

NOTICE WARNING CONCERNING COPYRIGHT RESTRICTIONS

The copyright law of the United States [Title 17, United States Code] governs the making of photocopies or other reproductions of copyrighted material. Under certain conditions specified in the law, libraries and archives are authorized to furnish a photocopy or other reproduction. One of these specified conditions is that the reproduction is not to be used for any purpose other than private study, scholarship, or research. If a user makes a request for, or later uses, a photocopy or reproduction for purposes in excess of "fair use," that use may be liable for copyright infringement. This institution reserves the right to refuse to accept a copying order if, in its judgement, fulfillment of the order would involve violation of copyright law. No further reproduction and distribution of this copy is permitted by transmission or any other means.

Cleveland State University ILL



ILLiad TN: 269620

Borrower: PMC

Lending String:

*CSU,VYF,UBY,VXW,KFP,IAC,NYG,GYG,UCW,XI
I,GDC,MRW,GZQ,TEU,OPU

Patron:

Journal Title: Perception of faces, objects, and
scenes : analytic and holistic processes /

Volume: **Issue:**

Month/Year: **Pages:** 295-334

Article Author:

Article Title:

Imprint: Oxford ; New York : Oxford University
Press, 2003.

ILL Number: 166800839



Call #: b BF241 .P434 2003

Location: 2

ODYSSEY ENABLED

Charge

Maxcost: 35.00IFM

Shipping Address:

Carnegie Mellon University-Hunt Library-ILL
Office
4909 Frew St.
Hunt Library Room 305
Pittsburgh, Pennsylvania 15213
United States

Fax: (412)268-6944

Ariel: 128.2.21.4/128.2.21.96

Odyssey: 128.2.20.146

Neuropsychological Approaches to Perceptual Organization

Evidence from Visual Agnosia

MARLENE BEHRMANN

The visual world consciously perceived is very different from the raw visual information or retinal mosaic of intensities and colors that arises from external objects. From the overwhelming influx of different colors and shapes that stimulate the individual retinal receptors, an object is seen as detached and separable from the adjacent objects and surfaces. This organization occurs despite the fact that parts of a single object may be spatially or temporally discontinuous, may have different colors, or may even transect several different depth planes. Additionally, because most surfaces are opaque, portions of objects are routinely hidden from view and, as we move around, surfaces continually undergo occlusion and fragmentation. As is apparent from this description, the objects of phenomenal perception are not given in any direct way in the retinal image. Some internal processes of organization must clearly be responsible, then, for producing a single, coherent percept. The goal of this chapter is to explore how the multitude of visual inputs contained in an image are integrated such that coherent entities are ultimately derived.

The processes “by which bits and pieces of visual information that are available in the retinal image are structured into the larger units of perceived objects and their interpretations” (Palmer, 1999) are generally classified under the umbrella term “perceptual organization.” The study of these visual processes has a relatively short history; roughly 100 years

ago, the Gestalt psychologists began to recognize and articulate the complexity of perceptual organization, and much of the real progress made today can trace its roots to the insights of these psychologists (Kellman, 2000). Although the Gestalt work on perceptual organization has been widely accepted as identifying crucial phenomena of perception, there has been, until the last decade or so, relatively little theoretical and empirical emphasis on perceptual organization. And, to the extent that progress has been made, there still remain many open questions. This paucity of understanding is well captured by the comment by Palmer (2003) that “We have not got the answers (to perceptual organization) yet; indeed, it is not entirely clear what the questions are!” (p. 1). As is evident from this, there is considerable work to be done in order to understand the behavioral mechanisms underlying perceptual organization.

In addition to trying to understand the functional processes involved in perceptual organization, there is much to be done to understand how these principles are neurally instantiated and what brain mechanisms might be involved. Recent neurophysiological advances have revealed much about the specificities of neuronal responses such as orientation selectivity, ocular dominance, and wavelength and directional selectivity. However, it is not clear how the fragments represented by these local analyzers are assembled to provide a unified percept.

One possible approach to understanding both the psychological and the neural mechanisms involved in perceptual organization is to study the performance of individuals whose visual behavior is impaired following brain damage. In particular, the patients described in this chapter have problems with processes involved in structuring pieces into larger units—the very definition of perceptual organization—and, therefore, their performance can shed light on issues related to perceptual organization. This approach, together with the emerging and converging evidence from other research domains such as cognitive psychology, functional neuroimaging, and neurophysiology, potentially offers important insights into the perceptual system.

The first section of this chapter will outline three main empirical issues falling under the domain of perceptual organization: figure-ground organization, visual interpolation, and grouping. The second section will contain a description of the patients with whom we are concerned, followed in the third section by an examination of the nature of the impairment in perceptual organization, in relation to figure-ground organization, visual interpolation, and grouping. We then provide some summary observations and comments about both the psychological and the neural aspects of agnosia and perceptual organization.

Processes of Perceptual Organization

Central questions that are being investigated in studies of perceptual organization concern the nature, ordering, and interactivity of the different

processes of perceptual organization. It is in the context of these questions that we examine the neuropsychological data. There has been growing awareness that perceptual organization is not a monolithic entity, but, rather, comprises a multiplicity of processes. Because the neuropsychological work mainly revolves around three of these processes—figure-ground segregation, visual interpolation, and grouping—we focus on them specifically. As will be evident shortly, however, the exact ordering of these processes is controversial and there is far more interaction between them than independence.

The crucial goal of *figure-ground* segregation is to assign contours in the image as belonging to the figural regions, thereby giving them shape, while the ground region extends behind them shapelessly. The figure appears closer to the observer and has the shape imparted by the dividing contour whereas the ground appears farther away and extends behind the contour. Figure-ground segregation also relies on depth information, particularly pictorial cues from occlusion, and, hence, processes such as visual completion and interpolation may play a role here, too. Just as the Gestalt psychologists proposed principles that govern grouping of elements in a display, so there are principles that govern figure-ground segregation. These include relative size of regions, repetition of regions, orientation, contrast, symmetry, parallelism and even conscious intent (Rubin, 1921). Contemporary psychologists have added others, including familiar shape, convexity/concavity contrast, surroundedness, and lower region (see Palmer, 2000, 2002; Peterson, 2003, for review).

Visual interpolation is the term applied to a variety of processes by which partially present information appears to be extended and continued. Partially occluded surfaces and objects are perceived as being complete in a rather effortless and automatic fashion, and this perception appears to include their shape, texture, and color. The process by which this completion occurs is often referred to as amodal completion to indicate that the completed portion is not supported by local stimulation or sensory information. Exactly what underlies amodal completion is under much discussion; while some argue that past experience with a square, for example, drives one to complete an occluded square, others suggest that the simplicity or Pragnanz of the display determines the completion. Yet others, such as Kellman and Shipley (1991), argue that the Gestalt principle of good continuation applies here. The relatability theory (Kellman, 2003; Kellman & Shipley, 1991; Kellman & Shipley 1992) that formalizes the Gestalt principle of good continuation suggests that the visual system connects two noncontiguous edges that are relatable (collinear). The likelihood of “seeing” a completed figure increases systematically with the size of the angle that must be interpolated, with the 50% threshold of completion occurring at around 90° and increasing probability of seeing it as complete as the angle approaches 90°. According to this view, relatability is a general principle of unit formation and applies not only to amodal completion but also to illusory or sub-

jective contours in which contours that do not actually exist in the image are perceived.

It has been proposed that contour interpolation that supports relatability occurs early in the visual system (Kovács, 2000). Physiological evidence suggests that neurons in early visual areas (such as V2) respond to the presence of illusory contours, with about 40% of neurons in this area becoming active when presented with stimuli that induce illusory contours in human perception (Heitger, von der Heydt, Peterhans, Rosenthaler, & Kubler, 1998; Peterhans & von der Heydt, 1991; von der Heydt, Peterhans, & Baumgartner, 1984). Neurons in V1 also respond to illusory contours, although their response is both weaker and slower than that observed in V2; the temporal sequence of these data is consistent with the claim that the V1 response is a consequence of feedback from later areas (Lamme & Roelfsema, 2000; Lee & Nguyen, 2001). Other neuropsychological data from patients with hemispatial neglect are consistent with this; several studies have shown that collinear contours may be completed pre-attentively and may influence the extent to which contralesional information, which is usually extinguished, may be preserved and reported (Gilchrist, Humphreys, & Riddoch, 1996; Humphreys, 2002; Mattingley, Davis, & Driver, 1997). Recent neuroimaging data have also shown that occipital regions and posterior temporal regions play a role in the integration of contours into a whole image (Gerlach et al., 2002).

The organizational processes concerned with *grouping* were a central focus of the work of the Gestalt psychologists, particularly that of Max Wertheimer, and his observations and principles are still referred to today. The well-known Gestalt laws of grouping include grouping by proximity, similarity, common fate, good continuation, and closure. A number of other principles have been added to the list more recently (Palmer, 1999, 2003, 2002; Sekuler & Bennett, 2001). These include synchrony (visual events that occur at the same time will be perceived as going together), common region (elements located in the same visual space will be grouped together), and element connectedness (elements that are connected by other elements tend to be grouped together). Once elements that belong together are determined, they can be grouped to form a superordinate, wholistic object or, alternatively, can be decomposed into their constituent parts.

Although we have laid out these processes in a sequential order, it is worth noting at this stage that there is much debate concerning the strictly serial and feedforward model of stages of processing. The debate essentially involves the relative independence and ordering of the different stages of processing. One might think, for example, of figure-ground segregation not as a separate process entirely but rather as an instance of perceptual grouping given that the contour is not only assigned to the figure but is also bound to or grouped with it (Palmer, 2003; Palmer & Brooks, 2000). Additionally, figure-ground segregation might not even be a separate process but rather the outcome of an interaction between con-

figural cues and depth cues (Peterson, 2002) and may involve top-down feedback from object representations (Vecera & O'Reilly, 1998). Amodal completion may also be thought of as an instance of perceptual grouping: both visible and invisible contours might be computed from local, oriented operators that are grouped by good continuation, as in relatability theory (Kellman & Shipley, 1992), and then the output of these operators contributes to the global shape.

The temporal staging of these various processes has been the subject of a number of other empirical studies and is undergoing much heated debate. The perceptual processes underlying classical grouping phenomena have traditionally been assumed to work in parallel on an early, 2D representation and to create an initial set of discrete elements on which later perceptual operations are performed. On some accounts, these processes operate pre-attentively to represent units to which attention is deployed (Moore & Egeth, 1997). Whether this is indeed so is debatable. Some researchers have argued that grouping does not occur as early as has been widely assumed. Instead, they have suggested that it operates after depth information has been extracted (Rock & Brosnole, 1964), and after lightness constancy (Rock, Nijhawan, Palmer, & Tudor, 1992) and perceptual completion (Agostini & Galmonte, 2002; Palmer, Neff, & Beck, 1996; Palmer, 2003) have been achieved.

Other findings have supported the arguments in favor of early grouping but have proposed that the representations derived by these early principles are much more complex and detailed than has been considered previously. For example, early levels of processing are sensitive to complex, scene-based properties (Enns & Rensink, 1990; He & Nakayama, 1992), to complete configurations rather than to components (Rensink & Enns, 1995) and to configural and to part-whole information (Kimchi, 1998). Finally, there are also recent data that show that some high-level cues, which have always been assumed to operate in a later, top-down fashion and to reflect access to memories of the structure of known objects, can influence perceptual processing very early on. For example, much recent work by Peterson and colleagues has shown that object knowledge can come into play early on, at pre-figural levels potentially, to influence figure-ground segregation (Peterson, 2003; Peterson & Gibson, 1994) and perceptual grouping (Kimchi & Hadad, 2002). Palmer and Rock (1994b), in their influential view of perceptual organization, did not order the stages strictly so that processing at one stage must necessarily be complete before the next stage is initiated; instead, they suggested that the various operations can occur in cascaded fashion. However, they also claimed that there is an architectural ordering of the stages that is required by the logical constraints of the task, which supports some of the seriality of the system (Palmer, 2003). Taken together, these findings rule out a pure "early" view of grouping and suggest that organizational factors likely do not operate solely at the level of the two-dimensional retinal image but may also play a role once some organization and interpretation have occurred.

The above debate suggests that the early operation of grouping principles is more complex than originally thought and may be a result both of the feedforward pass and the recurrent sweep of the connectivity of the visual system. It is well known that there are considerable feedback connections in the visual system (Felleman & Van Essen, 1991; Lamme & Roelfsema, 2000) and neurophysiological (Bullier, Schall, & Morel, 1996; Lee & Nguyen, 2001) and electrophysiological data support the role of recursive feedback mechanisms in perceptual organization (Doniger et al., 2000), involving even very early visual areas (Hopfinger, Buonocore, & Mangun, 2000). As is apparent from this discussion, there is a general lack of consensus regarding the functional properties of the perceptual organization system as well as its temporal characteristics. A full review of the evidence is beyond the scope of this chapter, but we do raise these challenges to alert the reader to the complexity of the problem. Two recent books deal with these issues directly and may be consulted for further information: one is on segmentation and grouping by Shipley and Kellman (2001) and the other is on the psychological and neural bases of visual perceptual organization by Kimchi, Behrmann, and Olson (2003).

The focus of the present work is restricted to the neuropsychological data and it is to those data that we now turn to examine the evidence.

