Published in final edited form as:

Cognition. 2018 May ; 174: 1–18. doi:10.1016/j.cognition.2018.01.008.

Contour Interpolation: A Case Study in Modularity of Mind

Brian P. Keane

Rutgers—Robert Wood Johnson Medical School, 671 Hoes Lane West, Piscataway, New Jersey 08854, USA

Rutgers University Center for Cognitive Science, 152 Frelinghuysen Road, Piscataway, New Jersey 08854, USA

Rutgers—University Behavioral Health Care, 151 Centennial Ave, Piscataway, New Jersey 08854, USA

Abstract

In his monograph *Modularity of Mind* (1983), philosopher Jerry Fodor argued that mental architecture can be partly decomposed into computational organs termed modules, which are characterized in terms of nine co-occurring features such as automaticity, domain specificity, and informational encapsulation. Do modules exist? Debates thus far have been framed very generally with few, if any, detailed case studies. The topic is important because it has direct implications on current debates in cognitive science and because it potentially provides a viable framework from which to further understand and make hypotheses about the mind's structure and function. Here, the case is made for the modularity of *contour interpolation*, which is a perceptual process that represents non-visible edges on the basis of how surrounding visible edges are spatiotemporally configured. There is substantial evidence that interpolation is domain specific, mandatory, fast, and developmentally well-sequenced; that it produces representationally impoverished outputs; that it relies upon a relatively fixed neural architecture that can be selectively impaired; that it is encapsulated from belief and expectation; and that its inner workings cannot be fathomed through conscious introspection. Upon differentiating contour interpolation from higher order contour representational abilities ("contour abstraction") and upon accommodating seemingly inconsistent experimental results, it is argued that interpolation is modular to the extent that the initiating conditions for interpolation are strong. As interpolated contours become more salient, the modularity features emerge. The empirical data, taken as a whole, show that at least certain parts of the mind are modularly organized.

Keywords

modularity; contour interpolation; contour integration; illusory contours; amodal completion; salience

Corresponding Author: Brian P. Keane, Rutgers, The State University of New Jersey, Brian.Keane@Rutgers.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

“[Although] great and extraordinary men have gone before me...I am not without some hopes, upon the consideration that the largest views are not always the clearest, and that he who is short-sighted will be obliged to draw the object nearer, and...by a dose and narrow survey discern that which had escaped far better eyes”
 -- -- George Berkeley, (1734/1996), *A Treatise Concerning The Principles of Human Knowledge*

1. Introduction

In his seminal book *Modularity of Mind* (1983), Jerry Fodor postulated perceptual and linguistic mechanisms that can be characterized by a cluster of nine co-occurring features. Modules are domain specific in that they solve a specific computational problem and respond to a narrow range of input. They are informationally encapsulated in that the cognitive information that they bring to bear on the problem is limited in comparison to what could be deployed. Modules mature in an innately paced manner such that there will be characteristic milestones at which time one or more capacities come on line. They rely upon fixed neural circuitry that can be selectively impaired. Modules obligatorily and rapidly generate output upon receiving specific types of input. Central access to the goings-on of a module is limited in that we cannot introspectively discern the rules that a module implements. Modular outputs are also shallow; they cannot express conceptual content and certainly cannot express sophisticated phenomena such as whether an image is of a “proton trace”, to use Fodor’s example (e.g., pp. 86, 93).

Fodor’s thesis has generated enormous controversy in diverse fields such as linguistics, philosophy, anthropology, computer science, and evolutionary biology. As with many broad ranging debates in cognitive science, the topic has created more controversy than consensus. Some have argued that moral cognition, music cognition, theory of mind, or syntactic judgments take on some of the properties that Fodor originally described (Fedorenko, Behr, & Kanwisher, 2011; Haidt & Joseph, 2007; Scholl & Leslie, 1999). Others have argued that the evidence for a modular mind is scant at best and that the whole concept offers little help in cognitive science (Prinz, 2006). A problem is that the debate has been framed in very general terms with few, if any, detailed case studies. Moreover, many of the debates have drifted from Fodor’s original formulation. Some, including Fodor himself, have maintained that informational encapsulation is at the heart of modularity (Fodor, 2001), others have argued that functional (domain) specificity is the most important criterion (Barrett & Kurzban, 2006; Coltheart, 1999; Pinker, 2009), while still others have emphasized the mind’s relatively fixed and functionally specialized neural circuitry (Kanwisher, 2010). What is needed and what I provide here is a *detailed* case study of a mechanism that fits Fodor’s original and much broader formulation (Footnote: While there have indeed been case studies using Fodor’s original definition such as that by Wagemans on visual shape determination (1988, pp. 67–75), few, if any, go into detail for each feature. Moreover, the present work has the luxury of being able to draw upon a larger and more recent literature (>800 articles; see below) and thus can benefit from the full gamut of findings from modern neuroscience, psychology, and related disciplines.).

There are several reasons why it is valuable to re-inspect Fodor's original modularity thesis. One is that it directly impinges on more specific controversies in cognitive and vision science. Firestone and Scholl (2015) have vehemently argued that perception is encapsulated from high-level cognition and that alleged counterexamples suffer from serious methodological flaws. Establishing a module would obviously strengthen their position. Likewise, some have argued for the functional specialization of numerous brain regions (e.g., the fusiform face area) whereas others have upheld the opposite view (Hanson & Schmidt, 2011; Kanwisher, 2010; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). The modularity perspective, again, takes a stand. Fodorian modularity also implies that certain perceptual or cognitive abilities unfold in an orderly manner over the course of normal development, and that these are "surprisingly insensitive to deprivation of environmental information" (Fodor, 1983, p. 100). This claim too is subject to ongoing investigation (Gandhi, Kalia, Ganesh, & Sinha, 2015; M. M. Murray, Matusz, & Amedi, 2015). The relevance of modularity to these and other important questions may explain why Fodor's book has garnered over 14000 Google Scholar citations to date, with more than 500 in 2017 alone.

Another reason to value the modularity thesis is that it yields a broad theoretical framework in which to couch an understanding of the mind and from which to formulate new testable predictions. Establishing a module would raise questions such as: How or in virtue of what do the modularity features co-occur? What stimulus conditions are needed to activate a module? What happens in the brain computationally and physiologically when a process expresses or fails to express modularity features? Do modules make organisms more evolvable in the face of direct selection pressures (Clune, Mouret, & Lipson, 2013)? Are modules like tiny islands in the vast ocean of equipotentiality or are they instead like phrenological continents sprawled across neocortex? Therefore, because Fodorian modularity has ramifications for how the mind works and how it can be investigated, and because it continues to be relevant in ongoing debates, Fodor's framework should be seriously scrutinized by practicing vision and cognitive scientists.

In the upcoming discussion, I focus specifically on *contour interpolation*, which is a visual process that represents non-visible edges on the basis of how surrounding physically visible edges are spatiotemporally configured. I use the term "interpolation" in a generic sense to include any instance where multiple non-contiguous edge elements are combined to form a greater contour and where the inter-element gap must be "filled-in", that is, treated as if it contained something physically visible (Fig. 1). Examples include combining spatially segregated oriented edge segments into a unified boundary (contour integration), forming illusory contours between locally aligned elements (modal completion), completing a contour behind an occluding surface (amodal completion), and seeing a line that emerges from a series of line endings (Varin, 1971). I do not consider more exotic forms of interpolation such as when an observer must move his or her head or body to see the integrated elements, nor do I include instances of contour extrapolation (Halko, Mingolla, & Somers, 2008; Singh & Fulvio, 2005). Therefore, the focus is on the basic boundary formation process that ensues when the visual system is confronted with two or more appropriately aligned, spaced, and oriented edge elements.

Interpolation is of interest because it is a *prima facie* likely candidate for modularity. It plays a critical role in normal seeing, helping to recover the shape, number, size, and persistence of objects that linger in our field of view (Kellman & Shipley, 1991). A canonical illusory or “Kanizsa” square (Fig. 1A) is seen not as four notched circles but as four complete circles partially occluded by a shape whose color and texture matches that of the background (Fig. 1A) (Kanizsa, 1955). A partly occluded bar is seen not as two dangling objects abutting a common surface, but as a single entity poking out from behind (Fig. 1B). A shape gliding behind a holed occluder is experienced as a single, gradually-appearing object rather than as a kaleidoscope of individual elements that flash in and out of existence (Fig. 1H) (Keane, Lu, & Kellman, 2007; E. M. Palmer et al., 2006). Four line segments that translate back-and-forth orthogonally to their respective slant directions are perceived as a single orbiting diamond rather than as four unrelated motion events (Fig. 1G) (Lorenceanu & Alais, 2001; Lorenceanu & Shiffrar, 1992). These distal properties of object shape, number, size, and persistence are arguably among the most important to recover; depriving the visual system of such features would wipe out much of what distinguishes vision from the other senses. (Footnote: The spatial character of audition, while important, lacks higher spatial frequency content and thus holds less value for determining object shape, number, and size. Moreover, in contrast to haptic perception, vision recovers properties of the *distal* environment, which do not immediately impinge on the transducing organs.) If any function should be hard-wired into our cognitive architecture, interpolation should be chief among them. Underscoring interpolation’s importance is its sweeping prevalence in the animal kingdom: mice, fish, bees, sharks, newborn chicks, and countless other species all rely upon the process (Fuss, Bleckmann, & Schluessel, 2014; Kogo & Wagemans, 2013; Nieder, 2002; Nieder & Wagner, 1999; Regolin & Vallortigara, 1995).

A module should also be suspected whenever a complex function would be difficult or cumbersome to perform on the fly within behaviorally relevant time scales. Interpolation’s function again is suggestive. It impressively determines at each moment how hundreds of scene segments form contours and closed surfaces (objects) (Field et al., 1993; Hess, Hayes, & Field, 2003). Leaving this computationally daunting task to the vicissitudes of a slow and effortful “system 2” type of mechanism (Kahneman, 2011) would seem impractical given the dynamics of natural scenes and the retina’s constantly changing spatial relation to the distal layout.

