & Landis, T. (2001). Explicit and implicit perception of illusory contours in unilateral spatial neglect: behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia, 39*(6), 597-610.

Walker, J. T., & Shank, M. D. (1988a). Interactions between real and subjective contours in the Bourdon illusion. *Perception & Psychophysics, 43*, 567-574.

Wasserstein, J. (1981). *Differentiation of perceptual closure: Implications for right hemisphere functioning*. Unpublished doctoral dissertation, City University of New York, New York.

Wasserstein, J., Zappulla, R., Rosen, J., & Gerstman, L. (1984). Evidence for differentiation of right hemisphere visual-perceptual functions. *Brain and Cognition, 3*(1), 51-6.

Wasserstein, J., Zappulla, R., Rosen, J., Gerstman, L., & Rock, D. (1987). In search of closure: subjective contour illusions, Gestalt completion tests, and implications. *Brain Cogn, 6*(1), 1-14.

Weisstein, N. (1966). Backward masking and models of perceptual processing. *J Exp Psychol, 72*(2), 232-40.

Weisstein, N., & Matthews, M. L. (1974). *Illusory contours can mask real contours*. Paper presented at the Psychonomic Society Bulletin.

Yin, C., Kellman, P. J., & Shipley, T. F. (1997). Surface completion complements boundary interpolation in the visual integration of partly occluded objects. *Perception, 26*, 1459-1479.