Visual Agnosia

“Visual agnosia” refers to the failure to identify or recognize even common objects presented in the visual modality. This recognition deficit is not secondary to a generalized intellectual dysfunction nor to a fundamental sensory problem (such as an hemianopia). That patients fail to name objects also cannot be attributed to a deficit in their knowledge of objects nor to a failure in producing the name for the object; when the patients are blindfolded and the same objects are presented for haptic recognition, for example, object recognition is normal. Additionally, the patients are able to provide definitions of the objects, given the auditory label. Agnosia reflects a modality-specific deficit in gaining access to long-term representations from vision and is not attributable to a conceptual failure of some sort. Importantly, when an agnosic patient fails to recognize an object, there is no evidence for the availability of information about the object through another response modality; for example, the patient is unable to gesture the use of the object correctly. This pattern distinguishes patients with agnosia from those with optic aphasia who are able to gesture the response correctly despite the failure to name the object (Lhermitte & Beauvois, 1973).

At one end of the spectrum, the term “visual agnosia” includes a fairly low-level visual deficit manifest as the inability to extract featural elements from a display despite intact sensation of the basic properties of the stimulus (for example, brightness perception). Many patients with this form

of deficit have suffered carbon monoxide poisoning, resulting in small, disseminated lesions in the cortex, or mercury or lead poisoning or a closed head injury, all of which have diffuse effects in the brain. At the other end of the spectrum, agnosia includes a rather higher level deficit reflecting the failure to assign meaning to an object despite the derivation of an intact percept (Farah, 1990; Humphreys & Riddoch, 2001), although the extent to which perception is truly normal is debatable. It is this latter form of agnosia that has been referred to as "perception stripped of meaning" (Teuber, 1968). These two ends anchor the dichotomy between apperceptive and associative agnosia originally proposed by Lissauer (1890). While the apperceptive agnosic patients appear to be impaired at deriving the form of the object, associative agnosic patients supposedly can derive percepts well but have difficulty matching form information with stored memories (see Farah, 1990; Humphreys & Riddoch, 1987).

Although the dichotomy between apperceptive and associative agnosia is useful, recent studies have attested to its inadequacy and have attempted to elaborate the spectrum of impairments (Humphreys, 1999; Warrington & Taylor, 1978). By the classic definition of these two types of agnosia, the apperceptive patients are those who cannot copy or match visual forms, whereas the associative patients can copy and match forms but cannot associate them with knowledge that would allow them to name or categorize them. One clear challenge to this dichotomy comes from a third type of patient labeled "integrative agnosia" (IA), and it is this type of agnosia with we are primarily concerned here.

Patient CK is a good example of an individual who suffers from integrative visual agnosia. CK was only able to recognize 16 out of 23 (70%) three-dimensional common objects presented to him for an unlimited period of time (normal subjects score 23/23); (Behrmann, Moscovitch, & Winocur, 1994; Behrmann, Winocur, & Moscovitch, 1992; Moscovitch, Winocur, & Behrmann, 1997). His errors include calling a smoking pipe "a straw," a card of matches "a card with writing," a padlock "an earring," a saw "a knife," pliers "clothes peg." He was, however, able to identify all 23 of the same objects with tactile presentation. He also defined in detail all the objects correctly when presented with the name auditorily. For example, he defined a duck as "an animal, marine life, with webbed feet and a bill"; a card of matches as "a cardboard container, the container flipped open, the log sticks are struck against the cordite strip"; and a pipe as "a short, hollow object, larger on one end, 120° angle, for leisurely smoking using tobacco." The detailed and descriptive definitions, which he was able to provide in response to the auditory label of the very objects he failed to recognize from visual input, reflect the preservation of his knowledge of objects.

Patient CK produces a reasonably good rendition of targets consisting of black and white geometric figures, as shown in figure 11.1. However, he does so in an unusual way: the numbers assigned to the different strokes indicate the order in which the lines were drawn. Instead of deriving the

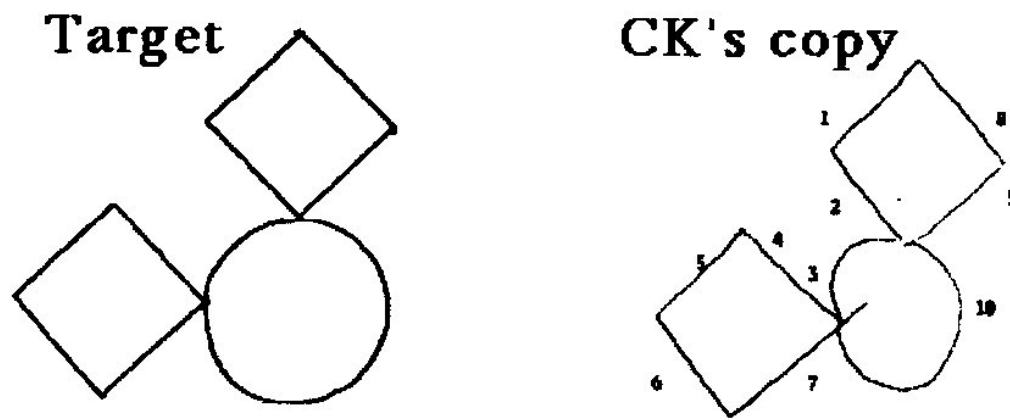


FIGURE 11.1. Copy of target (left) by CK with the numbers indicating the order of the strokes (from Behrmann et al., 1992).

holistic percept of two diamonds and a circle as unimpaired subjects might do, CK copies the individual lines slavishly and segmentally, without appearing to appreciate the identities. A similar pattern is noted when he copies text; CK copies the text in the same font as the target and does not appreciate the identity of the letters. This pattern poses a quandary for the classical agnosia dichotomy: CK can clearly copy figures or text and should, thus, be classified as an associative agnosic but the manner in which the copying is done is piecemeal and segmental and is clearly not normal. This slavish bit-by-bit copying is considered one of the hallmark features of integrative agnosia in which the impairment appears to affect mid- or intermediate level vision.

The label "integrative agnosia" was coined by Riddoch and Humphreys (1987) on the basis of their studies with patient HJA (Humphreys, 1999; Humphreys & Riddoch, 1987; Humphreys et al., 1994; Humphreys, Riddoch, Quinlan, Price, & Donnelly, 1992). The term was originally used to refer to the patient's inability to integrate disparate elements of a display, which are themselves available, into a coherent form. For example, they reported that HJA was impaired at search tasks that require the binding of visual elements in a spatially parallel manner across a field containing multiple stimuli; he was disproportionately slowed, relative to control subjects, in detecting the presence of an inverted T among upright Ts. In contrast, his search was efficient and rapid for targets that did not require a combination of elements such as a target "/" among multiple "|"s (Humphreys, 1999; Humphreys & Riddoch, 1987; Humphreys et al., 1994, 1992). Note that when the demands for integration are low, HJA and other integrative agnosic patients perform significantly above chance levels: they can make same/different judgments accurately on two stimuli, which share area and brightness but not shape (aspect ratio changes from square to rectangle; Efron, 1968; see figure 11.2).

Two problems emerge in trying to refine the definition of integrative agnosia. The first is that there are very few studies of such individuals

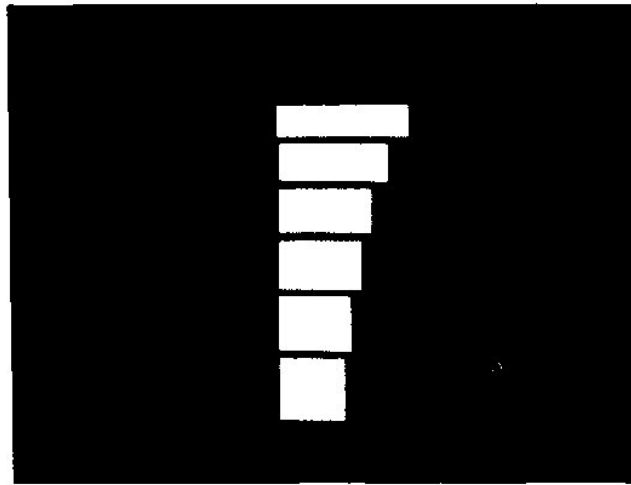


FIGURE 11.2. Efron shapes equated for area and brightness: two stimuli are placed before the patient for same/different judgments. Integrative agnosic patients usually perform reasonably well on this test of geometric form discrimination.

and so there is much to be done in delineating the key features of the disorder (see Humphreys, 2000, for a useful review). The second, related point is that, of those studies that have been done, the patients are not always fully characterized, and the focus of the work is usually rather circumscribed with a particular emphasis on one aspect of the problem. As such, we are left with uncertainty about the definition of the problem and about which patients can be classified by this term. The apparent failure to consider all parts of the stimulus in deriving a unitary representation of the input is probably key to IA. It is this inability to integrate the elements into a well-formed shape, the failure to group features into a larger, meaningful whole, and the overzealous parsing of the display that make these patients ideal for further investigations of perceptual organization. The purpose of this chapter is to elucidate the central features of IA and to discuss them in relation to the three processes of perceptual organization alluded to above. In doing so, we will first outline some exclusion criteria for IA and then describe the inclusion criteria.

What Is Not IA

Among the exclusion criteria for IA is a severe perceptual deficit: patients whose perceptual deficit is so extensive that it affects the extraction of simple features from a display are not classifiable as having IA. For example, patients who perform at chance on the Efron test (see figure 11.2) are considered to have a more marked deficit in encoding basic properties of form (more in line with apperceptive agnosia). These patients will not be considered further (see Benson & Greenberg, 1969; Campion & Latto, 1985; Davidoff & Warrington, 1993; Goodale & Milner, 1992; Mapelli & Behrmann, 1997; McMullen, Fisk, Phillips, & Maloney, 2000; Vecera & Behrmann, 1997; Warrington & Davidoff, 2000). Additionally, patients

who show normal performance on simple geometric form matching but who appear to be limited in the amount of perceptual information they can process are also excluded. These patients' performance deteriorates when the perceptual characteristics of the target itself are made more complex and when resource demands are increased even if the perceptual judgment required is simple (Grossman, Galetta, & D'Esposito, 1997). Such difficulties have occasionally been attributed to an attentional or working memory limitation (Coslett, Stark, Rajaram, & Saffran, 1996; Thaïs & de Bleser, 1992) and, although these patients fit the definition of integrative agnosia in some respects, they have additional problems and will not be considered further.

At the other extreme are patients whose perceptual performance is too good even if their object recognition is not. Such patients fit the standard classification of associative agnosia, although, again, as mentioned above, this is a rather coarse description for what is likely to be a host of different disorders. One example that fits this definition is an individual who was able to match nonsense figures well and who matched the size and position of stimuli well but showed significant problems in face, letter, and object recognition (Kertesz, 1979). That the matching task was done well suggests that the stimuli are probably reasonably well perceived, distinguishing him from patients with integrative agnosia.

A second type of associative agnosic patient to be excluded is an individual whose deficit in recognizing objects extends beyond perception. Though the patient's perceptual performance resembles integrative agnosia, the patients have an accompanying recognition deficit in another input modality or a problem in the long-term representation of objects. De Renzi and Lucchelli (1993), for example, report that their patient, Annalisa, has relatively good performance on the Efron test, along with reasonably good copying and poor performance on overlapping objects (see below for more on this). These patterns fit the definition of IA. However, Annalisa clearly had additional problems extending beyond a visual perceptual deficit. For example, she was impaired at recalling perceptual details of items from long-term memory. Also, when given the auditory labels of two objects, she was unable to describe the perceptual difference between them and she was in the intermediate range of severity on tactile recognition (see also patient of Davidoff & Wilson, 1985). The patient of Grailet, Seron, Bruyer, Coyette, & Frederix (1990) also showed many of the diagnostic features of integrative agnosia. However, he too appeared to have a deficit that extended beyond visual perceptual processing in that he was impaired at tactile object recognition and drew poorly from memory. These additional deficits call into question the competence of his long-term knowledge. We will not consider these patients as suffering from IA *per se* and will restrict our discussion to patients whose long-term representations are intact. It is worth noting, however, that longstanding IA may have adverse effects on long-term representations; visual memories might begin to deteriorate if not refreshed or updated by intact perceptual descriptions and,

unfortunately, this may be the case for patient HJA (Riddoch, Humphreys, Gannon, Blott, & Jones, 1999).

What Is IA?

A rough criterion for inclusion in this category is that the patients should have the features from the display available to them but be unable to utilize them further. Additionally, they should be able to make discriminations between forms that place minimal demand on integration. Thus, individuals with IA have relatively well preserved low-level visual processes including discrimination of line length, spatial localization of dots, color and motion processing. They can also make line orientation and size judgments at normal levels (Davidoff & Warrington, 1993; Gauthier, Behrmann, & Tarr, 1999; Humphreys, 1999).