A pragmatic reason to consider interpolation is that we know a lot about it. A PubMed search for a union of relevant terms yielded 863 results (terms—“contour integration”, “illusory contours”, “amodal completion”, “modal completion”, “subjective contours”, “contour interpolation”, “contour completion”, “boundary completion”; search date—9/29/2017). The search dramatically underestimates the volume of research on the topic not just because it excludes books, periodicals, and non-English journals, but also because many more generic or unusual key terms could have been included but were not, including “perceptual completion”, “visual completion”, “phenomenal contours”, “quasiperceptive contours”, “visual binding”, and “feature binding”, to name a few. A bibliography compiled over 25 years ago found 445 entries on subjective contours alone (Purghé & Coren, 1992). The jury should now be in as to whether interpolation qualifies as a module.

In what follows, I go through Fodor's nine criteria to make the case that contour interpolation fits his original description. The evidential base from which I construct my argument is necessarily broad in scope, incorporating a variety of methodologies—psychophysics, TMS, fMRI, EEG, eye movements, lesion studies, single-cell recording, two-photon calcium imaging—and drawing from a variety of subject populations—human and non-human primates, infants and adults, and persons with and without psychiatric or neurological disorders. Upon arguing for a module and upon differentiating contour interpolation from a superficially similar high-level contour representation process (“contour abstraction”), I go on to consider studies showing that at least some forms of interpolation depend on learning, top-down experience, conceptual priming, and attention. I accommodate the seemingly contradictory data by suggesting that contour interpolation is modular to the extent that the conditions for the process are favorable. When interpolated contours are rendered salient by one or more well-established stimulus manipulations, contour interpolation will take on the features that Fodor originally described. This salience constraint can be partly understood in the context of the competitive interactions hypothesis in neuroscience (Beck & Kastner, 2005; 2009; Desimone & Duncan, 1995; McMains & Kastner, 2010; 2011), according to which top-down influences become relevant when bottom-up factors fail to resolve stimulus ambiguities.

2. Evidence for a Classically Modular Interpolation Device

2.1. Interpolation is domain specific

Interpolation is domain specific in that it is dedicated to carrying out one kind of task: It determines whether spatially segregated edges belong together and also how they combine to form a continuous edge. The “how” goal is less obvious, but involves representing contours in a spatially well-defined way and treating those contours as if they were fully visible in front of the eyes (Pessoa, Thompson, & Noe, 1998). Consider, for example, a fat/thin shape discrimination task in which subjects discriminate quartets of pac-men that either form or do not form Kanizsa shapes (Ringach & Shapley, 1996). Placing distractor lines near the illusory contours worsens discrimination performance but the effect disappears when the pac-men are rotated to prevent illusory shape formation. This suggests that the regions on or near the interpolated boundaries are being queried as if they contained shape contour information (Ringach & Shapley, 1996; J. Zhou, Tjan, Zhou, & Liu, 2008). Similar findings have been uncovered in a reverse correlation study: Contrast noise near interpolated but not fragmented shape boundaries alters discrimination even though such regions are objectively useless (Gold & Shubel, 2006; Gold, Murray, Bennett, & Sekuler, 2000; Keane et al., 2007). In a dot localization paradigm, subjects determined whether a briefly appearing dot appeared within or outside of an interpolated shape. Despite brief presentation times (200 ms) and a disruptive backward mask, subjects were remarkably precise and accurate in judging the dot's location (e.g., see Fig. 2C) (Guttman & Kellman, 2004). When the inducing edge elements (“inducers”) were badly blurred or misaligned, the localization errors and imprecision increased appreciably (Guttman & Kellman, 2004; Stanley & Rubin, 2003). Ramachandran and colleagues viscerally demonstrated interpolation's sensitivity to filled-in regions by placing a Kanizsa shape on top of a seemingly irrelevant checkerboard texture: the shape stood out more clearly when the texture and contours perfectly aligned, but less

clearly otherwise (Ramachandran, Ruskin, Cobb, Rogers-Ramachandran, & Tyler, 1994 see Fig. 2D–F). These behavioral and phenomenological findings cohere with neurophysiological studies, which have found that V1 and V2 cells respond strongly to real and interpolated boundaries but very little to contours that are nudged away from the receptive field centers (Lee & Nguyen, 2001; Peterhans & Heydt, 1989) (See Fig. 2A). The foregoing suggests that interpolation augments sensitivity to a series of specific locations along the connecting path and that physically disturbing the appearance at those locations either worsens the precision of the contour or changes its perceived position or shape (Keane, Lu, Papathomas, Silverstein, & Kellman, 2013; Ringach & Shapley, 1996).

To some, the filling-in that accompanies interpolation might seem obvious, but it really should not be taken for granted. It did not have to be this way. The visual system could just as well have specified *that* elements belong together without also tracing the exact path that linked the elements or without causing observers to treat the path as if it contained something real. In other contour grouping variants—the grouping of orthogonal elements (“ladder” stimuli), for example—the elements do not form a well-defined edge along a precise boundary and perhaps as a result are not as easy to pick out when embedded within a sea of randomly oriented elements (Bex, Simmers, & Dakin, 2001; Field et al., 1993; Vancleef, Wagemans, & Humphreys, 2013). Grouping by other spatially punctate features (e.g., common orientation) does not incline subjects to rely upon a contiguous series of locations between the elements grouped. As we shall see in Section 2.4, observers can group some non-interpolating edge configurations without having any precise idea as to how the elements connect (see Fig. 5). Therefore, to summarize, the goal of interpolation is to decide not only which contour elements fit together but also *how* they fit together by filling-in between elements in a spatially precise and behaviorally consequential way.

The domain specificity of interpolation is also evident in that it operates over a highly restricted set of inputs. Scenes that lack fragmentation, that consist of smoothly varying surfaces, or that contain highly blurred contour elements will not interpolate. Scenes that do contain appropriate (e.g., step-edge) elements *may* interpolate, but only under very specific circumstances. If adjacent elements are scattered far from one another, if they are severely misaligned, or if they require a large turning angle (typically larger than 90 degrees in static displays), interpolation will not ensue. A first pass on the stimulus requirements for interpolation was expressed in the early part of the 20th century as the Gestalt law of good continuation (Wertheimer, 1923/2012). The law says very simply that, all else equal, two elements will be grouped when they can be joined by a smooth contour (S. E. Palmer, 1999). Kellman and Shipley formalized the geometric conditions for good continuation with a “relatability” theory, according to which edges interpolate when they can be connected by a smooth curve that monotonically bends no more than 90 degrees (Kellman & Shipley, 1991). The construct of relatability has been expanded to account for when edge elements are separated in stereoscopic depth or by temporal gaps (Kellman et al., 2005; E. M. Palmer et al., 2006). Others have argued for a related “association field” theory, which refers to the conditions under which a subset of oriented sinusoidal elements (Gabor) form an elongated contour, although the exact geometric determinants that veto or approve the process were never made explicit (Field et al., 1993). Geometric theories of interpolation have been bolstered by studies on natural scene statistics, which show that the likelihood that edge

elements will belong to the same contour can be strongly predicted by their relative proximity and alignment (Elder & Goldberg, 2002; Geisler, Perry, Super, & Gallogly, 2001).

Notwithstanding the repeated attempts of generations of vision scientists, there is not yet any single theory that fully explains when edge elements will co-connect. The process has turned out to be more complex and nuanced than what the early pioneers in Gestalt psychology originally thought. As an example, the visual system may be more permissive in its binding practices when elements are presented with low contrast, low spatial frequency, high temporal frequency, or high eccentricity (properties traditionally associated with the magnocellular pathway, Lorenceau & Alais, 2001). Adjacent elements that share spatial frequency, phase, or chromaticity may be more readily integrated versus those that differ in these qualities (Dakin & Hess, 1998; Field, Hayes, & Hess, 2000; Mullen, Beaudot, & McIlhagga, 2000). Subtle alterations to junction structure (Rubin, 2001)—such as rounding the corners of a T junction—can greatly change how interpolated contours are experienced and acted upon (see also Fig. 7D below) (Keane, Mettler, Tsoi, & Kellman, 2011; Lorenceau & Shiffrar, 1992; E. M. Palmer et al., 2006; Rubin, 2001). Global layout also matters: Four plus signs centered on the vertices of a square fail to yield the appearance of a contour as compared to four pac-men similarly arranged, even though the physically visible lines that participate in the contour are the same in each case (Kanizsa, 1976; Leshner, 1995; Rock, 1983; Sekuler, Palmer, & Flynn, 1994; van Lier, van der Helm, & Leeuwenberg, 1994) (footnote: For a model of how global layout influences border ownership and illusory contour formation, see work by Kogo and colleagues (2013; 2010)). Other contributing factors include increasing the total contour length, connecting opposite ends of a contour (so as to form an enclosed shape), minimizing curvature changes (of an open contour), and ocularily tracking the centroid of a partly visible shape (Braun, 1999; Elder & Zucker, 1993; Hafed & Krauzlis, 2006; Kovács & Julesz, 1993; Pettet, 1999). Just as linguists must work hard to discern the eligible phonemes and computational rules that ultimately lead to the well-formed syntax of a native speaker, so too must vision scientists carefully design experiments to figure out the features and compositional rules that govern interpolation.

2.2. Interpolation is fast

Interpolation bridges edge elements with astonishing speed. Lee and Nguyen (2001) showed that superficial V2 cells in awake monkeys responded differentially to illusory and amodal contours relative to a control no-contour condition within 50 ms of stimulus onset; a peak response was observed in the following 100 ms (See Fig. 2). In a dot localization task, human adults needed 120 ms to optimally decide whether a transient dot fell within or outside of an interpolated shape (Guttman & Kellman, 2004). Scalp recorded visual evoked potentials demonstrated an intact illusory contour formation signature within 88 and 100 ms of stimulus onset over lateral occipital areas (M. Murray et al., 2002). A behavioral study using a disruptive backward mask found that subjects needed 100 ms of stimulus presentation to reliably detect an illusory-contour-defined shape (R. I. Reynolds, 1981). Behavioral experiments with monkeys have shown that 30–60 ms of presentation time was needed to detect an integrated Gabor boundary that was followed immediately by a disruptive backward mask (Mandon & Kreiter, 2005). A caveat in these investigations is that interpolation may be slower in the presence of potentially competing edge elements (as in

noisy contour integration displays), when interpolated elements are more distantly spaced, when there is a forward mask (prior to stimulus onset), when the elements are presented with degraded features (e.g., a luminance noise field), or when the interpolated elements are nonenclosing or non-dynamic (Gold & Shubel, 2006; Mandon & Kreiter, 2005; E. M. Palmer et al., 2006). However, as argued further below, when the conditions for interpolation are ripe, interpolation effects materialize within the first 100 ms and continue to strengthen within the following 50 ms. It is worth emphasizing in passing how impressive this achievement truly is. Contour integration displays typically contain hundreds of elements. The visual system registers not just the orientation and position of each element, and not just their spatial relation to one another, but also a host of non-geometric properties, such as relative phase, spatial frequency, closure, and element dynamics that modulate contour salience. Because the process happens so often, so quickly, and so effortlessly, it is easy to underestimate the computational prowess involved.

2.3. Interpolation is obligatory

Interpolation is also modular in that it produces its output in an automatic, mandatory fashion (Vandenbroucke, Fahrenfort, Sligte, & Lamme, 2014). In a single unit study, figures delineated by abutting line gratings elicited similar responses in monkey V1 and V2 regardless of whether those figures were actually attended (Marcus & Van Essen, 2002). V1/V2 cell responses to interpolated contours have been documented with fully anaesthetized animals (Grosf, Shapley, & Hawken, 1993; Heydt, Peterhans, & Baumgartner, 1984; Sheth, Sharma, Rao, & Sur, 1996). Computational models, based completely on bottom-up, local-grouping mechanisms, accurately predicted human performance on certain interpolation tasks (Geisler et al., 2001; Kalar, Garrigan, Wickens, Hilger, & Kellman, 2009). Neural activation (BOLD response) to a Kanizsa shape was shown to be the same regardless of whether or not it was overtly noticed (Vandenbroucke, Fahrenfort, Sligte, & Lamme, 2014). In an attentional neglect investigation, a parietal lobe patient ignored contralesional hemifield objects that were co-presented with ipsilesional hemifield objects; the neglect was largely removed if interpolation could connect the objects across hemifields (Mattingley, Davis, & Driver, 1997). An electrophysiological investigation of Kanizsa shape discrimination found that the magnitude and scalp topography of the initial VEP response (124–186 ms) remained constant regardless of whether subjects were correct in their shape judgment (M. M. Murray, Imber, Javitt, & Foxe, 2006). More impressively, other studies have shown that interpolation ensues even when contrary to task demands. Subjects attempting to track multiple target objects among moving distractors (Pylyshyn & Storm, 1988), track less well when the distractors and targets form illusory or occluded contours (Fig. 3) (Erlikhman, Keane, Mettler, Horowitz, & Kellman, 2013; Keane et al., 2011; Pylyshyn & Storm, 1988). Subjects who discriminate fat and thin Kanizsa shapes perform worse when distractor lines are placed near the illusory boundaries; the effect persists even when subjects are explicitly and repeatedly told to ignore the lines throughout the experiment (Keane et al., 2013). In visual search, interpolation can actively work against the observer, transforming distractors into target lookalikes, necessitating a slow serial target hunt (Davis & Driver, 1998; He & Nakayama, 1992).

2.4. Interpolation is cognitively encapsulated

If interpolation is mandatory, then it should also be impervious to the effects of belief, desire, expectation, and other higher order cognitive states—that is, it should be cognitively encapsulated. Interpolation again fits the bill. Even though common experience and contextual regularities should incline us to see a fourth lobe in Fig. 4A or an octagon in Fig. 4B, interpolation demands the percept of an irregular shape in each case. And even though we disbelieve in 7-foot human arms and impossibly structured cubes, amodal completion compels us to behold such images (Fig. 4C,D). Psychophysical data lend further support. In a “motion linking” paradigm, a partly occluded polygon orbits upright about a central point (without rotating), and subjects report whether the shape moves clockwise or counterclockwise (Lorencean & Alais, 2001; Lorencean & Shiffrar, 1999). Accuracy of the motion judgments did not improve when subjects were told immediately before each trial as to the true shape of the completed object (Fig. 4E). Thus it appears that subjects cannot use prior knowledge to amodally complete a figure into a rigidly moving object.

The foregoing does not mean that cognitive expectation is always irrelevant for constructing visual shape from fragmentary information. Anybody who has witnessed RC James’ classic Dalmatian dog example (Fig. 5A) knows that there is some problem-solving going on here—hints about the semantic category will steer the observer to the right answer (Gregory, 1970; Rock, 1983). But solving the puzzle is not a matter of slipping conceptual clues down to a low-level contour linking process. Indeed, it is doubtful that interpolation plays any significant role at all. Neighboring pairs of edge elements either i) are not appropriately geometrically arranged (not “relatable”), ii) have inadequate support ratio (only a small proportion of the total edge length is physically specified), or iii) lack the junction structure that signals when one contour is occluding or blending in with another surface. If the mystery animal were subtly altered so that there were a smooth series of interspersed relatable edge elements along the outlying boundaries, the image would become instantly recognizable and no more noteworthy than those first documented by Gaetano Kanizsa in the 1950s (Fig. 5B). Therefore, it is not the fragmentation or the two-tone nature of the image that makes recognition of the Dalmatian so difficult; it is the fact that the image prohibits modal or amodal completion. Our brains are left with no choice but to seek conceptual assistance.

The Dalmatian dog is but one example of a broader class of phenomena in which high-level knowledge parses and completes ambiguous or vague images into cohesive and meaningful units. The process that generates such boundaries might be called *contour abstraction*. Examples of abstraction abound in psychology. Mooney figures (Mooney & Ferguson, 1951) are similar to the Dalmatian, but are blurred prior to two-tone conversion (Imamoglu, Kahnt, Koch, & Haynes, 2012). The blurring dissolves high spatial frequency texture elements that might be confused with a global contour, but also removes T and L junctions, which signal occlusion or camouflage (Rubin, 2001). Pareidolia-inducing images—which cause us to see meaningless shapes as familiar—may also activate contour abstraction. Seeing a cloud as a rabbit or a piece of toast as a holy figure involve carving the figure into reticulated parts that are not given via interpolation (Voss, Federmeier, & Paller, 2012) (see Fig. 5D). Implicit beliefs or attitudes may interpret a symmetric blob of a Rorschach image

as a coherently structured object, introducing new contours where none were seen before (Rorschach, 1921).

There are also hybrid examples where contour interpolation and contour abstraction work in tandem. In a classic object recognition paradigm, subjects try to name the objects depicted in partly visible line drawings (see Fig. 5H.). The spatial distribution of the fragmentation decides the extent to which interpolation plays a role. If the available line fragments are mostly relatable to one another and if the support ratio of the edges is reasonably good (T. F. Shipley & Kellman, 1992), then the task becomes easy—interpolation does all the work. If only non-relatable edges are visible, if the support ratio is very low, or if the junction structure is incompatible with interpolation, subjects will resort to the slower, more effortful process of matching memory templates to what's in view, perhaps by first recognizing a small part of the stimulus and then thereby inferring the rest of the image (Biederman, 1987). The same holds true for other types of image fragmentation, including bubble stimuli, in which object parts are selectively sampled through randomly distributed Gaussian windows; luminance noise paradigms, where small bits of edge elements may be chipped away by stochastic luminance fluctuations (Gosselin & Schyns, 2001; Pratte, Ling, Swisher, & Tong, 2013); and fragmented object recognition tasks, in which randomly selected segments of line drawings are added or torn away to render an object more or less recognizable (Sehatpour, Molholm, Javitt, & Foxe, 2006; Sehatpour et al., 2008). In all of these cases, unless the fragmentation is strategic, the aforementioned paradigms will not yield information solely about interpolation.

The varieties of contour abstraction are pointed out because they present a sort of red herring, misleading researchers into thinking they are studying one process when in fact they are studying another. It is understandable to confuse the two—both allow us to represent the entirety of an object from partial information and both are dependent upon the geometry of edge elements. But just underneath the similarities lurk stunning differences. Foremost, abstracting contours involves representing an object *as* something familiar or at least as something that was initially entertained on a conceptual level. Subjects first have an idea of what it is that they are seeing perhaps by using a local cue (e.g., the leg of the Dalmatian), and then envision the rest of that shape using knowledge of how that object typically appears (Biederman, 1987). Interpolation works in the opposite way. It first fills-in missing boundaries from locally aligned edge elements, and then delivers a well-defined contour or shape representation that may or may not lead to recognition. If the above sketch is accurate and in particular if interpolation, but not abstraction, operates independently of object recognition, then the former should be carried out more quickly and with less difficulty than contour abstraction. There is some evidence for this implication. Kanizsa shapes may be detected faster relative to non-interpolating “inferred” shapes (Ritzl et al., 2003). Partly visible line drawings of ordinary objects are recognized more accurately and rapidly when the visible line segments are relatable rather than unrelatable (Biederman, 1987). Another difference between abstraction and interpolation is that the former is domain general, depending much less on edge element geometry and appearance. I may see the head of a dog peering from behind a surface and on that basis infer the approximate location of the rest of its body (Kellman et al., 2005) (Fig. 5E). In a dark room, I may fail to see *any* part of the dog but still use my knowledge of where and how the dog likes to sit in order to represent

(imagine) its approximate boundaries. Contour abstraction differs also in that it strongly hinges on processing within prefrontal cortical structures. Neuroimaging studies have shown that when subjects consciously recognize Mooney faces, there is greater functional connectivity between dorsolateral prefrontal cortex and extrastriate cortex (Imamoglu et al., 2012); in MEG studies, the same recognition corresponds with greater frontoparietal activity in the high gamma range (60–120 Hz) (Sun et al., 2012). In human intracranial recordings, apprehending the objects depicted in randomly degraded line drawings activates the hippocampal formation, occipitotemporal cortex, and the lateral prefrontal cortex (Sehatpour et al., 2008). Although orbitofrontal cortex and some frontal areas may be active during visual shape completion tasks (Halgren, Mendola, Chong, & Dale, 2003), these structures are probably not necessary to link simple contours (Ciaramelli, Leo, Del Viva, Burr, & Ladavas, 2007). Contour abstraction is also more susceptible to the will of the observer. Different shapes or contours can be readily extracted from a single ambiguous image (e.g., Fig. 5F) but this is not so for well-defined, highly salient contour stimuli (e.g., Fig. 1D). A final difference is that abstracted contours are represented with more positional uncertainty. As already noted, subjects can precisely and accurately assess when a briefly presented dot falls within or outside of a classic Kanizsa shape; the same is not true when the inducers are either misaligned, rounded, or replaced with dotted arrows so that subjects must cognitively infer the contour (Fig. 2C) (Guttman & Kellman, 2004; Stanley & Rubin, 2003). Taken together, contour abstraction is not a modular process. In fact, it is the exact opposite—a central or horizontal process, to use Fodor’s terminology. When presenting putative counterexamples to an encapsulated interpolation process, the two must not be conflated.