As mentioned above, one way in which the IA deficit manifests is in copying performance. RN and SM1 (to be differentiated when SM2 is introduced below) are two other IA patients, who, like HJA and CK, are able to copy well, as evident in their copies of complex figures such as the Rey-Osterrieth figure (see figure 11.3) and a copy of a beach scene

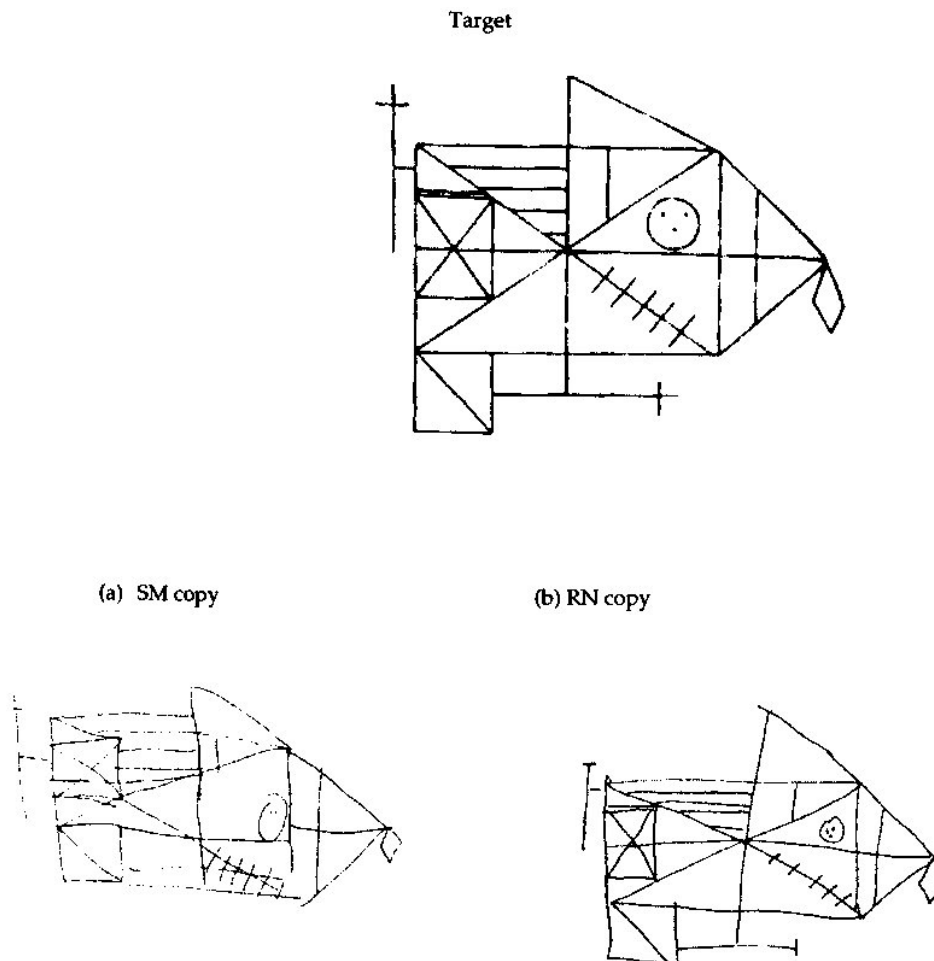


FIGURE 11.3. Copies of Rey-Osterrieth figure by patients RN and SM1.

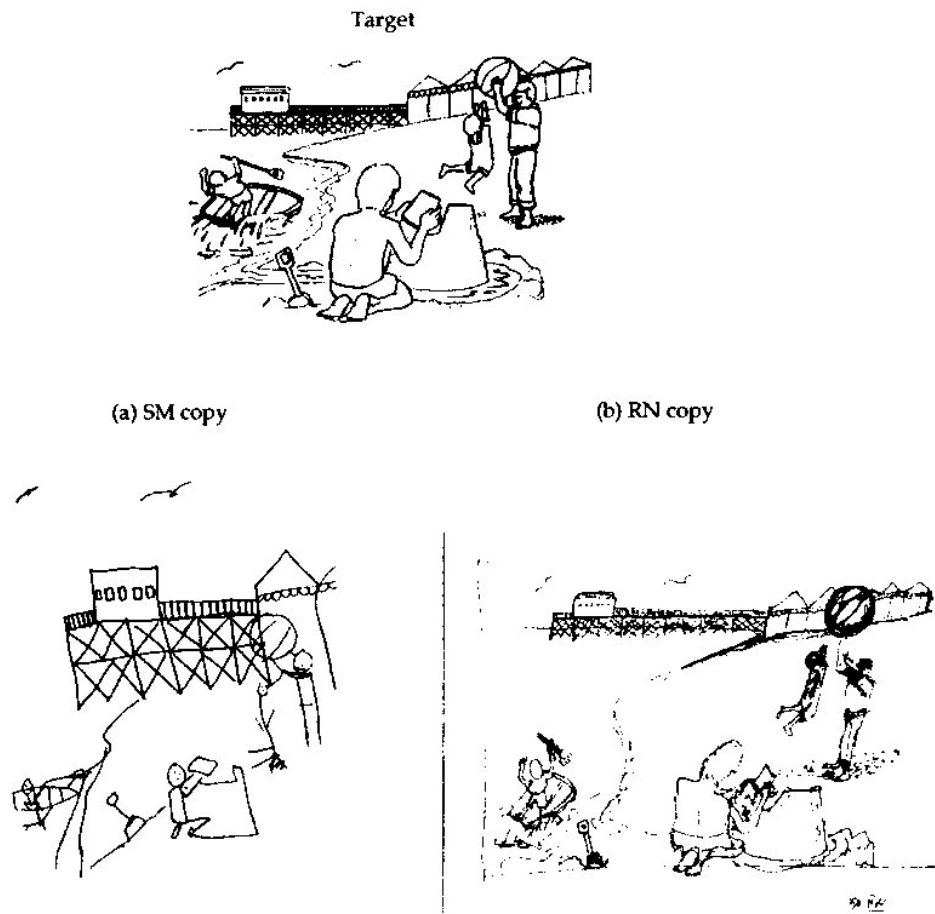


FIGURE 11.4. Copy of beach scene by SMI and RN.

(see figure 11.4). Both, however, are noticeably slow and segmental in their copying with laborious slavish efforts.

Another way in which the IA deficit manifests is in the patients' performance on segregating items, which are presented in an overlapping display. For example, in the stimulus displayed in figure 11.5, patient CK performed extremely poorly. He was, on occasion, able to match the features that protrude from the overlapping display, like the edge of the stick of the flag, but was unable to decide which objects were present. This was true even when he was not required to identify the objects per se but merely to match them to an array of choices placed below the overlapping display. The impairment in segmentation was also seen when he was given the set of overlapping figures, as shown at the top of figure 11.5, and asked simply to trace the outline of each different object with a different colored crayon. He first outlined in different colors the components of the object that did not overlap in the central region and that did not require segmentation. Once this was done and he now had to segment the overlapped region, he picked up a crayon, placed it at the intersection of two contours, and held it there for a long time without proceeding. He then had a strong emotional reaction and refused to complete the task, arguing

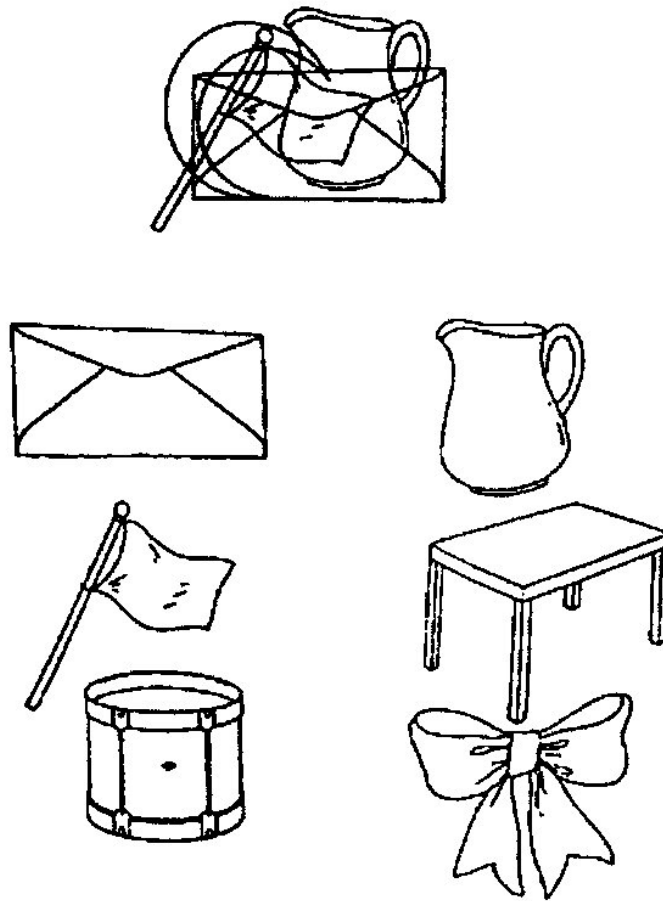


FIGURE 11.5. Display of overlap and choices for matching. Overlapping section at top also used for coloring contours.

that he had no idea in which direction to continue, as he did not know which lines belonged to which objects. HJA shows a very similar pattern and his outlining of overlapped objects is demonstrated in Humphreys & Riddoch (2001).

The fragmented nature of the patients' perception also comes through clearly in their object-recognition errors. Their responses to black-and-white line drawings (see figure 11.6) are consistent with the claim that they can extract some, but not all the relevant information from the display. Patient RN, for example, identified the harmonica as a "stereo or computer," presumably picking up on the little "keys" (air holes). He also called an octopus a "bug" and a pretzel a "snake." We see a similar pattern in patient SM1 who called an octopus a "spider" and a harmonica a "cash register." The piecemeal description of objects is characteristic of other IA patients. HJA, for example, tends to oversegment objects so that even when presented with a single item such as a paintbrush, he is convinced that two separate objects are present in the display. In his response to a picture of a pepperpot, he responded "a stand containing three separate pans; the top has a design on its lid, the second has a slightly smaller diameter than the top pan; the bottom pan has a wider diameter than the

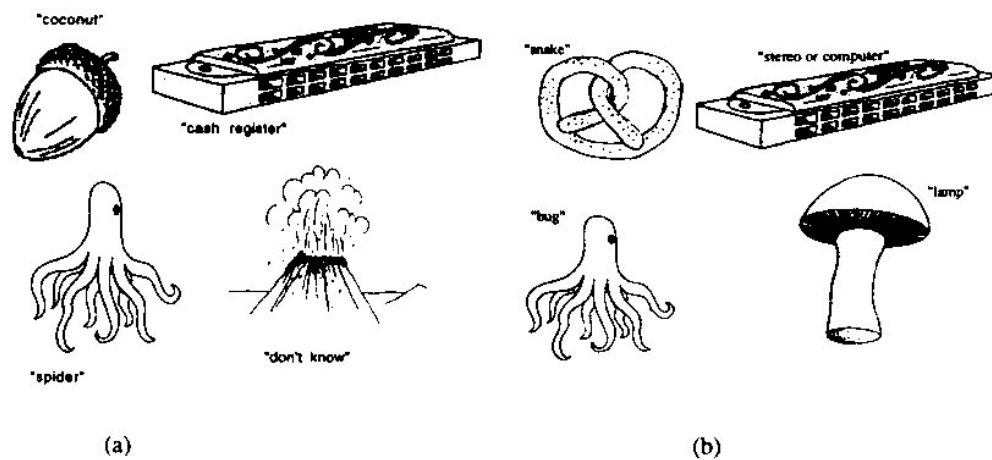


FIGURE 11.6. (a) RN's and (b) SM1's naming errors on Boston Naming Test.

second pan and is longer in length" (p. 399, Humphreys & Riddoch, 1984). This oversegmentation is also seen in SM2 (Butter & Trobe, 1994) who, when presented with a display of a few items, stated that several objects were present as he identified parts as separate items. Shown a cup and asked to identify it, he stated that it was "a large oval item together with a smaller oval item (pointing to the handle)." This oversegmentation can also apply to individual letters; patient FGP (Kartsounis & Warrington, 1991) selected subparts of individual letters, reporting R as D and Q as O.

Almost all of the IA patients are impaired at face recognition, with the exception of CK, as well as object recognition, and are also alexic, although this is not true of every patient. Their alexia usually manifests in very slow reading (Mycroft, Behrmann, & Kay, 2003); for example, SM1 is able to read accurately (98% correct) but requires roughly 104 ms to process each letter in a word. Accuracy is also high for HJA, but he requires a significant amount of time (355 ms per letter) for letter processing (Oßwald, Humphreys, & Olson, 2002). RN also requires a substantial increase in time (178 ms) for each additional letter, although his accuracy is also affected, as he reads only 80% of words correctly. The patterns reported here are all in contrast with the minimal increase required by normal subjects for words up to 6 or 7 letters in length (Frederiksen & Kroll, 1976).

A final common characteristic of the performance of these patients is that they typically benefit from the addition of surface information. Color, motion, or other surface cues seem to help the integration of form elements into a coherent perceptual whole. Thus, HJA identifies real objects correctly about 60% of the time in contrast with photographs (40%) and line drawings (30%). The same is true of patient CK, who also benefits from color and other surface cues, which lead to roughly 25% improvement in his object identification (Behrmann et al., 1992). Through the addition of surface information such as luminance and texture, contrasting parts may be observed and used especially in cases where edge-based segmentation

is impaired. In addition, depth information, conveyed both by binocular disparity cues as well as head movements, assists with the segmentation of parts of an object and allows partially occluded surfaces to be recovered (Chainay & Humphreys, 2000).

In sum, at the present time, we take as the defining features of IA the disproportionate impairment in perceptual processing when there are multiple elements to be encoded and integrated and when exposure duration or stimulus quality is affected. This manifests in overlapping displays, in copying and in object and word identification (although the deficit may also be evident under many other conditions). When sufficient time is available and encoding can be done serially, or when cues to the segmentation are present (for example, color or other surface properties), performance is somewhat better.

We should also note one other dramatic finding observed in some, but not all IA patients; because this pattern is not evident in all patients, we have not included it as a core characteristic of the deficit. The pattern under discussion concerns the fact that the patients' perception of silhouettes may be better than of line drawings. Interestingly and counterintuitively, in some cases, the presence of local information may even reduce the efficiency of visual recognition. For example, both patients HJA (Lawson & Humphreys, 1999; Riddoch & Humphreys, 1987) and SM2 (Butter & Trobe, 1994) were better at identifying pictures presented as silhouettes rather than line drawings as the internal details apparently led to incorrect segmentation. HJA scored 72% for silhouettes and 64% for line drawings when tested in 1997 (reported by Riddoch et al., 1999). The difference between stimulus types was even more dramatic in patient SM2, who identified 23% of black-and-white line drawings and 48% silhouettes. Note that, in both cases, performance on silhouettes is still far from normal (control subjects for SM2 scored 92.5%). Nevertheless, the advantage for silhouettes over line drawings is in direct contrast to the behavior of non-neurological subjects who benefit significantly from the presence of additional contours. Not all patients do better on silhouettes, as neither CK, SM1, nor RN show this advantage and FGP identified only 3 out of 12 silhouette drawings of common objects.

Neuropsychological Evidence

In the following section, the evidence from patients with agnosia concerning perceptual organization is reviewed for each of the three processes outlined above. Again, although there may be other patients in the literature who fit the IA definition, we have selected only those patients ($n = 7$) for whom sufficient information is provided in the reports. In an attempt to coordinate the findings across the different studies, in table 11.1 we have summarized the neurological status of the different patients and their performance on the three processes.

TABLE 11.1: Biographical data and summary of performance of 7 patients with integrative agnosia across a range of perceptual organization measures

Patient	Biographical Details	Lesion Details	Figure Ground	Overlapping	Amodal Completion	Illusory Contours	Grouping
HJA (Humphreys, 1999; Humphreys & Riddoch, 1987; Humphreys et al., 1994; Humphreys, Riddoch, Quinlan, Price, & Donnelly, 1992; Riddoch & Humphreys, 1987; Riddoch, Humphreys, Gannon, Blott, & Jones, 1999)	61-year-old male; right-handed; detailed testing at many ages, currently 80 years old	Stroke at age 61; bilateral lesions of occipital cortices extending forward to temporal lobes; Bilateral superior altitudinal defect	Poor	Poor	Poor	?	Poor
CK (Behrmann, Moscovitch, & Winocur, 1994; Behrmann, Winocur, & Moscovitch, 1992; Moscovitch, Winocur, & Behrmann, 1997)	41-year-old male; right-handed	Car accident; bilateral thinning of occipital cortices and hypoperfusion on SPECT; Left hemianopia largely resolved	Poor as noise increases	Poor	Poor	Poor	?
SM1 (Behrmann & Kimchi, 2002; Behrmann & Kimchi, 2003a; Gauthier, Behrmann, & Tarr, 1999; Marotta, McKeef, & Behrmann, 2002)	26-year-old male; right-handed	Car accident; contusion in the right anterior and posterior cerebral regions accompanied by deep shearing injury in the corpus callosum and left basal ganglia; no field defect	Good	Poor	Poor	Good	?
CR (Gauthier et al., 1999)	22-year-old male	Metabolic encephalopathy affecting right temporal lobe	Good	Poor	Poor	?	Good (?)
RN (Behrmann & Kimchi, 2002; Behrmann & Kimchi, 2003a; Marotta et al., 2002)	43-year-old male	Stroke following myocardial infarction; negative MRI scan; no field defect	Good	Poor	Good	Good	Poor
SM2 (Butter & Trobe, 1994)	43-year-old male; right-handed	Right hemianopia; MRI—high-intensity signal abnormalities, consistent with progressive multifocal leukoencephalopathy	?	Poor on complex displays	?	Poor	Poor
FGP (Kartsounis & Warrington, 1991)	71-year-old female; handedness?	Left hemianopia; Mild cerebral atrophy	Poor	Poor	Poor	Poor	Poor

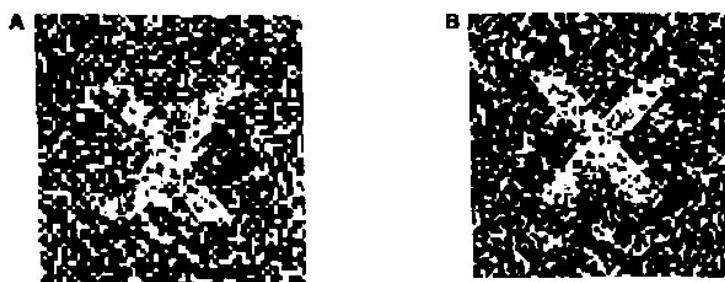


FIGURE 11.7. Figure-ground segregation task modified from VOSP, Warrington and James (1991).

Figure-Ground Segregation

One way used to assess figure-ground processing in the patients is to present a display in which a figure is embedded in a noisy background and then to require the subject to detect the presence or absence of the figure. Such a task is incorporated into the Visual Object and Space Perception battery (VOSP; Warrington & James, 1991) and an example of a stimulus from this task is shown in figure 11.7. Patient FGP (Kartsounis & Warrington, 1991) failed consistently (13/20, 8/20, and 12/20) on this task, whereas CK performed reasonably well on this standard version of the task. When the task was adapted, however, so that the level of noise became progressively greater, CK became more impaired at detecting the presence of the X although normal subjects still continue to do well (see figure 11.7, left panel, for example of the display with increasing complexity of the background; Behrmann et al., 1994). Both SM1 and RN scored 20/20 on the original version and CR scored 18/20, failing to detect the X twice when it was present. Of course, we do not know whether the performance of these three patients would be adversely affected when the degree of background noise is increased and so the data remain somewhat equivocal in this regard.

We should note that the failure to derive the figure is not obviously attributable to a problem in processing the spatial frequency information. One may notice that in displays such as this, the background (noise) is carried by the high spatial frequency components and the figure is carried by the low spatial frequency components. To the extent that this is known, the patients do not have a specific problem in processing either high or low spatial frequency information (see Behrmann and Kimchi, 2003a) and therefore, this does not explain the failure to segregate figure from ground. Additionally, this spatial frequency explanation cannot account for the patients' problems in segregating overlapping line drawings so this explanation is unlikely to hold.

As noted above, the impaired performance on overlapping displays relative to displays containing the same stimuli presented in isolation may also be attributable to poor figure-ground segregation. Patient FGP, for

example, performed poorly at identifying a whole range of displays in which the shapes overlapped. This included displays where the contour of the shapes overlapped, where the contours were nonoverlapping but the items were totally superimposed (for example, a circle drawn entirely within the boundaries of a square), and where the overlapping shapes were solid rather than transparent. She was also impaired at identifying how many objects are present in three-dimensional displays. HJA also performs more poorly on overlapping than nonoverlapping displays (Riddoch & Humphreys, 1987). In the recent follow-up study with him, it took him only 0.6 s to name an individual letter when it was nonoverlapping but 1.5 s when it overlapped. This contrasts with the normal subjects who required a mean of 0.4 s in both conditions.

Performance on overlapping versus nonoverlapping displays is also worse for CR, SM1, and RN on visually embedded Poppelreuter figures (similar to figure 11.5) where multiple figural overlaps require complex contour analysis. Interestingly, SM2 was impaired on overlapping displays depending on the extent of the overlap. Asked to identify objects presented overlapping, he scored 94% correct when the borders of the objects did not overlap extensively but only roughly 66% when the overlap was increased (in contrast with the 99% correct by the control subjects). This is also true of HJA (see following discussion of Giersch, Humphreys, Boucart, & Kovacs, 2000). The ability to make use of features that do not overlap also exemplified the performance of patient CK, as described above, and when he was forced to segment the image by the contours that overlapped, he was completely unable to do so. We have chosen to ascribe the problems in overlapping figures to the more general problem of figure-ground segregation, but this may not be absolutely correct. Patients may be impaired on overlapping shapes for a variety of reasons; for example, they may fail tasks with such shapes because of the susceptibility of contour completion processes to noise (intersecting lines; see below) or they may be laboriously tracing out the contours as they would do if they were copying. This ambiguity highlights the fact that perceptual organization processes are not well understood and much remains to be explained. For the current purpose, however, we would just point out that the patients perform poorly on overlapping shapes and that such displays clearly tap into the need for deriving coherence from complex images.

Visual Interpolation

Many real-world conditions require visual interpolation processes, including conditions of occlusion where amodal completion is engaged and where illusory contours are perceived. Indeed, as stated above, according to some accounts, these different conditions may entail the same mechanisms (Kellman, Yin, & Shipley, 1998; Shipley & Cunningham, 2001). We will consider the perception of amodal completion and illusory con-

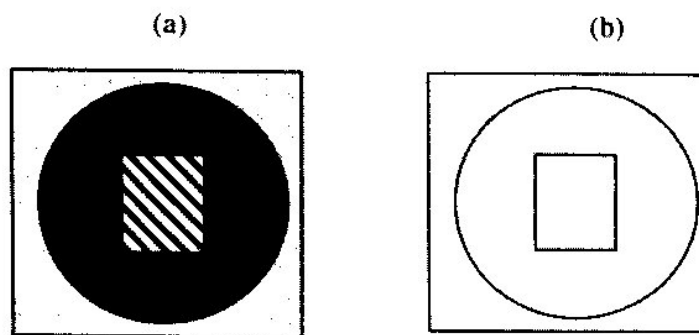


FIGURE 11.8. (a) Overlapping geometric shapes in different, solid colors and (b) the same displays but rendered as line drawings with the different contours in different colors.

tours separately, however, in order to determine whether there are any dissociations evident between them in the patient performance.

AMODAL COMPLETION

Several studies have examined amodal completion in IA patients, although the methods (and results) vary quite widely. For example, patient FGP was asked to identify simple geometric shapes, which were solid in color and displayed one superimposed on top of the other—in one display, a small solid red triangle might appear on top of and in the center of a larger green square which, in turn, was placed on top of and in the center of a larger blue circle (for example, see figure 11.8a). FGP succeeded in identifying all three shapes on only 4 out of 15 trials even with prolonged stimulus duration. Interestingly, she was able to identify all the shapes placed in the center, and fewer of those in the intermediate and outer positions, which require completion. A similar problem was noted for colored line drawings of concentric geometric shapes (figure 11.8b). Although we do not know this definitively, we assume that report of the shapes was better when the shapes were presented in isolation. The failure to derive the shapes when overlapping suggests a problem in interpolation and completion when only a partial image is evident. Similar data from patient FGP are presented in the previous section on figure-ground segregation, reflecting the close relationship between figure-ground segregation and amodal completion.

My colleagues and I have also been interested in the extent to which the patients can complete occluded images, and we have had occasion to test some IA patients on an experiment that uses displays that require completion. The experiment was originally designed to examine whether normal subjects can attend to features of an occluded object as well as they can attend to features of a single object—that is, whether they exhibit object-based attention to occluded objects. To explore this, we used a

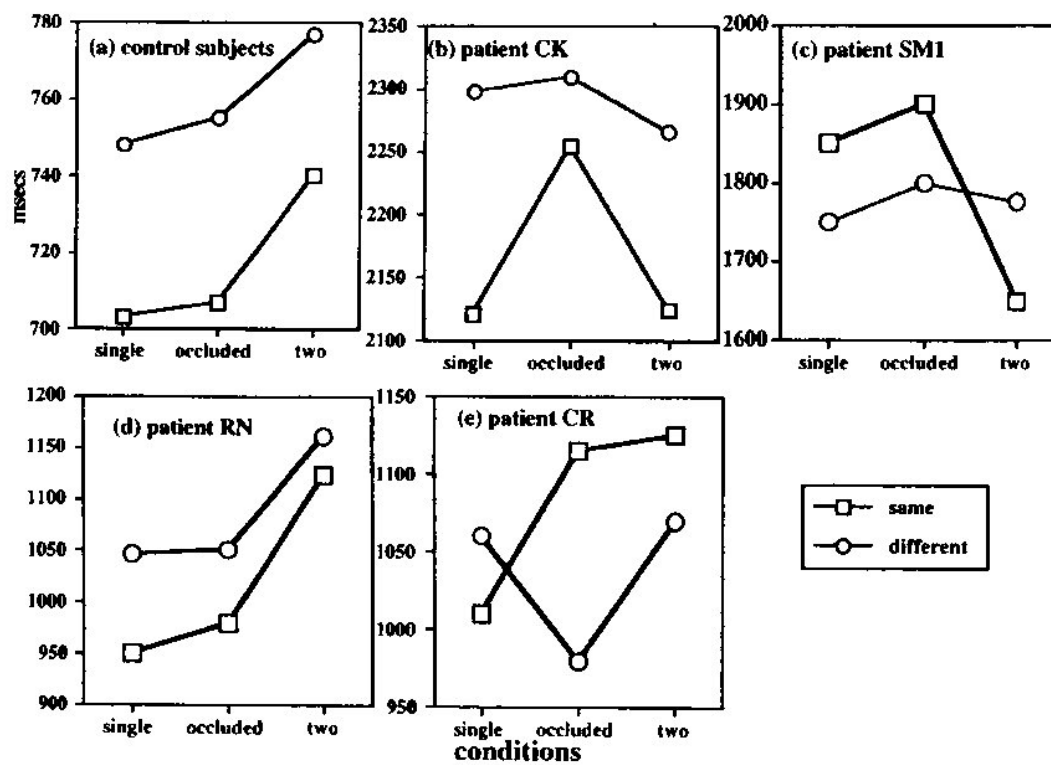
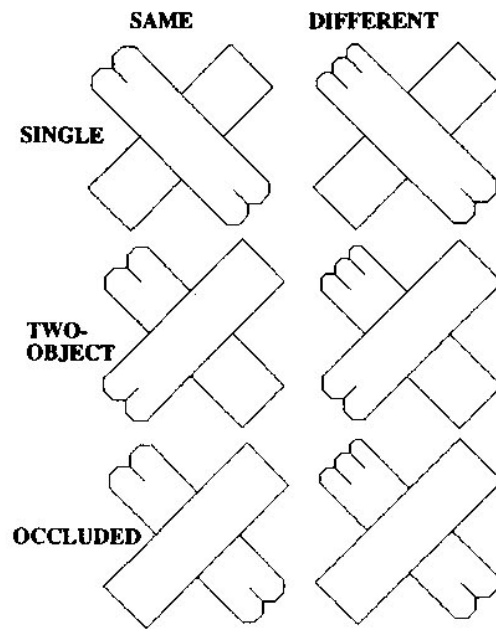


FIGURE 11.9. (Upper panel) Examples of display from Behrmann et al. (1998); (Lower panel) Performance of (a) normal subjects and four patients with integrative agnosia, with each display (b-e) reflecting the data of a single patient.

paradigm in which subjects were required to decide, as quickly as possible, whether the number of bumps appearing at two of the four possible ends of overlapping rectangle were the same or not (Behrmann, Zemel, & Mozer, 1998, 2000). As shown in figure 11.9 (upper panel), there are three conditions in this task, reflected in the rows, all of which are crossed with same/different judgments, as reflected in the columns. In the single-object condition, the bumps appear at the ends of a single, unoccluded object. In the two-object condition, the bumps appear at the end of two different objects, and, in the occlusion condition, the bumps appear at the ends of a single, occluded object.