The abstraction/interpolation distinction is not a post-hoc attempt to save the modularity thesis from falsification; its existence has been suggested by leading vision scientists at least since the 1960’s. Michotte and colleagues (1964) argued that amodal completion has a clear “perceptual character” in that it relies on the Gestalt “laws of structural organization” without regard to cognitive expectation; such a process was claimed to differ from an “analogous” operation, which creates “vague and indeterminate” shape representations on the basis of object familiarity (as when seeing a half-occluded face as a whole; pp. 182–184, 203) (Footnote: For a review of Michotte’s contributions to perceptual and cognitive psychology, including contour completion, see Wagemans, Scholl, and Pylyshyn, (2006)). Gaetano Kanizsa distinguished “cognitive integrations” from “perceptual interpolations”, where the former was subject to the observer’s will and unconstrained by the incoming stimulus input (Kanizsa, 1985), and the latter operated “according to autonomous principles of organization” and “without regard to logic, expectations, and knowledge” (pp. 31, 33). Biederman (1987) described a difference between “recoverable” and “non-recoverable” partly visible line-drawings of objects (Fig. 5H). In the former, the mid-segments of contours are removed and the object’s components (geons) can be quickly and rapidly recognized via filling-in (p. 133); in the latter, interpolation is absent and subjects must laboriously figure out the object from other cues (p. 136). More recently, Kellman and colleagues coined the related notion of “recognition from partial information” or RPI for short, where subjects first recognize an object part and then infer that shape’s global boundary (Fig. 5E). According to Kellman and colleagues, RPI activates a memory representation of an entire form but this does not interfere with lower-level contour linking

(Kellman et al., 2005; Kellman, Guttman, & Wickens, 2001). In short, despite the venerable origins of the interpolation/abstraction distinction and despite its continued relevance in contemporary psychological research, the distinction is rarely made explicit and is often overlooked, leading to confusion for those seeking to evaluate interpolation's alleged encapsulation.

To consider a specific example of how the interpolation/abstraction distinction has led to confusion, it is worth briefly considering—as an aside—a controversy concerning a classification image or reverse correlation technique employed in the perception literature (Ahumada, 1996; for a review, see Murray, 2011). Gold et al (2000) investigated contour filling- by having subjects repeatedly discriminate noise embedded fat and thin shapes, whose contours were either interpolated (illusory/amodal), luminance-defined (real), or fragmented (absent). A spatial map of the correlations between noise pixel contrast and observer response indicated that the noise altered discrimination when appearing near luminance-defined and interpolated contours but not when appearing near broken or fragmented contours. The influential noise regions were thought to signify the receptive field locations of cells in early visual cortex. Others have since disputed this interpretation and have argued that the classification images reflect the high-level shape templates that subjects hold in mind as they perform the task (B. L. Anderson, 2007; Gosselin & Schyns, 2003). In support of the objection, Gosselin and Schyns (2003) conducted an experiment in which subjects determined whether a complex noise-embedded object (e.g., a letter) was present or absent on each trial. Unbeknownst to the subjects, only Gaussian noise fields were shown. Despite the subjects never having seen the stimulus on any trial, the resulting classification images contained shapes that vaguely resembled the target objects (Gosselin & Schyns, 2003).

It is first pointed out that Gosselin and Schyns results do not seriously threaten Gold et al.'s original interpretation of the classification images. First, when subjects discriminate contours embedded in dynamic luminance noise, the noise alters responses earlier for luminance-defined than for illusory contours (Gold & Shubel, 2006; Keane et al., 2007), which is consistent with what we know about the time course of the two contour types (Guttman & Kellman, 2004; Lee & Nguyen, 2001; M. M. Murray et al., 2006). Second, the contrast polarity of the classification image features is best explained in terms of an accompanying lightness induction process (Keane et al., 2013), which again would not be predicted if cognitive strategy were dominating the images. Third, whereas the images of Gosselin and Schyns differ considerably from observer to observer, there is remarkable inter-subject consistency in the spatial position and precision of the classification image contour features (Gold et al., 2000), which provides yet another footprint of mid-level vision (Lee & Nguyen, 2001).

The results of Gosselin and Schyns are nevertheless important because they demonstrate a bonafide confound that must be reckoned with when applying the classification image technique; they convincingly show that accompanying arguments must be provided as to why high-level influences are not unduly generating the classification image features of interest. In Gold et al.'s study, two contour formation processes could theoretically be at play: interpolation, which will occur when the inducing edges are visible and relatable; and

abstraction, which arises on trials when the luminance noise cancels out or strongly spatially deviates an inducing edge, or when the instructions cause observers to imagine connecting boundaries. This confound is in no way specific to classification images but will arise whenever the image degradation is randomly applied, such as in bubble stimuli or fragmented line drawings (Fig. 5G,H). In each paradigm, if the goal is to provide the cleanest possible picture of interpolation, the solution is to ensure that the conditions for the process are intact on every trial.

Contour abstraction aside, another important role of cognitive expectation is that it helps decide how interpolated contours are used for shape discrimination. As already noted, sets of individually rotated pac-men can be better distinguished when the composing elements are relatable rather than unrelatable (Guttman & Kellman, 2004; Pillow & Rubin, 2002; Ringach & Shapley, 1996; Rubin, Nakayama, & Shapley, 1997; J. Zhou et al., 2008). The reason for this relatability advantage has not been articulated but likely owes to the fact that the largest positional difference between a convex and concave illusory contour is bigger than the largest difference between an inducer that forms each of those alternatives. What's important for the present discussion is that this relatability advantage is not guaranteed. For example, when observers were biased through instructions and pictures to see the relatable inducers as disconnected (an “ungroup” strategy), performance worsened relative to when they were biased to see the configuration as unitary (“group” strategy) (Keane, Lu, Papathomas, Silverstein, & Kellman, 2012). The ungroup strategy per se was not more difficult, since it did not lower performance in the unrelatable condition. The ungroup strategy also did not interfere with illusory contour formation since, regardless of strategy, distractors imposed a negative effect only in the relatable condition (See Fig. 6). Therefore, although cognitive expectation cannot prevent or induce the formation of illusory contours, it does strongly influence how well those contours are used for shape discrimination.

Additional evidence for the dissociability of illusory contour formation and illusory shape discrimination derives from psychophysical and electrophysiological investigations of schizophrenia. The illness is defined in terms of delusions, hallucinations, disorganized thought, erratic behavior, and negative symptoms, but is also increasingly viewed as a disorder that disrupts aspects of perception and cognition (Kahn & Keefe, 2013; Silverstein & Keane, 2011). As a most relevant example, patients engaging in a fat/thin task performed as if they steadfastly adopted an ungroup strategy: they responded normally to distractor lines (being affected in the relatable condition only), performed near normally in the unrelatable condition, but were worse at discriminating illusory shapes (Keane, Joseph, & Silverstein, 2014b). Intriguingly, patients most clearly demonstrating these patterns were those who suffered from conceptual disorganization, a clinical symptom that impedes clear thinking and verbal communication. In a methodologically similar follow-up study, schizophrenia patients benefitted normally from improvements in illusory contour salience, despite an overall worse ability to distinguish Kanizsa shapes (Keane, Erlikhman, Kastner, Paterno, & Silverstein, 2014a). It may seem counterintuitive to tease apart the logically linked processes of illusory contour and shape formation, but other research teams have reached the same conclusion with different methods. Foxe and colleagues (2005), for example, had schizophrenia patients and healthy controls determine whether or not a Kanizsa shape was present on each trial. Their patients demonstrated an intact early

electrophysiological signature of illusory contour formation (106–194 ms) over lateral occipital regions but an aberrant late “closure- negativity” (N_{cl}) waveform (240–400 ms) over right inferior frontal regions. In a non-clinical electrophysiological study of fat/thin shape discrimination, Murray et al. (2006) found that—at earlier time epochs (124– 186 ms; N_1 component)—response magnitude and scalp topography of the VEP depended on the presence of illusory contours but not on response accuracy. At later time epochs (330–406 ms; N_{cl} component), these same measures strongly depended on discrimination accuracy. The embraced conclusion was that an early boundary formation is automatic and dissociable from a later response-dependent visual shape completion stage. Additional corroborating evidence derives from a study with macaque monkeys: ablations applied to inferior temporal cortex (IT) impaired the discrimination of illusory-contour defined shapes but not luminance defined shapes (Huxlin, Saunders, Marchionini, Pham, & Merigan, 2000), indicating that IT may help observers harness illusory contours to discern subtle shape differences. If a two-stage model is correct—which I believe the data support— then there is no contradiction in saying that observers form illusory contours at an early encapsulated stage and use those contours with varying degrees of success at a later conceptual stages for global shape categorization.

To summarize, high-level cognitive states—beliefs, biases, or expectations—allow contours to be abstracted from impoverished or ambiguous object images and they influence how effectively such contours can be use for higher-level tasks such as shape discrimination. Nevertheless, the evidence suggests that high-level knowledge cannot block or launch interpolation when the edge geometry would ordinarily lead to the opposite outcome.

2.5. Interpolation is innate and matures predictably through adolescence

A fifth feature of interpolation is that it develops in a predictable way, emerging first at birth and developing through early adolescence. A key type of evidence derives from infant looking time behavior. When shown a smoothly-translating, partly-occluded rod and then either a fragmented or complete rod, infants aged between 2 and 4 months gaze longer at the fragmented rod (Johnson & Aslin, 1996; Kellman & Spelke, 1983). The accepted explanation is that visual completion leads to a single object expectation, violation of which leads to prolonged visual inspection. Smoothly translating stimuli do not evoke visual completion behavior in neonates but this is plausibly because the ability to detect speed and motion direction is immature prior to two months of age (Wattam-Bell, 1991; 1996) (E. Valenza, Leo, Gava, & Simion, 2006). Inducers that flicker and move stroboscopically may be necessary. With such stimuli, newborn infants exhibit looking time behavior that resembles that of the 2–4 month-old infants, not only for partly occluded contour stimuli but also for Kanizsa-style objects (E. Valenza & Bulf, 2007; 2010).

Results with neonates have been corroborated by studies on congenitally blind adults who had their sight recently restored (Ostrovsky, Meyers, Ganesh, Mathur, & Sinha, 2009). One adult and two children initially had visual acuity of either 20/900 or light perception (LP), and received optical correction or cataract surgery to improve their vision to at least 20/120. After visual restoration, all three individuals were able to trace a segmented contour embedded in noise and all three could amodally complete an outline of a triangle that

dynamically overlapped with an outline of a square. Considering that one of these individuals was an adult who recovered sight within two weeks post-surgery, the evidence again suggests an innate ability to interpolate and create structure from sparse distal arrays.

For normally sighted individuals, contour interpolation ability continues to develop in a predictable way through early adolescence, at least when the integrated stimuli are non-dynamic, noisy, or more distantly separated (Kovács, 2000). In EEG experiments, an enhanced N1 component was taken as a signature of illusory contour formation; this waveform arose in children 6–9 years of age, but the latency shortened and the time-window narrowed for older age groups (Altschuler et al., 2014). Others have shown that the ability to discriminate static illusory shapes continues to mature up through age 12 (Hadad, Maurer, & Lewis, 2010). In cross-sectional studies, the capacity to detect noise-embedded, enclosed Gabor shapes improves from 5 to 19 years of age, especially for more distantly spaced elements (K. Benedek et al., 2010; Kovács, Kozma, Fehér, & Benedek, 1999). Additional research is needed to determine whether the interpolation's developmental milestones are as fixed and predictable as those reached in other more studied areas of cognitive and motor development (e.g., gross motor skills, language acquisition, etc.).

2.6. Interpolation yields shallow outputs and restricts introspective access

A sixth feature of a module is that its outputs are shallow, viz., they lack conceptual content. According to Fodor, this means that they cannot express sophisticated events like what a particle physicist might observe, such as “proton trace” (Fodor, 1983, p. 93). While it is true that the governing rules of interpolation are complex, the resulting representational content is surprisingly basic. The representations indicate what edges belong together, how they join across space, and perhaps also how they persist over time (E. M. Palmer et al., 2006). But the representations do not specify much more than this. The representations are not jeopardized if a subject's conceptual framework is distorted, fragmented, biased, or altogether absent. Interpolation proceeds normally in schizophrenia patients with disorganized thinking (Keane et al., 2014b), in healthy individuals with a bias to interpret objects as fragmented (Fig. 6) (Keane et al., 2012), and in newborn infants or phylogenetically primitive organisms, with little or no conceptual resources (Nieder, 2002; E. Valenza et al., 2006). The paths traced out by interpolation do not depend on whether the contour was seen before, whether it is expected, or even whether it is physically possible, further suggesting that process is not conceptually mediated. Despite being shallow, the interpolation's outputs are not *too* shallow: they are ordinarily accessible phenomenologically at least in non-pathological cases where the subject has plentiful time to inspect or re-inspect the contours. The outputs of interpolation can generally support the more sophisticated sort of cognitive inferences that Fodor originally envisioned.

Central access to the goings-on of interpolation is also limited. According to Fodor, the mind's architecture consists in ascending levels of representation, starting from the level of input transducers stretching all the way up to occurrent thought and complex object recognition. Through effort and introspection, we can reach down into the representative hierarchy to figure out what is going on, but only so far; at some point, the introspective hand will bump into a module's cold exterior and the informational content will become off-

limits. Therefore, we vision researchers cannot fathom through introspection the integrative rules governing interpolation; we must instead perform experiments to determine what those rules are. We must painstakingly construct new experiments to understand all the properties that weaken, strengthen, spatially deviate, or otherwise alter the process.

2.7. Interpolation has a well-defined neural substrate that may be selectively impaired

Interpolation has a well-defined neurobiological substrate that relies upon a plexus of long-range horizontal excitatory connections between orientation-tuned spatial frequency filters or end-stopped cells in V1/V2. Higher-visual areas—most specifically V4 or lateral occipital complex (LOC)—may shuttle signals to and from lower-level retinotopic areas to sharpen or refine the contours that have already been formed in grosser fashion (M. Chen et al., 2014; Cox et al., 2013). The methodologies whose data have converged on these brain structures (hereafter the “classical” structures) include fMRI (Altmann, Bühlhoff, & Kourtzi, 2003; Seghier & Vuilleumier, 2006), EEG (M. M. Murray et al., 2006), behavioral psychophysics (Pillow & Rubin, 2002), single-unit recording (R Von der Heydt, Peterhans, & Baumgartner, 1984; Lee & Nguyen, 2001; Peterhans & Heydt, 1989), MEG (Halgren et al., 2003), lesion studies (see immediately below), and two photon calcium imaging (Iacaruso, Gasler, & Hofer, 2017). Alternative regions—although less well-established and probably secondary to contour interpolation—may also be implicated: inferotemporal cortex (for discriminating interpolated contours, Huxlin et al., 2000), area V3b or KO (for dynamic interpolation, Seghier et al., 2000) and orbitofrontal cortex (possibly for matching the interpolated stimulus to shape templates stored in memory, Halgren et al., 2003).

There is evidence that individuals lose interpolation but not other capacities as a result of selective deactivation or injury to classical structures. A patient, LG, with developmental object agnosia had profoundly deactivated intermediate visual areas (V2-V4). This person’s LOC did not respond selectively to objects as compared to unstructured patterns during fMRI experiments (Gilaie-Dotan, Bentin, Harel, Rees, & Saygin, 2011; Gilaie-Dotan, Perry, Bonne, Malach, & Bentin, 2009). LG was poor at recognizing partly occluded objects, disentangling overlapping line drawings, and detecting certain types of Kanizsa shapes (Gilaie-Dotan et al., 2009; 2011). When presented with overlapping line drawings, LG required long periods of time to identify the target object. LG’s V2-V4 deactivation imposed an equally profound effect on everyday subjective experience, as can be gleaned by this first-person report:

“Looking at objects further than about 4 m, I can see the parts but I cannot see them integrated as coherent objects, which I could recognize; however, closer objects I can identify if they are not obstructed; ...” (p. 1690).

It seems therefore that reduced activation in V2-V4 may cause LG to see interpolated shapes as if they were non-recoverable (to use Biederman’s term), as if they were variants of the Dalmatian dog, requiring a slow effortful abstraction process.

At the same time, LG was normal in other respects. This person had intact reading skills and above average grades in school. LG was normal at naming complete objects and matching features, had normal biological motion and global/local processing (as assessed with Navon figure displays), and exhibited normal selectivity to houses and places in functional

neuroimaging experiments. It is true that LG had great difficulty at recognizing faces, but this could be because the FFA is in close proximity to V4 (and LOC) and thus the former may also be adversely affected. Therefore, once again, the deficit is about as specific as what one could hope for from a neuropsychological case study.

There are other complementary pieces of evidence for selective impairment. Contour interpolation can survive ablations or injuries to areas like TEO, IT, right posterior parietal, and ventromedial prefrontal cortex (Ciaramelli et al., 2007; Huxlin et al., 2000; Vancleef et al., 2013), suggesting that the process may be fairly well-localized in the brain. Parietal neglect patients with damage only to thalamus or inferior parietal cortex were able to form illusory contours as evidenced by a line bisection task; patients with the same condition but a damaged lateral occipital cortex were unable to form such contours (Vuilleumier, Valenza, & Landis, 2001). Liang and colleagues applied a conditional Granger causality analysis to monkey spike train and local field potential data within a contour integration task. They found that activation in V4 promoted lateral interactions in V1 and vice versa, and that the synergistic effects were reduced on trials where the contour was incorrectly identified (Liang et al., 2017). In a TMS study, stimulation applied to LOC at earlier time-frames (100–122 ms) or to V1/V2 at slightly later time frames (160–182 ms) impaired the discrimination of fat/thin Kanizsa shapes; the same stimulation applied at different time epochs produced no impairment (Wokke, Vandenbroucke, Scholte, & Lamme, 2013). A caveat here again is that it remains unclear how much these deficits were specific to contour interpolation (e.g., it is unclear whether the same stimulation would interfere with face recognition).