The main result using this task was that normal subjects make the bumps decision equally quickly on the single and occluded objects, and both of these conditions are faster than the two-object condition (see figure 11.9 leftmost upper panel), consistent with notions of object-based attention. Note that object-based attention here likely emerges from the ability to complete the display amodally, as we have argued previously (Behrmann, et al., 2000).

Importantly, the advantage for the single and occluded object over the two-object condition was not obtained for three of the four agnosic patients we tested (see remaining panels in figure 11.9). Only patient RN performs similarly to the control subjects, although his intercept is considerably raised (note, however, that he is somewhat older than the control subjects reported here and so this may account for the overall slowing in base reaction time). The other patients are all slower than the control subjects, despite the fact that they are all fairly close in age. Of interest is that, although some of these patients do show an advantage for the single-object condition relative to the two-object condition, as in the case of CR, none really shows the pattern whereby single and occluded conditions are equivalent and both differ from the two-object condition. Note that the distance between the ends of the objects in the single and occluded cases is larger than the distance between the ends in the two-object condition; this may explain why SM1 performed better in the two-object case than in the other two conditions.

Patient HJA's ability to complete images has also been tested fairly extensively. For example, in a recent study, Giersch, et al. (2000) tested him on a task containing three stimuli that were either separated, transparently superimposed, in silhouette, or occluded (see examples in figure 11.10, Experiment 2). HJA and the control subjects were required to match the reference stimulus to one of two choices where the alternative choice contained the same three stimuli but in a different spatial arrangement. There was a 500 ms delay between the target and choice displays. HJA was significantly slowed at making decisions on occluded displays relative to all other displays. Interestingly, his performance with silhouettes was good, as has been reported previously (Riddoch & Humphreys, 1987) and no different from that on separated or superimposed displays. The good

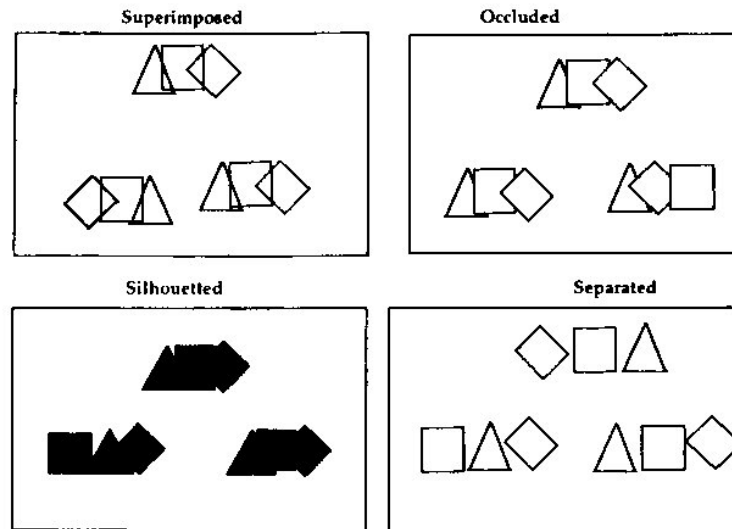


FIGURE 11.10. Superimposed, occluded, silhouetted, and separated displays from Giersch et al. (2000).

performance on silhouettes is consistent with data reported below, showing that he is disadvantaged by the presence of local details.

Despite the ability to compute collinear line segments, HJA's performance on occluded displays is not normal and reveals that the local contours are poorly bound into more global representations of shape even though they themselves might be correctly computed. In a different experiment containing three occluded or superimposed stimuli from which HJA had to select a single stimulus, which matched the central shape, he chose the completed shape as often as he chose the mosaic or partial, incomplete shape. This is in contrast to the control subjects, who chose the mosaic most often (consistent with the 2D representation). Whereas the control subjects could ignore the completion, HJA could not. That HJA could complete occluded contours but not always use this information correctly is most obviously evident in a copying task on which he drew in the occluded contour as if the real contour were present. For example, when a shape interrupted the collinear line of a square so that it was no longer visible, HJA drew in the missing collinear segment on 26 out of 47 trials. He did not include additional contours in displays where there was no occlusion. These findings all suggest that he can interpolate occlusion correctly, although he appears not to be able to exploit it for the purpose of figure-ground differentiation.

Based on the apparent ability to compute the occluded shape but the failure to match this shape when it appears in the presence of other shapes, Giersch et al. (2000) argue that contour interpolation is an early visual process, that occurs prior to the assignment of the contours to more global shapes. They attribute HJA's preserved ability to the more elementary operation of binding form elements into contours, which, they show, is in-

deed normal (for further discussion, see Humphreys, 2002). Using a set of cards containing displays of a smoothly aligned, closed path of Gabor elements embedded in a random array of Gabor elements of the same spatial frequency and contrast (Pennefather, Chandna, Kovacs, Polat, & Norcia, 1999), they required HJA to trace the Gabor contour on each card. They then used a staircase procedure to establish a threshold. This procedure has been used successfully with various pathological populations (Kovács, Polat, Pennefather, Chandna, & Norcia, 2000) and examples of the cards are shown in figure 11.11. Threshold is reflected in terms of parameter Δ , which is the ratio of average background spacing over contour spacing, and it ranges between 1.2 to 0.5 in steps of 0.05. This parameter expresses “relative noise density” and reflects signal-to-noise ratio; the smaller the Δ value, the better performance (Kovács et al., 2000). HJA obtained a Δ of 0.65, well within the normal range of performance, which is around 0.69 (SD 0.09). The preserved ability on this test is thought to reflect the intact pattern and spatial extent of long-range interaction among orientation-tuned neurons in primary visual cortex.

That contour interpolation can be intact and underlie amodal completion but still not suffice for figure-ground segregation may also explain the performance of SM1 who, on the identical contour-integration task described above, obtained a threshold of 0.6, clearly within normal limits. Of interest is that he still performed poorly on the amodal completion task (see figure 11.9c). On this latter task, he did not obtain an advantage in processing features from a single object, either occluded or complete, compared with two objects. The findings indicate that intact contour interpolation may not suffice for object-based attention just as it may not suffice for figure-ground segregation. Instead, both object-based attention and

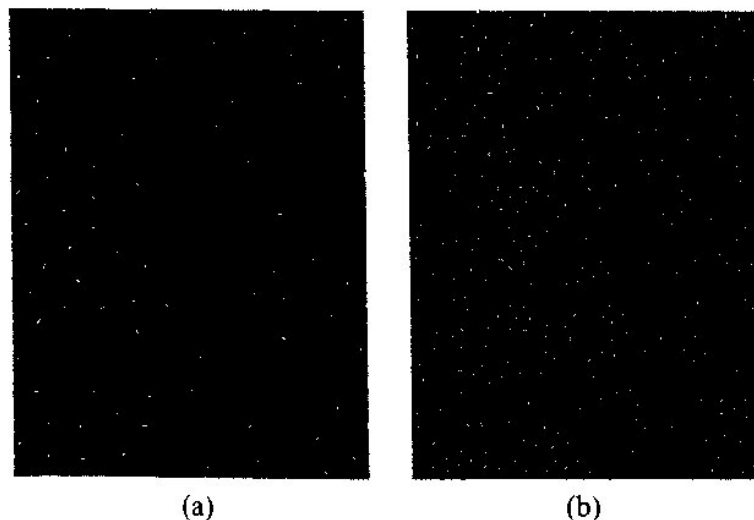


FIGURE 11.11. Examples of displays from Kovacs et al., (2000) of contours made of local Gabor units. (a) easy and (b) difficult. The target is a line made of the Gabor units and the target is located toward the bottom left in (a) and upper right in (b).

figure-ground segregation require that form elements be bound into coherent object descriptions.

ILLUSORY FIGURES

Illusory figures are perceived where inducing elements are positioned so that their contours align to form the edges of a closed figure. Under the correct circumstances, observers then perceive an opaque figure of about the same reflectance as the background surface in front of and partly occluding the black elements, which are then amodally completed behind the illusory figure.

Patient FGP was dramatically impaired on any task requiring the perception of subjective contours. For example, shown Kanisza-type figures of circles, triangles, and squares, not only did she comment that she only perceived little curves and no real shape, but she was even unable to discriminate the geometric shape given the choices. Additionally, she was impaired at deciding which of two outline shapes would make up a triangle (see figure 11.12). She stated that she only saw "three little L's," suggesting a fundamental impairment in deriving the completed contours. Using a two-choice procedure, she scored 13/20 on the easy and 10/20 on the difficult discriminations; of course, one might easily also attribute this to a problem in good continuation and, indeed, as noted below, she performs poorly on tasks of continuation and closure. When she was shown displays in which a contour was created by aligned line terminators to give the impression of one shape superimposed on another, she failed to detect the illusory contour.

The findings from the various patients indicate that IA individuals are mostly impaired at various forms of visual interpolation, including amodal completion and illusory contours, although this is not perfectly consistent across all patients. We examine the implications of the variability in the final section.

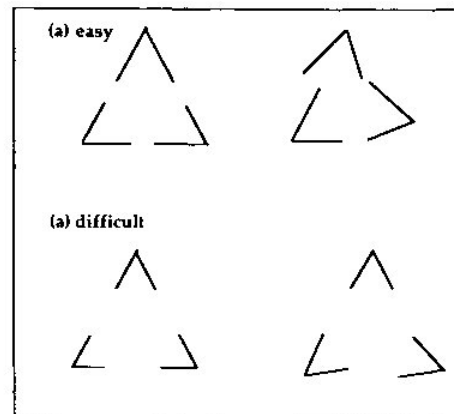


FIGURE 11.12. (a) easy and (b) difficult discriminations of illusory shapes from Kartsounis and Warrington (1991).

Perceptual Grouping

The final organization process we discuss is perceptual grouping, and of all the different processes of perceptual organization, this has been the one most extensively explored in IA. Of course, there are many ways in which elements can be grouped and some, but not all these ways have been explored in patients.

HJA is apparently unable to exploit the Gestalt principle of collinearity. For example, in one study he was required to make perceptual matches with fragmented line drawings (Boucart & Humphreys, 1992). The fragments in the line drawings could be aligned and collinear, or they could be misaligned so they were no longer collinear but the overall shape had the same spatial frequency as before. In contrast to normal subjects who showed an advantage for the collinear displays, this was not the case for HJA. This is somewhat surprising given his intact contour detection discussed above and his ability to compute occlusion (even though this may not aid in his depth assignment for figure-ground segregation). One might have expected that the ability to link contour elements into elongated contours would assist in the computation of collinearity. Interestingly, HJA did show a sensitivity to the global form; his performance was better when he was required to discriminate between items that had different global orientation than between those with the same orientation. HJA's failure to deal with collinear fragmented forms is suggestive of a problem in integrating local, intact contours into more global, multicontour shape representations and is also compatible with his failure to use the local information for object recognition. This impairment may explain his preference for silhouettes and, as we shall see below, it may be compatible with his performance on hierarchical stimuli.

The ability to use collinearity may also be important for successful performance on other tests of fragmented objects (although undoubtedly many other perceptual skills are also required). Patient SM2 performed poorly on the Hooper Visual Recognition test in which fragments of a contour are shown and subjects assemble these to determine the item (items are not that different from figure 11.12). For example, when displays containing fragmented parts of objects rotated from their normal position were shown to SM2, he was unable to recognize any (normal controls 89%). Two other paradigms have been used extensively to investigate grouping and they are the visual search task and the global/local task. These are discussed in turn.