3. Contrary Evidence and an Appeal to Salience

3.1. Salience and top-down effects

Affirmative evidence notwithstanding, there are seemingly inconsistent results in which top-down factors guide the discovery of segmented contours embedded in noise. In a series of single-cell studies, responses within primary visual cortex strongly depended on whether integrated contours were attended, expected, or repeatedly encountered over time (Gilbert & Li, 2013; Ito & Gilbert, 1999; W. Li, Piëch, & Gilbert, 2004; 2006; McManus, Li, & Gilbert, 2011; Ramalingam, McManus, Li, & Gilbert, 2013; Volberg, Wutz, & Greenlee, 2013). As an example, Li, Piëch and Gilbert (2008a) found that—as monkeys were trained on a contour integration task—contour integration performance improved and V1 cell responses to the contours increased. Ramalingam and colleagues (2013) had monkeys perform line bisection or vernier tasks and found that the correlational structure and informational content communicated between V1 sites depended on the type of task performed. McManus and colleagues (2011) invoked an adaptive procedure to find the optimal contour integration stimulus for activating specific cells in monkey V1; cell responses crucially depended on the type of integrated object shown during an initial cueing phase of a trial.

These carefully crafted studies and others like them do not invalidate the modularity hypothesis. They instead show that *interpolation is modular to the extent that bottom-up factors resolve grouping ambiguities* (Beck & Kastner, 2009; Desimone & Duncan, 1995; McMains & Kastner, 2010; 2011). In the vast majority of contour integration experiments, inter-element grouping strength is necessarily limited. First, the line segment endings (or

terminator s, as they are sometimes called) appear intrinsic to the lines, rather than being caused by an overlapping object (e.g., see Fig. 1F). Whenever interruption of an otherwise continuous contour cannot be clearly attributed to an intervening surface, inter-element grouping will weaken (Berzhanskaya, Grossberg, & Mingolla, 2007; Bregman, 1981). Another somewhat obvious but seldom-discussed factor that mutes salience in almost all contour integration studies is the noise field itself. Some noise elements will accidentally align with one another, misleading the observer into detecting these elements rather than the target; other noise elements will join with and branch off of the target, making the observer think that the target has a different shape, length, or location than it actually has. Consistent with this assertion, it has been found that an integrated target contour becomes easier to see when immediately surrounded by orthogonal noise elements and harder to see when surrounded by parallel elements (Dakin & Baruch, 2009). The effect makes sense because nearby orthogonal elements lack the requisite geometry to join with the target, allowing the target to stand out unequivocally from the background. Parallel noise elements, by contrast, will join with one another, providing a competing pseudo-target that must be ignored during target detection. Of course, there are many other ways to increase target salience besides those just mentioned—adding motion, reducing target inter-element spacing, adding more target elements, allowing target contours to form an enclosed shape, etc. The point here is not so much *how* contour saliency is augmented but the fact that it *can* be augmented well beyond levels typically used. I argue that as the contours become more convincing, classic top-down factors including attention, learning, and expectation, will become much less relevant.

Additional seemingly contrary evidence derives from a collinear facilitation paradigm, in which a central low-contrast Gabor element becomes easier to see when flanked by collinear (rather than orthogonal) high contrast Gabors (Polat & Sagi, 1994b; 1994a). Monkey single-cell neurophysiology suggests that the effect is mediated by long-range horizontal connections between orientation-tuned spatial frequency filters in V1/V2 (Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). At the same time, the effect may be attentionally gated. In the so-called “dual axis” displays, a central low contrast Gabor target is flanked by two collinear Gabors along one diagonal axis and by two orthogonal Gabors along the other diagonal axis. If subjects perform a Vernier task on and thus attend to the orthogonal flankers, the collinear flankers along the other diagonal no longer confer an advantage for target detection (Freeman, Sagi, & Driver, 2001). These results, while interesting, do not pose any special problem for modularity. First, it is debatable whether collinear facilitation should qualify as interpolation. Collinear facilitation does not occur under dichoptic viewing conditions or within young children; it requires that elements have a more similar phase or rotation angle and that they fall within a few degrees of fixation (Doron, Spierer, & Polat, 2015; Hess, May, & Dumoulin, 2013; Huang, Hess, & Dakin, 2006). Contour integration and other forms of interpolation, on the other hand, occur in infancy (Baker, Tse, Gerhardstein, & Adler, 2008; Kellman & Spelke, 1983), and when the elements are more rotated, more peripheral, alternating in spatial phase, or split between the eyes (Hess et al., 2013; Huang et al., 2006; Lorenceau & Alais, 2001; Nugent, Keswani, Woods, & Peli, 2003; Spehar & Clifford, 2003). Even if collinear facilitation were a more rudimentary form of interpolation, attentional modulation would still not be problematic because it depends on

the multistable and ambiguous “dual axis” display just mentioned. Freeman and Driver (2005) had subjects perform different secondary tasks on the two flankers, judging relative alignment, orientation, contrast, or chromaticity. This was done for dual and single-axis displays (with four and two flankers, respectively). In the former, modulation arose only when subjects attended to the relative spatial properties (relative alignment) of the flankers; in the latter, facilitation arose regardless of the secondary task. The authors argue—quite reasonably—that in the dual-axis displays, attention serves to reinforce the grouping of relevant items and exclude the grouping of irrelevant items (p. 635) and that, in the single-axis displays, attention is irrelevant because the grouping is automatic. The view that top-down modulation is efficacious primarily when there are competing interpretations of an ambiguous image dovetails with the view proposed here. A logical corollary is that if the competitive interactions of the dual axis display were somehow reduced—for example, if the orthogonal Gabors were shifted further away (e.g., 8x rather than 4x the Gabor wavelength)—then competition between the two axes would be reduced and attentional modulation would significantly diminish.

Only a handful of studies have directly manipulated contour salience while measuring top-down effects, but the results so far are encouraging. McMains and colleagues (2011) parametrically varied the individual rotation of pac-man elements so that they grouped strongly (into a Kanizsa shape), weakly, or not at all. A secondary task ensured that the pac-men were either attended or not attended. Attentional BOLD modulation in areas V1, V2, V3, and V4 was smallest for the strongly grouping elements and largest for the non-grouping elements relative to a control condition in which the pac-men were shown sequentially without grouping. In a single cell neurophysiology study of contour integration, Li, Piëch, and Gilbert (2006) varied the number or spacing of elements composing a contour. They found that neuronal responses depended most obviously on top-down influence for contours of intermediate grouping strength and much less so for strongly grouping contours. If their “salient” contours were rendered even more salient (e.g., by removing border ownership problems or by inhibiting noise element competition), top-down modulation would probably be even weaker than what was reported.

Taken together, when the intermittent appearance of a contour cannot be explained in terms of an occluding surface, when integration must occur in a dense array of noise elements, or when the salience is limited due to any other type of factor, the resulting contour representation will be weakened and so too will its encapsulation from higher-level effects. By contrast, when conditions for interpolation are conducive—that is, when stimulus properties (e.g., motion) strongly bias competitive interactions towards bottom-up grouping (W. Li et al., 2006)—interpolation will behave much as Fodor originally described.

3.2. Salience modulates other modularity features

A case has already been made that salience gates interpolation from top-down interference; the case is now made that salience modifies other modularity features. Let’s first consider interpolation’s reliance on V1, V2, V4, and LOC—what I have termed the “classical” structures. V1 BOLD activation is stronger for translating than for static illusory contours (Seghier & Vuilleumier, 2006). V1/V2 neuronal response is enhanced for flickering or

abruptly appearing inducers relative to those that are fixed and unchanging (Coren, 1991; Lee & Nguyen, 2001). Abutting line gratings produce a more salient V1/V2 response than Kanizsa shapes, whose inducing edges are further apart (Mendola et al., 1999). A transcranial magnetic pulse applied to V1/V2 and LOC within appropriate time frames (see above) worsen Kanizsa shape discrimination for high support ratio but not low support ratio shapes (Wokke et al., 2013). Increasing inter-element spacing, rotation, or misalignment reduces the firing rates of cells in monkey V1 (Kapadia et al., 1995). Prefrontal cortical damage worsens human contour integration performance for elements separated by 3 or 4 degrees of visual angle, but not for those that are within 2 degrees (Ciaramelli et al., 2007).

Salient contours are also processed faster. Contours that curve, that are non-enclosing, or that have more distantly spaced elements take longer to integrate than those that are straight, that enclose, or that have more contour elements per unit distance (Beaudot & Mullen, 2001; Elder & Zucker, 1993). Shape contours that are more occluded take longer to complete than those that are less occluded (Guttman, Sekuler, & Kellman, 2003; Shore & Enns, 1997). The relative alignment of relatable edges can be determined more quickly for dynamic rather than static presentations; the same is not true for unrelatable edges (E. M. Palmer et al., 2006).

Salient contours also require less experience to be perceived. Stroboscopically moving contours evoke contour completion looking time behavior in neonates; static illusory contour stimuli do not do this (E. Valenza & Bulf, 2007). Overlapping moving outline shapes can be readily distinguished by congenitally blind, recently sighted adults; the same is not true for overlapping static contours (Ostrovsky et al., 2009). Illusory contours with higher support ratio (66%) can be perceived earlier in development (3–4 months) than those that have lower support ratio (37%; 7–8 months) (Otsuka, Kanazawa, & Yamaguchi, 2004) (see also, Hadad, Maurer, & Lewis, 2016). Contour integration behavior of children and adults differ most obviously from one another when the inter-element distance is increased from .9 to 1.8 degrees (Kovács et al., 1999).

Salient contours are also more likely to be processed automatically and obligatorily. Popout visual search—a behavioral hallmark of automatic visual processing in which target detection speed is approximately invariant to the number of distractors—has been documented with abutting line grating contours or with high support ratio Kanizsa figures, but not with Kanizsa stimuli that have ambiguous border ownership or non-optimal junction structure (Davis & Driver, 1994; 1998; X. Li, Cave, & Wolfe, 2008b). During multiple object tracking, illusory contours tug attention away from targets and towards distractors, but the effect is diluted when the contours have reduced support ratio or increased curvature (Erlikhman et al., 2013; Keane et al., 2011)(Fig. 3B). Kanizsa shapes centered within visual space are seen as unitary by parietal extinction patients but this automatic grouping largely dissipates when rings are drawn around the pac-men to diminish contour clarity (Mattingley et al., 1997).

3.3. Using salience to further test (and potentially falsify) interpolation's modularity

An implication so far is that modularity comes in degrees and can be gradually switched on or off by turning the dial on contour salience. As shown in Fig. 7, there are many ways to

move the dial in favor of stronger contours; these include increasing the support ratio (T. F. Shipley & Kellman, 1992), distributing inducing edge material along the interpolated path (Maertens & Shapley, 2008), resolving border ownership ambiguities (Bregman, 1981; McDermott, Weiss, & Adelson, 2001; Rubin, 2001), adding motion cues (Ni, Wang, Wu, Wang, & Li, 2003; Ostrovsky et al., 2009; Seghier et al., 2000), adding abrupt onsets or flicker (Coren, 1991; Lee & Nguyen, 2001), decreasing the turning-angle between adjacent elements (Fulvio, Singh, & Maloney, 2006), decreasing the ambiguity of whether an element connects to its neighbor or to some other nearby distractor (e.g., by excluding noise in contour integration displays), having the contour form an enclosed shape (Gerhardstein, Tse, Dickerson, Hipp, & Moser, 2012), and extending the total contour length (W. Li & Gilbert, 2002). These are just some examples. It is predicted that as the conditions for interpolation become more favorable, interpolation will regain its modularity features—it will become faster, less subject to the goals or beliefs of the observer, more likely to arise in early infancy, more reliant on classical circuitry, less likely to lead to outputs that are conceptual in nature, less flexible in the range of input that it will find acceptable, and less likely to operate by rules that can be extracted, created or implemented through effort and introspection. The most convincing way to discredit the putative modularity of interpolation, therefore, is to first identify a set of stimulus parameters that modulate the salience of the phenomenon, then adjust the parameters so that the phenomenon is robust, and then to go through the Fodor criteria—one-by-one—to show that they do not apply. For example, the *most* convincing debunking of contour interpolation's modularity would involve taking a series of contiguous line elements that are closely spaced, perfectly aligned, with no ambiguity in border ownership or relative connectedness, that are presented in motion and with large support ratio. If such a stimulus yields top-down effects that are dependent on observer knowledge, if it happens slowly or subject to the whims of the observer, if it does not happen in early infancy, if it does not critically rely on long-range horizontal excitatory connections in V1/V2 or top-down feedback from lateral occipital complex or V4, then all of these findings would be important pieces of disconfirmation. Of course, this does not mean that there is no value in testing the modularity of other more weakly grouping contour elements. If salient contours largely count as modular, then it will still be important to figure out where and under what conditions the modularity comes undone. But the point here is that if the modularity view is to be convincingly discredited, the appropriate stimulus conditions must be chosen.

4. Addressing General Objections

Several objections may be waged against the modularity perspective and each is worth considering in turn. One is that modular devices are inflexible and almost all aspects of cognition can be changed through effort, learning, attention, or expectation. Many might therefore greet the modularity thesis with a prolonged stare of incredulity. I first state without hesitation that interpolation *is* inflexible in several important respects: for certain element layouts, there is no amount of learning or top-down strategy that will get the elements to link together in a spatially precise way; and for other configurations (a abutting line grating), interpolation will be inescapable. But this inflexibility is really not so confining; the number of unique interpolating configurations is nearly limitless. The visual

system can encounter edge configurations that were never encountered in the past (different colors, spatial positions, contrasts, etc.) and that might never be expected in the future. More importantly, for those who insist that the mind must meet the constantly changing needs of the observer and demands of the environment, interpolation may become susceptible to high-level processes when the conditions for the process are weakened, as repeatedly noted above.

If interpolation sheds its modular features under non-optimal stimulus conditions, doesn't this mean that it is not a module at all? The answer is "no" and the reason is that virtually any input domain will be inherently fuzzy at its edges, and that a domain-specific device can be expected to act out of character when the input lies out at the outer extremes of what is acceptable. The idea is related to David Marr's (1982) "principle of graceful degradation" (p. 106), according to which a process will be engaged to a lesser extent (and its output only partly provided) when the visual input is degraded. Just as a visible light detector may respond tepidly to ultraviolet or infrared electromagnetic radiation, so too should interpolation be allowed to express modularity features to a greater or lesser extent. This graded character of modularity is very much in line with Fodor's original proposal, when he wrote that the "notion of modularity ought to admit of degrees" and that a modular system need only to express its qualities "to some interesting extent" (Fodor, 1983, p. 37).

It may also be argued that because salient interpolated contours arise only in highly specific situations, the process might take on modularity features only in rare circumstances. On this view, even though interpolation *in principle* behaves like a module, in practice it does not, rendering the current case study of little interest to those interested in how the mind typically works. The objection is weakened by studies of natural scene statistics. An examination of two-dimensional grayscale photographs of natural landscapes and objects indicate that contour fragmentation is the norm, and that a subset of the visible edge elements strongly group together by sharing a similar location, orientation, alignment, and contrast (Elder & Goldberg, 2002; Geisler et al., 2001; Geisler & Perry, 2009). Moreover, the prevalence of strong contour grouping is almost certainly underestimated in these studies. Motion and stereoscopic depth, for example, are not included as relevant stimulus dimensions, even though both are pervasive in natural environments and both contribute importantly to contour salience. Therefore, the available evidence tilts in a direction *opposite* to that proposed above: because most natural scenes are perceived to have at least some strongly grouping edge elements, interpolation should behave as a Fodorian module for most of our waking moments.

Another generic objection is that, if modular mechanisms are encapsulated, how is it that they can act so intelligently, for example, when taking into account global scene properties to arrive at a plausible stimulus interpretation (Gregory, 1972; Rock, 1983)? This sort of objection has been addressed by others (Pylyshyn, 1999) but the crux of the confusion is that a low level module can encompass integration algorithms that look ingenious from the outside (Runeson, 1977). It may initially seem unlikely that a smart process can be packaged into a module, but the data so far are leading us to this conclusion. Moreover, the intelligence of modularity should not be over-stated: although interpolation furnishes a by-and-large veridical picture of the external world and although it elegantly and effortlessly

takes into account a variety of stimulus properties to produce this representation, there are clear circumstances (albeit contrived) in which it reaches the wrong conclusion by stubbornly ignoring high-level knowledge and expectation (e.g., Fig. 4A–D).

Yet another potential obstacle to the modularity viewpoint is that salience and modularity appear to be circularly defined: Interpolation acts as a module if the processed contour stimuli are salient, and contour stimuli count as being salient if they generate modularity features (fast, automatic, etc.). The circularity can be remedied in two non-mutually exclusive ways. First, the notion of salience can be anchored in phenomenology—contours that can be easily seen and that make a clear subjective impression would be categorized as salient. There is rarely disagreement in the literature about what contours are or are not salient (at least in the extreme cases), and modularity is not critically defined in terms of phenomenology, and so inter-subjective agreement on phenomenal salience may offer a viable off-ramp from the circular reasoning. Another perhaps more satisfactory solution is to simply embrace the inter-definition. One can argue that whatever properties increase the likelihood of finding one modularity property will increase the chances of finding others. Salience-making properties will be those that increase the chances of finding all modularity features in one fell swoop. On this view, if a given property change increases the speed of interpolation, it will also elicit stronger activity in classical structures, increase the contour's spatial precision and accuracy (e.g., in dot localization tasks), make the contour more readily perceived by young infants, render the process more impervious to cognitive expectation, and so forth. My central claim is that stimulus arrangements exist such that all of the modularity features will be found together at once.

A related concern is that the proposed account initially seems immune to falsification—whenever a potential modularity counterexample is discovered one can quickly blame the stimulus conditions as not being sufficiently salient or write off the example as an instance of contour abstraction. This concern has been addressed in Section 3.3 above, but the response is worth repeating: There are established stimulus conditions under which interpolated contours are crisp and obvious. If the modularity thesis does not describe interpolation even under these circumstances, then it does not hold true for the process at all.

5. Outstanding Questions

I do not pretend to have answered all questions regarding the modularity of interpolation; many aspects of the process require further exploration. One such area is the relation between contour abstraction and interpolation. The former is supposed to be slower, more effortful, less spatially precise, conceptually mediated, later developing, more reliant on prefrontal cortical structures, more broad ranging in its initiating stimulus conditions, and less reliant on classical structures. However, many of these assertions are in need of further support and more studies need to explicitly compare the two processes side-by-side.

Above, it was also argued that interpolation is cognitively encapsulated in that stimulus properties—most notably, edge element geometry—determine whether inducers form a single bounded elongated contour. However, encapsulation in its strongest form entails that other modularity features should also be shielded from high-level influence; these include

speed, dependence on classical neural structures (V1, V2, LOC), and spatial precision. It is proposed that there are no such effects, but this strong supposition is in need of further testing. Relatedly, it has been argued that beliefs and expectations determine how well interpolated contours are used at decisional stages for tasks such as shape discrimination. However, the evidence most directly supporting this claim derives from contours of intermediate salience (static inducers with modest support ratio ~25%; Fig. 6A) (Keane et al., 2012). Had more salient contours been used, subjects may have successfully discovered and used the contours regardless of task strategy. It is therefore possible that beliefs/expectations have a limited impact on even the outputs of interpolation, when the contours are salient.