The ability to group is also useful under some conditions in visual search tasks. In normal subjects, when the distractors are homogeneous and can be grouped together, target detection is efficient and rapid whereas search is slowed and inefficient when the distractors are heterogeneous and require serial encoding. When searching for a T among inverted Ts in a field, HJA showed a similar serial pattern to the control subjects when the distractors were heterogeneous. Of interest is that he could not exploit

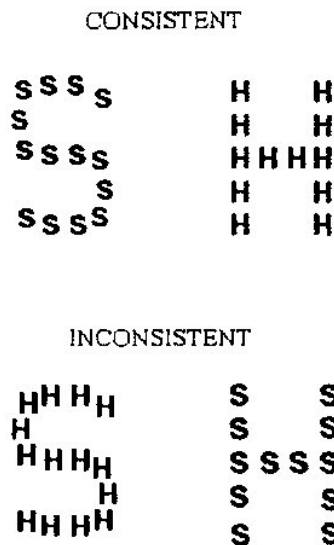


FIGURE 11.13. Stimuli used in local/global tasks in which the local and global stimuli are consistent (above) or not (below).

the similarities and potential for grouping among the homogeneous distractors, with the result that he made many errors and his search function was slow and affected by the number of distractors present (Humphreys et al., 1994, 1992). A similar pattern was seen when HJA searched for abstract forms rather than letters. In contrast, HJA manifested normal search functions when the target was of a different orientation from the distractors. Taken together, these findings reflect the fact that the impairment in integrative agnosia is reflected in tasks that require the binding of visual elements in a spatially parallel manner across a field (Humphreys & Riddoch, 2001; Humphreys et al., 1994).

The final domain we discuss is that of processes involved in deriving hierarchical configurations from discrete elements. These processes are engaged frequently in the real world; bicycles have wheels, which, in turn, have spokes and this requires that parts of objects must be bound into global wholes. The paradigm most often exploited to study the ability to deal with elements and wholes is modelled after that of Navon (1977) in which hierarchical stimuli are used and in which the local elements may or may not be consistent with the global item. For example, stimuli may consist of a global letter H made up of small letter Hs or small letter S. Whereas the former are consistent, the latter are not (see figure 11.13). Such stimuli are useful in order to examine whether global identity can be derived and whether local information interferes with this derivation or vice versa. It is generally thought that the local elements are grouped to form the global shape and grouping of the elements may be based, for example, on proximity, similarity of luminance or shape, or good continuity (Han & Humphreys, 2002).

In one block of trials, subjects report the identity of the global letter and in a second, they report the identity of the local letters. Typically, normal observers exhibit a global advantage such that the global item is identified more rapidly than the local items (the so-called forest-before-the-trees effect; Navon, 1977; Yovel, Yovel & Levy, 2001). Additionally, global interference is observed such that in cases where the local and global information are inconsistent, there is interference from the global identity onto naming the local item but not vice versa. Much recent research has been concerned with identifying the neural substrate that mediates the processing of the local and global elements. One result from this research is that the right hemisphere appears to be biased for global processing whereas the left hemisphere appears to be biased for local processing (Fink et al., 1996), although these hemispheric asymmetries may be relative rather than absolute (Polster & Rapcsak, 1994).

Given the compositional nature of the stimuli and the tendency of patients to oversegment, one would predict that the integrative agnosic patients would be easily captured by local elements or parts and would then have difficulty deriving unified wholes from the input. This is precisely the case for patients RN (Behrmann & Kimchi, 2003a, 2003b) and CR (Behrmann and Kimchi, 2003c). Figure 11.14 below shows the data from the control subjects as well as from three patients (we return to a discussion of SM1 shortly). As is evident from this figure, the normal control subjects show the expected global advantage and a trend toward global-to-local interference (under foveal presentation with unlimited exposure durations, one does not always obtain a strong interference effect). Of particular interest are the data from RN and CR, which contrast with the normal subjects and in which there is local dominance; performance is faster for local than global shapes and there is interference from local to global in the inconsistent case. These findings strongly support the claim that the patients' processing is directed toward the elements rather than the configuration *per se*.

But this pattern of local capture is not seen in all integrative agnosic patients. This pattern was not observed in HJA nor in patient SM1. Let us consider HJA first: he responded more quickly to global than to local stimuli (roughly 300 ms difference). His responses to global letters were relatively normal and it was his response to local letters that was slowed, although he showed no impairment when the local elements were presented in isolation (Riddoch & Humphreys, 1987). However, unlike normal subjects, he showed no interference from global to local identification (although, as we see above, even the normal subjects do not always show this and it is paradigm-dependent). The explanation offered for HJA's pattern is that there is separate and independent processing of global and local forms (Humphreys, 1999) and this is supported by the presence of a global advantage without global-to-local interference. The idea is that global shape can be derived by HJA but is not embellished with more

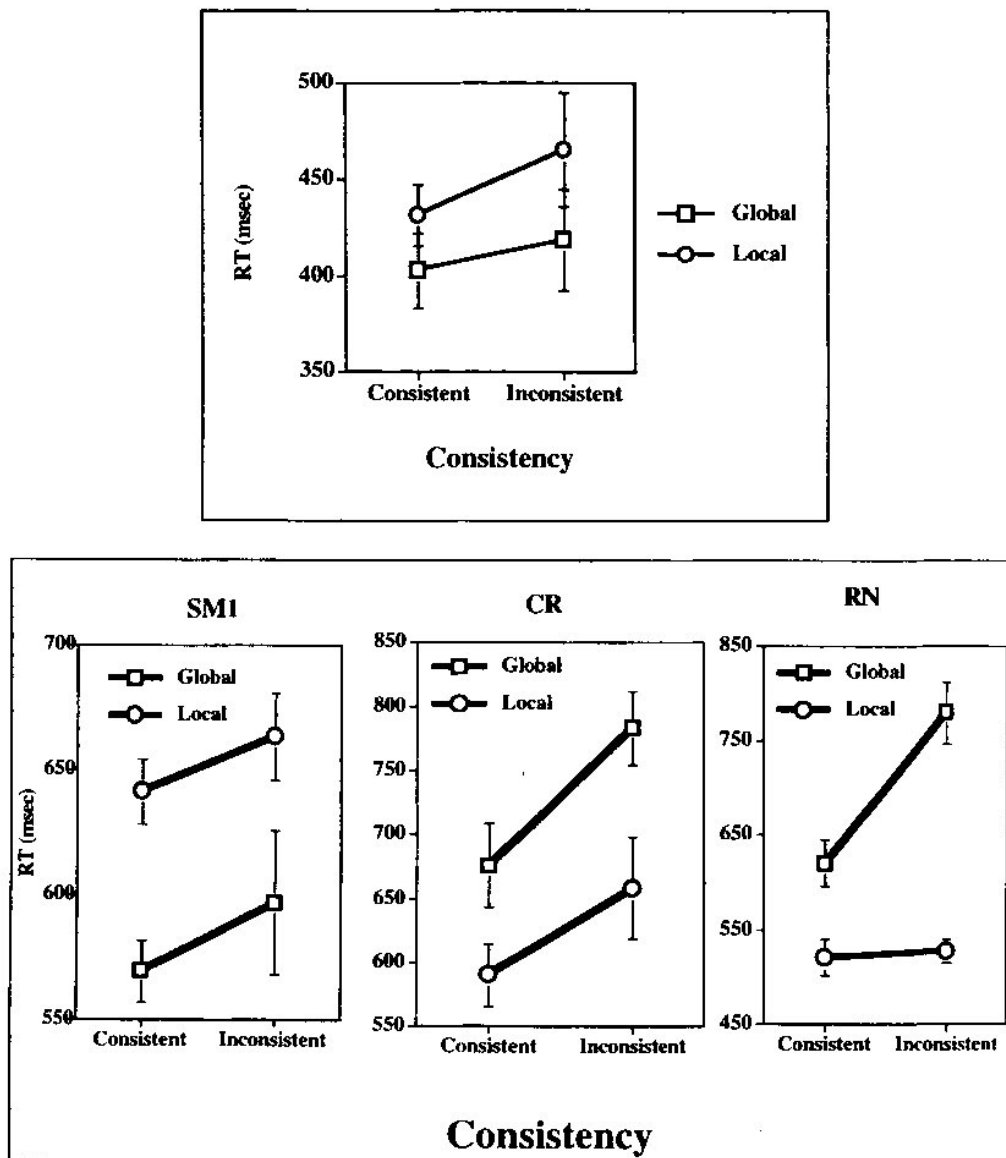


FIGURE 11.14. RT performance of control subjects (above) and three patients with integrative agnosia in a global/local letter identification task.

detailed local information and so the two forms are not synthesized. To derive sufficient local information for object identification, HJA may then have to process the parts serially, and this may lead to the segmental, piecemeal performance. This explanation is consistent with the data from Boucart and Humphreys (1992) mentioned above revealing his sensitivity to global shape despite the inability to exploit the collinearity of the fragmented elements. It also meshes well with his ability to derive form from the global outline of the silhouette in the absence of the internal features.

But not all the data seem compatible with this explanation. For example, HJA's ability to match and identify objects appears not to be greatly influenced by the global properties of objects under some conditions. For example, when an object is foreshortened and the global shape altered.

his performance is not greatly affected. Also surprising is that his performance appears to be more reliant on local distinctive features of an object; when a primary distinctive feature is no longer salient in an image, performance is adversely affected (Humphreys & Riddoch, 1984). But HJA is not the only IA patient exhibiting global precedence and no interference; this is the pattern shown by SM1 too (see figure 11.14). SM1's ability to derive the global configuration is particularly puzzling as he has a clear unilateral right-hemisphere lesion and in terms of hypotheses about right-hemisphere tuning for global properties of stimuli, he should be dramatically impaired.

We have previously offered an explanation for SM1's apparent success with these Navon figures. We have shown, for example, that when a hierarchical stimulus is presented for a brief exposure duration (unlike the unlimited duration used for presenting the Navon figures), SM1 no longer performs as well as normal controls in deriving the global configuration (Behrmann & Kimchi, 2003a). Additionally, under more challenging conditions, such as when there are few, rather than many, local elements that need to be grouped, SM1 does not derive the global form from the elements. These findings suggest that SM1 is indeed impaired at grouping, although his impairment might not be as severe as that of the other patients. Under the appropriate testing conditions, however, the deficit is easily revealed. This explanation might also apply to HJA but whether it does is not known at present.

Recent findings from the study of normal perceptual organization suggests that the impairment in deriving the global configuration may be a direct consequence of weakened grouping. For example, Han, Humphreys, & Chen, (1999) have proposed that there is an interaction between perceptual organization based on Gestalt laws and that based on hierarchical processing (see also Han & Humphreys, 1999). In their experiments, they required subjects to discriminate stimuli at the local or global level and manipulated the strength of grouping by including background distractors. When the grouping between local elements was weakened, the perception of global structure was impeded (Han & Humphreys, 1999), manifest as a reduction in the global advantage. These findings are relevant for IA and suggest that a reduction in grouping ability, as in CR and RN, directly results in the local advantage.

One other issue that may help us resolve and understand the relationship between hierarchical processing and grouping, as well as other forms of perceptual organization, is that of the microgenesis or detailed time course of these different processes. Recent studies by Kimchi (Kimchi, 1998, 2000) with normal subjects have revealed a change in the representation derived from the stimulus as a function of time. Whereas early on in the course of processing, subjects appear to represent the elements, later on at longer durations, the configuration is represented and this is the source of the global advantage. We have begun exploiting this method for more detailed analysis of the patients' performance in an attempt to un-

cover the mechanisms mediating the derivation of global configuration (Behrmann & Kimchi, 2003b). One possible explanation for the apparent differences observed across patients is that all integrative agnosic patients are impaired at deriving global configuration—however, with enough time, some of them (such as SM1 and HJA) may eventually succeed. Only a detailed analysis of the time course of processing in the patients can resolve this.

Taken together, the findings clearly indicate some pattern of impairment in grouping processes in almost all patients, although the vagaries of the studies and patients do not allow us to make good comparisons between the patients. This domain clearly requires further exploration.

Caveats and Qualifications

The focus of this chapter has been on a select subgroup of individuals with visual perceptual deficits acquired in adulthood. These patients exhibit integrative agnosia, a deficit in which they appear to have the building blocks of perception available to them but are unable to use them to configure shapes. We have deliberately excluded other types of patients (apperceptive agnosic, associative agnosic, attentional deficits) as well as integrative agnosic patients who meet our criteria but for whom insufficient detail is available. Before concluding, however, there is one other group of patients whom we have not discussed but deserves to be contrasted with IA patients and these are individuals with simultanagnosia. In some ways, IA and simultanagnosia are very similar and so comparing them is important.

Simultanagnosia is the term applied to those patients who, following lesions to the junction of parietal and occipital regions bilaterally, may be able to detect or identify individual visual objects or their features but may be unable to process multiple objects simultaneously. These patients may also exhibit a host of other impairments including spatial disorientation, abnormal eye movements, and inaccurate visually guided reaching (Balint, 1909), but our focus here is on the apparent problem in perceptual organization and its relationship to integrative agnosia. The simultanagnosic deficit has been labeled “dorsal simultanagnosia” to differentiate it from the impairment in interpreting visual arrays that occurs with letter-by-letter reading (Farah, 1990). This latter impairment occurs following lesions to more ventral areas, typically in the left hemisphere. Of relevance to us here, however, is that there are aspects of the performance of dorsal simultanagnosic patients that resemble the patterns described above in relation to visual agnosia. The striking feature of dorsal simultanagnosia is that the patient’s visual experience becomes captured by a local detail or individual object, to the exclusion of all other aspects of the scene (Coslett & Saffran, 1991; Rafal & Robertson, 1995).

Some recent case reports highlight the perceptual difficulties of these patients. For example, patient KB (Karnath, Ferber, Rorden, & Driver, 2000) could recognize a square or circle drawn on paper but when they overlapped, she was unable to identify both. She was able to identify only individual objects in a visual scene and was unable to recognize the general theme of the picture. The pathological visual capture of local elements was so striking that she was virtually unable to identify a global shape using Navon hierarchical stimuli even when the stimulus exposure duration was unlimited. Although she identified the local letter correctly on 91% of the trials, she managed to name the global letter on only 5 out of 96 trials and, on the incorrect trial, she gave the local letter as a response on 77 of the incorrect trials. This local capture resembles the pattern reported for the integrative agnosic patient, RN, reported above. It is interesting to note that KB was slowed in reporting the local letter when it was inconsistent with the global letter, revealing evidence for some processing of the global letter albeit insufficient for it to reach threshold for overt identification. One possible explanation is that local capture is not diagnostic of a particular perceptual problem. Indeed, similar, albeit milder impairments in selectively identifying the global hierarchical letter has been reported in patients with unilateral right-hemisphere lesions around the temporo-parietal junction (Doricchi & Incoccia, 1998; Robertson, Lamb, & Knight, 1988) and for patients with degenerative disorders and diffuse cortical atrophy (Coslett, Stark, Rajaram, & Saffran, 1995; Stark, Grafman, & Fertig, 1997).

Although there is some similarity between simultanagnosic and integrative agnosic patients, there are also major differences. Integrative agnosic patients do not show spatial disorientation, do not bump into objects, and do not exhibit optic ataxia. Moreover, they do not appear to be limited in their ability to report the presence of multiple objects even if they cannot identify them all correctly. Humphreys (1999) suggests that the distinction between the two phenomena is best characterized as a difference between spatial representation between parts of a single object (integrative agnosia) versus spatial representation between objects (simultanagnosia).

Conclusion

This chapter has been concerned with a specific subpopulation of patients who are unable to bind contours into wholistic shapes despite the apparent availability of the contours (as is known for some cases) and other low-level features of the image. Because these patients appear to have the building blocks for perception but cannot derive the final shape, they may provide some insight into normal mechanisms of perceptual organization. We examined the performance of these patients in relation to three main

processes of perceptual organization: figure-ground segregation, visual interpolation, and grouping. The study of these patients offers much potential for understanding perceptual organization.

A review of the findings from 7 patients all of whom have been tested relatively extensively leads to a few general conclusions. As a group, the patients appear to be impaired in the three processes we have dealt with. It is the case, however, that detailed examination of the individual patients does not reveal uniformity across the patients. Three of the patients are clearly impaired at figure-ground organization, while three patients are reasonably good and there are no persuasive data from the final patient. Five patients are impaired at amodal completion and one is reasonably good. There is similar discrepancy on some of the other dimensions. It is the case, however, that all patients are impaired on at least one of the organizational processes.

A critical question is where does the variability come from and is it informative? At this stage it is difficult to answer either question. The variability might emerge from the fact that patients may differ in severity. For example, whereas patients HJA and CK appear to be impaired on all processes, RN is impaired on only a subset. Degree of deficit may provide an explanation but it is not clear how to validate this claim. Additional testing with some means of external validation for these processes is clearly needed. A second explanation for the variability might be the lesion site and qualitative, not quantitative, differences between the patients. Again, this is notoriously difficult to nail down in a neuropsychological population because of the extent of the lesion site and so we cannot reach any definitive conclusions about lesion site and overt behavioral deficit. What is clear from all this is that much remains to be done to develop a further understanding of the relationship between neural mechanisms and perceptual organization but also to understand how the different perceptual processes are related to each other and to other forms of visual processing such as object discrimination and identification.

At this stage, suffice it to say that the available data are rich and interesting and provide clear suggestions for future research and clarification. We expect that these ongoing neuropsychological investigations, in conjunction with the emerging data from other methods such as single neuron recordings, functional imaging, and detailed behavioral studies with normal subjects, will help clarify the mechanisms, both psychological and neural, that mediate the organization of the chaotic input to the visual system.

Notes

This chapter was largely written while the author was on sabbatical at the Weizmann Institute of Science, Israel. The work was supported by grants from The Weston Visiting Professorship at the Weizmann Institute of Science, Israel; the

James McKeen Cattell Sabbatical award; a Binational Science Foundation grant to MB and Rutie Kimchi; and NIMH grant MH54766. I thank Rutie Kimchi, Mary Peterson, Gill Rhodes, Christan Gerlach, and Anjan Chatterjee for their valuable comments on this chapter.

References

- Adler, A. (1944). Disintegration and restoration of optic recognition in visual agnosia. *Archives of Neurology and Psychiatry*, 51, 243–259.
- Agostini, T., & Galmonte, A. (2002). Perceptual organization overcomes the effects of local surround in determining simultaneous lightness contrast. *Psychological Science*, 13(1), 89–93.
- Arguin, M., Bub, D. N., & Dudek, G. (1996). Shape integration for visual object recognition and its implication in category specific visual agnosia. *Visual Cognition*, 3(3), 221–275.
- Balint, R. (1909). Seelenlahmung des 'Schauens', optische Ataxie, raumliche Störung der Aufmerksamkeit. (Paralysis of "looking," optic ataxia, and the spatial disturbance of attention). *Monatsschrift für Psychiatrie und Neurologie* (25), 51–81.
- Bartolomeo, P., Bachoud-Lèvi, A., De Gelder, B., Dalla Barba, G., Brugieres, P., & Degos, J. D. (1998). Multiple-domain dissociation between impaired visual perception and preserved mental imagery in a patient with bilateral extrastriate lesions. *Neuropsychologia*, 36(3), 239–249.
- Bartolomeo, P., Bachoud-Lèvi, A. C., Degos, J. D., & Boller, F. (1998). Disruption of residual reading capacity in a pure alexic patient after a mirror-image right hemispheric lesion. *Neurology*, 50(1), 286–288.
- Behrmann, M., & Kimchi, R. (2003a). What does visual agnosia tell us about perceptual organization and its relationship to object recognition? *Journal of Experimental Psychology: Human Perception and Performance*.
- Behrmann, M., & Kimchi, R. (2003b). Perceptual organization in visual agnosia. In R. Kimchi, M. Behrmann, & C. Olson (Eds.), *Perceptual organization in vision: Behavioral and neural perspectives*. Hillsdale, NJ: Erlbaum.
- Behrmann, M. and Kimchi, R. (2003c). Studies with agnosic patient, CR. Unpublished observations.
- Behrmann, M., Moscovitch, M., & Winocur, G. (1994). Intact visual imagery and impaired visual perception in a patient with visual agnosia. *Journal of Experimental Psychology: Human Perception and Performance*, 20(5), 1068–1087.
- Behrmann, M., Winocur, G., & Moscovitch, M. (1992). Dissociations between mental imagery and object recognition in a brain-damaged patient. *Nature*, 359, 636–637.
- Behrmann, M., Zemel, R., & Mozer, M. C. (1998). Object-based attention and occlusion: Evidence from normal subjects and a computational model. *Journal of Experimental Psychology: Human Perception and Performance*, 24(4), 1011–1036.
- Behrmann, M., Zemel, R., & Mozer, M. C. (2000). Occlusion, symmetry, and object-based attention: Reply to Saiki (2000). *Journal of Experimental Psychology: Human Perception and Performance*, 26(4), 1497–1505.
- Benson, D. F., & Greenberg, J. P. (1969). Visual form agnosia. *Annual Review of Neuroscience*, 20, 82–89.

- Boucart, M., & Humphreys, G. W. (1992). The computation of perceptual structure from collinearity and closure: Normality and pathology. *Neuropsychologia*, 30(6), 527-546.
- Bullier, J., Schall, J. D., & Morel, A. (1996). Functional streams in occipito-frontal connections in the monkey. *Behavioural Brain Research*, 76, 89-97.
- Butter, C. M., & Trobe, J. D. (1994). Integrative agnosia following progressive multifocal leukoencephalopathy. *Cortex*, 30, 145-158.
- Campion, J., & Latto, R. (1985). Apperceptive agnosia due to carbon monoxide poisoning, an interpretation based on critical band masking from disseminated lesions. *Behavioral and Brain Sciences*, 15, 227-240.
- Chainay, H., & Humphreys, G. W. (2000). The real object advantage in agnosia: Evidence for a role of shading and depth in object recognition. *Cognitive Neuropsychology*, 12, 175-191.
- Coslett, H. B., & Saffran, E. M. (1991). Simultanagnosia: To see but not two see. *Brain*, 114, 1523-1545.
- Coslett, H. B., Stark, M., Rajaram, S., & Saffran, E. M. (1995). Narrowing the spotlight: A visual attentional disorder in Alzheimer's disease. *Neurocase*, 1, 305-318.
- Davidoff, J., & Warrington, E. K. (1993). A dissociation of shape discrimination and figure-ground perception in a patient with normal acuity. *Neuropsychologia*, 31(1), 83-93.
- Davidoff, J., & Wilson, B. (1985). A case of visual agnosia showing a disorder of presemantic visual classification. *Cortex*, 21(2), 121-134.
- de Gelder, B., Bachoud-Lévi, A. C., & Degos, J. D. (1998). Inversion superiority in visual agnosia may be common to a variety of orientation polarised objects besides faces. *Vision Research*, 38(18), 2855-2861.
- De Renzi, E., & Lucchelli, F. (1993). The fuzzy boundaries of apperceptive agnosia. *Cortex*, 29, 187-215.
- Delis, D. C., Robertson, L. C., & Efron, R. (1986). Hemispheric specialization of memory for visual hierarchical stimuli. *Neuropsychologia*, 24, 205-214.
- Doniger, G., Foxe, J. J., Murray, M. M., Higgins, B. A., Snodgrass, J. G., Schroeder, C. E., & Javitt, D. C. (2000). Activation timecourse of ventral visual stream object-recognition areas: High density electrical mapping of perceptual closure processes. *Journal of Cognitive Neuroscience*, 12(4), 615-621.
- Doricchi, F., & Incoccia, C. (1998). Seeing only the right half of the forest but cutting down all the trees. *Nature*, 394, 75-78.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96(3), 433-458.
- Efron, R. (1968). What is perception? *Boston Studies in Philosophy of Science*, 4, 137-173.
- Enns, J. T., & Rensink, R. A. (1990). Influence of scene-based properties on visual search. *Science*, 24, 721-723.
- Etcoff, N., Freeman, R., & Cave, K. R. (1991). Can we lose memories of faces? Content specificity and awareness in a prosopagnosic. *Journal of Cognitive Neuroscience*, 3(1), 25-41.
- Farah, M. J. (1990). *Visual agnosia: Disorders of object recognition and what they tell us about normal vision*. Cambridge, MA: MIT Press.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1, 1-47.

- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature*, 382, 626–628.
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1997). Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain*, 120, 1779–1791.
- Frederiksen, J. R., & Kroll, J. F. (1976). Spelling and sound: Approaches to the internal lexicon. *Journal of Experimental Psychology: Human Perception and Performance*, 2(3), 361–379.
- Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience*, 11(4), 349–370.
- Gerlach, C., Aaside, C. T., Humphreys, G. W., Gade, A., Paulson, O. B., & Law, I. (2002). Brain activity related to integrative processes in visual object recognition; Bottom-up integration and the modulatory influence of stored knowledge. *Neuropsychologia*, 40, 1254–1267.
- Giersch, A., Humphreys, G., Boucart, M., & Kovacs, I. (2000). The computation of occluded contours in visual agnosia: Evidence for early computation prior to shape binding and figure-ground coding. *Cognitive Neuropsychology*, 17, 8, 731–759.
- Gilchrist, I. D., Humphreys, G. W., & Riddoch, M. J. (1996). Grouping and extinction: Evidence for low-level modulation of visual selection. *Cognitive Neuropsychology*, 13(8), 1223–1249.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–24.
- Goodglass, H., Kaplan, E., & Weintraub, S. (1983). *Boston Naming Test*. New York: Lea and Febiger.
- Grailet, J. M., Seron, X., Bruyer, R., Coyette, F., & Frederix, M. (1990). Case report of a visual integrative agnosia. *Cognitive Neuropsychology*, 7(4), 275–309.
- Grossberg, S. (1997). Cortical dynamics of three-dimensional figure-ground perception of two-dimensional pictures. *Psychological Review*, 104(3), 618–658.
- Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures and neon color spreading. *Psychological Review*, 92(2), 173–211.
- Grossman, M., Galetta, S., & D'Esposito, M. (1997). Object recognition difficulty in visual apperceptive agnosia. *Brain and Cognition*, 33, 306–342.
- Han, S., & Humphreys, G. W. (1999). Interactions between perceptual organization based on Gestalt laws and those based on hierarchical processing. *Perception and Psychophysics*, 6(7), 1287–1298.
- Han, S., & Humphreys, G. W. (2002). Segmentation and selection contribute to local processing in hierarchical analysis. *Quarterly Journal of Experimental Psychology*, 55A(1), 5–21.
- Han, S., Humphreys, G. W., & Chen, L. (1999). Parallel and competitive processes in hierarchical analysis: Perceptual grouping and encoding of closure. *Journal of Experimental Psychology: Human Perception and Performance*, 25 (5), 1411–1432.
- He, Z. J., & Nakayama, K. (1992). Surfaces versus features in visual search. *Nature*, 359, 231–233.

- Heitger, F., von der Heydt, R., Peterhans, E., Rosenthaler, L., & Kubler, O. (1998). Simulation of neural contour mechanisms: representing anomalous contours. *Image and Vision Computing*, 16, 407–422.
- Hirsch, J., DeLaPaz, R. L., Relkins, 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. *Proceedings of the National Academy of Sciences*, 92, 6469–6473.
- Hochberg, J. (1981). Levels of perceptual organization. In M. Kubovy and J. R. Pomerantz (Eds.), *Perceptual organization* (pp. 255–278). Hillsdale, NJ: Erlbaum.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, 3(3), 284–291.
- Humphreys, G. W. (1999). Integrative agnosia. In G. W. Humphreys (Ed.), *Case studies in vision* (pp. 41–58). London: Psychology Press.
- Humphreys, G. W. (2003). Binding in vision as a multi-stage process. In R. Kimchi, M. Behrmann, & C. Olson (Eds.), *Perceptual organization: Behavioral and neural perspectives*. Hillsdale, NJ: Erlbaum.
- Humphreys, G. W., & Riddoch, M. J. (1984). Routes to object constancy: Implications from neurological impairments of object constancy. *Quarterly Journal of Experimental Psychology*, 36A, 385–415.
- Humphreys, G. W., & Riddoch, M. J. (1987). *To see but not to see: A case-study of visual agnosia*. Hillsdale, NJ: Erlbaum.
- Humphreys, G. W., & Riddoch, M. J. (2001). Neuropsychological disorders of visual object recognition and naming. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 4). Amsterdam: Elsevier Science.
- Humphreys, G. W., & Riddoch, M. J., Donnelly, N., Freeman, T., Boucart, M., & Muller, H. M. (1994). Intermediate visual processing and visual agnosia. In M. J. Farah & G. Ratcliff (Eds.), *The neuropsychology of high-level vision* (pp. 63–101). Hillsdale, NJ: Erlbaum.
- Humphreys, G. W., & Riddoch, M. J., Quinlan, P. T., Price, C. J., & Donnelly, N. (1992). Parallel pattern processing and visual agnosia. *Canadian Journal of Psychology*, 46(3), 377–416.
- Karnath, H. O., Ferber, S., Rorden, C., & Driver, J. (200). The fate of global information in dorsal simultanagnosia. *Neurocase*, 6, 295–306.
- Kartsounis, L., & Warrington, E. K. (1991). Failure of object recognition due to a breakdown in figure-ground discrimination in a patient with normal acuity. *Neuropsychologia*, 29, 969–980.
- Kellman, P. J. (2000). An update on Gestalt psychology. In B. Landau, J. Sabini, E. Newport, & J. Jonides (Eds.), *Essays in honor of Henry and Lila Gleitman*. Cambridge, MA: MIT Press.
- Kellman, P. J. (2003). Visual perception of objects and boundaries: A four-dimensional approach. In R. Kimchi, M. Behrmann & C. Olson (Eds.), *Perceptual organization in vision: Behavioral and neural perspectives*. Mahwah, NJ: Erlbaum.
- Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, 23, 141–221.
- Kellman, P. J., & Shipley, T. F. (1992). Perceiving objects across gaps in space and time. *Current Directions in Psychological Science*, 1(6), 193–199.

- Kellman, P. J., Yin, C., & Shipley, T. F. (1998). A common mechanism for illusory and occluded object completion. *Journal of Experimental Psychology: Human Perception and Performance*, 24(3), 859–869.
- Kertesz, A. (1979). Visual agnosia: The dual deficit of perception and recognition. *Cortex*, 15, 403–419.
- Kimchi, R. (1998). Uniform connectedness and grouping in the perceptual organization of hierarchical patterns. *Journal of Experimental Psychology: Human Perception and Performance*, 24(2), 1105–1118.
- Kimchi, R. (2000). The perceptual organization of visual objects: a microgenetic analysis. *Vision Research*, 40, 1333–1347.
- Kimchi, R., Behrmann, M. and Olson, C. (2003). *Visual perceptual organization: Behavioral and neural perspectives*. Hillsdale, NJ: Erlbaum.
- Kimchi, R., & Hadad, R. (2002). Influence of past experience on perceptual grouping. *Psychological Science*, 13, 41–47.
- Kohler, W. (1920/1950). Physical gestalten. In W. D. Ellis (Ed.), *A sourcebook of Gestalt psychology* (pp. 17–54). New York: Humanities Press.
- Kovács, I. (2000). Human development of perceptual organization. *Vision Research*, 40, 1301–1310.
- Kovács, I., Polat, U., Pennefather, P. M., Chandna, A., & Norcia, A. M. (2000). A new test of contour integration deficits in patients with a history of disrupted binocular experience during visual development. *Vision Research*, 40, 1775–1783.
- Lamb, M. R., Robertson, L. C., & Knight, R. T. (1989). Attention and interference in the processing of global and local information: Effects of unilateral temporal-parietal junction lesions. *Neuropsychologia*, 27(4), 471–483.
- Lamb, M. R., Robertson, L. C., & Knight, R. T. (1990). Component mechanisms underlying the processing of hierarchically organized patterns—inferences from patients with unilateral cortical lesions. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 16, 471–483.
- Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neuroscience*, 23(11), 571–579.
- Lawson, R., & Humphreys, G. W. (1999). The effects of view in depth on the identification of line drawings and silhouettes of familiar objects. *Visual Cognition*, 6(2), 165–195.
- Lee, T. S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences*, 98(4), 1907–1911.
- Lhermitte, F., & Beauvois, M. F. (1973). A visual-speech disconnection syndrome: Report of a case with optic aphasia, agnosic alexia and colour agnosia. *Brain*, 96, 695–714.
- Lissauer, H. (1890). Ein fall von seelenblindheit nebst einem beitrage zur theorie derselben. (A case of visual agnosia with a contribution to theory). *Archiv Fur Psychiatrie und Nervenkrankheiten*, 21, 222–270.
- Liu, Z., Jacobs, D., & Basri, R. (1999). The role of convexity in perceptual completion: beyond good continuation. *Vision Research*, 39, 4244–4257.
- Mapelli, D., & Behrmann, M. (1997). The role of color in object recognition: Evidence from visual agnosia. *Neurocase*, 3, 237–247.
- Marotta, J. J., McKeeff, T., & Behrmann, M. (2002). The effects of inversion and rotation on face processing in prosopagnosia. *Cognitive Neuropsychology*, 19(1), 31–47.

- Mattingley, J. B., David, G., & Driver, J. (1997). Pre-attentive filling in of visual surfaces in parietal extinction. *Science*, 275, 671–674.
- McMullen, P. A., Fisk, J. D., Phillips, S. J., & Maloney, W. J. (2000). Apperceptive agnosia and face recognition. *Neurocase*, 6, 403–414.
- Mendola, J., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. H. (1999). The representation of real and illusory contours in human cortical visual areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience*, 19, 8560–8572.
- Moore, C., & Egeth, H. (1997). Perception without attention: Evidence of grouping under conditions of inattention. *Journal of Experimental Psychology: Human Perception and Performance*, 23(2), 339–352.
- Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, 9(5), 555–604.
- Mycroft, R., Behrmann, M., & Kay, J. (2003). *Letter-by-letter reading in visual agnosia*. Manuscript in preparation.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9, 353–383.
- Oßwald, K., Humphreys, G. W., & Olson, A. (2002). Words are more than the sum of their parts: Evidence from letter-by-letter reading in normal and alexic readers. *Cognitive Neuropsychology*, 19(8), 675–695.
- Palmer, S. E. (1999). *Vision science: From photons to phenomenology*. Cambridge, MA: MIT Press.
- Palmer, S. E. (2003). Understanding perceptual organization and grouping. In R. Kimchi, M. Behrmann, & C. Olson (Eds.), *Perceptual organization: Behavioral and neural processes*. Hillsdale, NJ: Erlbaum.
- Palmer, S. E., & Brooks, J. L. (2000). *Common fate as a determinant of figure-ground organization*. Manuscript submitted for publication.
- Palmer, S., Neff, J., & Beck, D. (1996). Late influences on perceptual grouping: Amodal completion. *Psychonomic Bulletin and Review*, 3(1), 75–80.
- Palmer, S. E., & Rock, I. (1994a). On the nature and order of organizational processing: A reply to Peterson. *Psychonomic Bulletin and Review*, 1, 515–519.
- Palmer, S. E., & Rock, I. (1994b). Rethinking perceptual organization: The role of uniform connectedness. *Psychonomic Bulletin and Review*, 1(1), 29–55.
- Pennafather, P. M., Chandna, A., Kovács, I., Polat, U., & Norcia, A. M. (1999). Contour detection threshold: repeatability and learning with “contour cards.” *Spatial Vision*, 2(3), 257–266.
- Peterhans, E., & von der Heydt, R. (1991). Subjective contours—Bridging the gap between psychophysics and physiology. *Trends in Neuroscience*, 14(3), 112–119.
- Peterson, M. A. (2003). On figures, grounds and varieties of surface completion. In R. Kimchi, M. Behrmann, & C. Olson (Eds.), *Perceptual organization in vision: Behavioral and neural perspectives*. Mahwah, NJ: Erlbaum.
- Peterson, M. A., & Gibson, B. S. (1994). Must shape recognition follow figure-ground organization: An assumption in peril. *Psychological Science*, 9, 253–259.
- Peterson, M. A., de Gelder, B., Rapcsak, S. Z., Gerhardstein, P. C., & Bachoud-Lévi, A. C. (2000). Object memory effects on figure assignment: Conscious

- object recognition is not necessary or sufficient. *Vision Research*, 40, 1549–1567.
- Polster, M. R., & Rapcsak, S. Z. (1994). Hierarchical stimuli and hemispheric specialization: Two case studies. *Cortex*, 30, 487–497.
- Rafal, R., & Robertson, L. (1995). The neurology of visual attention. In M. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 625–648). Cambridge, MA: MIT Press.
- Rensink, R., & Enns, J. T. (1995). Preemption effects in visual search: Evidence for low-level grouping. *Psychological Review*, 102, 101–130.
- Ricci, R., Vaishnavi, S., & Chatterjee, A. (1999). A deficit of intermediate vision: Experimental observations and theoretical implications. *Neurocase*, 5, 1–2.
- Riddoch, M. J., & Humphreys, G. W. (1987). A case of integrative visual agnosia. *Brain*, 110, 1431–1462.
- Riddoch, M. J., Humphreys, G. W., Gannon, T., Blott, W., & Jones, V. (1999). Memories are made of this: The effects of time on stored visual knowledge in a case of visual agnosia. *Brain*, 122, 537–559.
- Robertson, L. C., Lamb, M. R., & Knight, R. T. (1988). Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *Journal of Neuroscience*, 8(10), 3757–3769.
- Rock, I., Nijhawan, R., Palmer, S. E., & Tudor, L. (1992). Grouping based on phenomenal similarity of achromatic color. *Perception*, 21, 779–789.
- Rubin, E. (1921). *Visuell Wahrgenommene Figuren*. Copenhagen: Glydenalske boghandel.
- Sekuler, A., & Bennett, P. (2001). Generalized common fate: Grouping by common luminance changes. *Psychological Science*, 12(6), 437–444.
- Shipley, T. F., & Cunningham, D. W. (2001). Perception of occluding and occluded objects over time: Spatiotemporal segmentation and unit formation. In T. F. Shipley & P. J. Kellman (Eds.), *From fragments to objects* (pp. 557–586). Amsterdam: Elsevier.
- Shipley, T. F., & Kellman, P. J. (2001) *From fragments to objects*. Amsterdam: Elsevier.
- Sparr, S. A., Jay, M., Drislane, F. W., & Venna, N. (1991). A historic case of visual agnosia revisited after 40 years. *Brain*, 114, 789–800.
- Stark, M. E., Grafman, J., & Fertig, E. (1997). A restricted “spotlight” of attention in visual object recognition. *Neuropsychologia*, 35(9), 1233–1249.
- Tarr, M. J., & Pinker, S. (1990). When does human object recognition use a viewer-centered reference frame? *Psychological Science*, 1(4), 253–256.
- Teuber, H.-L. (1968). Alteration of perception and memory in man. In L. Weiskrantz (Ed.), *Analysis of behavioral change*. New York: Harper and Row.
- Thaïs, L., & Bleser, R. D. (1992). Visual agnosia: A case of reduced attentional “spotlight”? *Cortex*, 28, 601–621.
- Vaishnavi, S., Greenberg, A., & Chatterjee, A. (1999). A preattentive visual deficit without visual agnosia. *Journal of the International Neuropsychological Society*, 5, 107.
- Vecera, S. P., & Behrmann, M. (1997). Spatial attention does not require preattentive grouping. *Neuropsychology*, 11, 30–43.
- Vecera, S. P., & O'Reilly, R. (1998). Figure-ground organization and object recognition processes: An interactive account. *Journal of Experimental Psychology: Human Perception and Performance*, 24(2), 441–462.

- von der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. *Journal of Neuroscience*, 9(5), 1731–1748.
- von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Sciences*, 224(4654), 1260–1262.
- Warrington, E. K., & Davidoff, J. (2000). Failure at object identification improves mirror image matching. *Neuropsychologia*, 38(9), 1229–1234.
- Warrington, E. K., & James, M. (1991). *The Visual Objects and Space Perception Battery*. Suffolk, UK: Thames Valley Test Company.
- Warrington, E. K., & Taylor, A. M. (1978). Two categorical stages of object recognition. *Perception*, 7, 695–705.
- Yovel, G., Yovel, I., & Levy, J. (2001). Hemispheric asymmetries for global and local visual perception: Effects of stimulus and task factors. *Journal of Experimental Psychology: Human Perception and Performance*, 27(6), 1369–1385.