Questions also remain as to *how* salience interacts with attention and expectation during interpolation. According to a competitive interactions hypothesis, multiple co-presented stimuli automatically compete for neural representation and the outcome of these interactions depend on stimulus driven factors (saliency) and top-down factors such as voluntary attention (Desimone & Duncan, 1995; J. H. Reynolds, Chelazzi, & Desimone, 1999). This influential theory has been further fleshed out in terms of an interface hypothesis, according to which top-down and bottom-up signals dynamically interact within the same local circuits to determine relative occlusion, contour connectedness, and border ownership (Qiu, Sugihara, & Heydt, 2007). In at least some varieties of contour grouping, the interface may be at the level of V4 (McMains & Kastner, 2011). Feedback from the pulvinar, frontal eye fields, and TEO (Gilbert & Li, 2013) could primarily stimulate V4 parvalbumin-expressing inhibitory interneurons (Mitchell, Sundberg, & Reynolds, 2007). Other areas like V1/V2 may provide additional interfaces through which descending and recurrent feedback connections influence interpolation (Gilbert & Li, 2013; Liang et al., 2017). Cognitive expectation influences may additionally trickle down to the interface cell populations (e.g., by way of IT) from prefrontal cortex (Bar, 2003). Computationally speaking, when competition is moderate or strong—that is, when interpolation fails to decisively unify a fragmented edge array—the issue as to *how to* represent the stimulus may be resolved through predictive coding (Friston, 2005; Rao & Ballard, 1999). On this view, the visual system may have priors as to what shape or contour is most likely, and these priors may influence in Bayesian fashion the final shape perceived; the priors may furthermore be updated when there is significant prediction error, that is, when there is mismatch between the predicted and actual (e.g., unoccluded) contour (Clark, 2013). A seductive hypothesis—and one that will undoubtedly need to be further tested—is that the “local circuits” which lie at the interface of bottom-up and top-down signals and which participate in predictive coding may also instantiate the nine Fodorian features. Processing in these circuits may be fast, innate, automatic, domain specific, informationally encapsulated, and so forth under appropriately favorable stimulus conditions.

Throughout, I have delineated a class of phenomena termed interpolation, which subsumes motion linking, illusory contour formation, abutting line gratings (including Varin figures), amodal completion, and contour integration (line segments or Gabors). But what falls within this class is subject to revision. For example, I have assumed a single interpolation process for modal and amodal completion even though this has been hotly contested (B. L. Anderson, 2007; B. Anderson, Singh, & Fleming, 2002; Barraza & Chen, 2006; Kellman,

Garrigan, Shipley, & Keane, 2007; Shpaner, Murray, & Foxe, 2009; J. Zhou et al., 2008). I have also assumed that abutting line grating stimuli create interpolated contours even though they are mediated by end-stopped rather than orientation-tuned cells in early visual cortex (R Von der Heydt et al., 1984; Soriano, Spillmann, & Bach, 1996). While I think that a good case can be made for a single process in each of these cases, I acknowledge that seemingly identical visual phenomena may sometimes be unrelated (e.g., Carandini & Heeger, 2012).

The tentatively hypothesized granularity of interpolation may also be too narrow. Spatiotemporal boundary formation, where contours are formed by discontinuities in sparse background elements, could belong to the interpolation family (Erlikhman & Kellman, 2015; T. F. Shipley & Kellman, 1993); second-order motion, where contours are formed from changes in individual pixels of a dense background (Ledgeway & Smith, 1994), could as well. Other tentatively excluded variants are: amodal continuation, where a single partly occluded shape phenomenally extends behind an opaque surface, (Kanizsa, 1979); contour extrapolation, where a contour shoots forth from where it intersects with an occluder (Halko et al., 2008; Singh & Fulvio, 2005); and collinear facilitation, which (as noted) fills-in between collinear high-contrast elements to facilitate the detection of a centrally aligned low-contrast target (Polat & Sagi, 1994a). Regardless of whether the currently circumscribed class of interpolation phenomena turn out to invoke multiple mechanisms or one, and regardless of whether it captures the entirety of interpolation, it will still satisfy Fodor's original description, so long as the initiating conditions are favorable.

6. Modularity Beyond Interpolation

In the foregoing discussion, I have concentrated on interpolation because the process is phylogenetically pervasive and behaviorally important, and because there is a large, varied literature on the topic stretching back to the 1950's. I have argued that it is more fruitful to focus on one specific process about which we have much information rather than grapple with the much more unwieldy question of whether all of early vision, all of perception, or all of language processing is modular. It is doubtful that any of these bigger questions can be convincingly settled in one research article. After surveying the large and still-growing literature on interpolation, I hope to have shown that the human mind comes stocked with at least one device that is fast, mandatory, informationally encapsulated, domain specific, restricted in its central access, productive of representationally impoverished content, and reliant upon a fixed neural architecture that can be selectively impaired. These modularity features may be turned on or off by twisting the dial on contour salience; this is the same dial that modulates the ability of bottom-up factors to exclude top-down factors during the competitive interactions hypothesized in neuroscience.

By championing Fodor's core concept of modularity, I do not ipso facto vouch for all his other commitments regarding cognitive architecture. I remain non-committal on whether only modular systems can be fruitfully investigated, whether central (non-modular) systems always lack modularity features (e.g., domain specificity, automaticity), whether concepts are innate, whether central systems are by their nature inferentially promiscuous ("isotropic" and "Quinean", to use Fodor's terms) and so forth. The major claim instead is

much more modest, namely, that the human mind comes equipped with at least one device that fits his original description.

Establishing a module is important. It directly bears on contemporary empirical debates such as whether there are functionally specialized neural circuits (Kanwisher, 2010), whether the mind can be decomposed into numerous domain-specific devices (Kurzban, 2011), whether perception is cognitively encapsulated (Firestone & Scholl, 2015), and whether mental capacities develop in a fixed and regimented way irrespective of past experience (M. M. Murray et al., 2015). Establishing a module also invites new research questions. It should incite us to search for a better understanding of how or in virtue of what all the Fodorian features hang together (e.g., Why are obligatory processes carried out quickly? Why do quickly executed processes also tend to develop earlier in life? Why are earlier developing processes more often neurally specialized?). It should prompt deeper inquiry into how and why the nine Fodorian features so intimately depend on salience (e.g., Why are contours with higher support ratio processed more quickly and at an earlier stage in development? Why is attention less able to modulate responses to dynamic contours?). It should motivate new experiments that directly compare contour interpolation and contour abstraction side-by-side (What distinguishes contour abstraction from weak interpolation, and can this distinction be altered with learning?). Establishing a module should direct inquiry into the alleged interface circuits that adjudicate between bottom-up and top-down signals and that effectively gate the expression of modularity features (see Section 5 above). Finally, discovering one module should prompt us to search more expansively for other such mechanisms not only in vision but across all sensory systems. Taken collectively, the present case study should breathe fresh air into an empirical research agenda that has been seriously doubted by many, fully embraced by few, and substantially qualified even by Fodor himself.

There still looms the grander question of whether a substantial portion of early perception is modular—this of course is the question that we all want answered. Only a broad, careful reading of the literature for each process will reveal the true answer. Just as salience plays a critical role in determining interpolation's modularity, so too may it for other visual processes such as stereopsis or face perception, or for non-visual processes such as auditory event segmentation or haptic object localization. And just as contour abstraction presented a red herring for contour interpolation, so too may related cognitive operations confuse or mislead cognitive scientists as they evaluate whether this or that process counts as modular. In each case, the most convincing disconfirmation will entail establishing and constructing highly salient stimuli and then testing the Fodorian modularity features, one-by-one, to determine which features hold. By addressing this grander question in a more systematic and progressive manner, we can provide an answer to one of the deepest problems in cognitive science, which pertains to how the human mind is functionally organized and evolutionarily designed.

Acknowledgments

The writing of this manuscript was supported by an NIH/NIMH National Research Service Award (F32MH094102) and an NIH/NIMH Mentored Career Development Award (K01MH108783). There are no conflicts of interest to declare. Portions of this work were presented as talks at Vision Sciences Society (2010), Rutgers University Center for Cognitive Science (2011), and the Society for Philosophical Psychology (2011, 2012). I am grateful to Randy

Gallistel, Sabine Kastner, Philip Kellman, Zenon Pylyshyn, and Steve Silverstein for helpful input and stimulating conversation. Last but certainly not least I am indebted to the late Jerry Fodor for sparking an enduring interest in modularity.

References

- Ahumada AJ (1996). Perceptual classification images from vernier acuity masked by noise. *Perception* [Abstract], 18.
- Altmann CF, Bühlhoff HH, & Kourtzi Z (2003). Perceptual organization of local elements into global shapes in the human visual cortex. *Current Biology: CB*, 13(4), 342–349. [PubMed: 12593802]
- Altschuler TS, Molholm S, Butler JS, Mercier MR, Brandwein AB, & Foxe JJ (2014). The effort to close the gap: Tracking the development of illusory contour processing from childhood to adulthood with high-density electrical mapping. *NeuroImage*, 90, 360–373. <http://doi.org/10.1016/j.neuroimage.2013.12.029> [PubMed: 24365674]
- Anderson BL (2007). Filling-in models of completion: Rejoinder to Kellman, Garrigan, Shipley, and Keane (2007) and Albert (2007). *Psychological Review*, 114(2), 509–525. 10.1037/0033-295X.114.2.509 [PubMed: 17500640]
- Anderson B, Singh M, & Fleming R (2002). The interpolation of object and surface structure. *Cognitive Psychology*, 44(2), 148–190. [PubMed: 11863323]
- Baker TJ, Tse J, Gerhardstein P, & Adler SA (2008). Contour integration by 6-month-old infants: Discrimination of distinct contour shapes. *Vision Research*, 48(1), 136–148. 10.1016/j.visres.2007.10.021 [PubMed: 18093632]
- Bar M (2003). A cortical mechanism for triggering top-down facilitation in visual object recognition. *Journal of Cognitive Neuroscience*, 15(4), 600–609. 10.1162/089892903321662976 [PubMed: 12803970]
- Barraza JF, & Chen VJ (2006). Vernier acuity of illusory contours defined by motion. *Journal of Vision*, 6(9), 923–932. 10.1167/6.9.6 [PubMed: 17083285]
- Barrett HC, & Kurzban R (2006). Modularity in Cognition: Framing the Debate. *Psychological Review*, 113(3), 628–647. 10.1037/0033-295X.113.3.628 [PubMed: 16802884]
- Beaudot WHA, & Mullen KT (2001). Processing time of contour integration: the role of colour, contrast, and curvature? *Perception*, 30(7), 833–853. 10.1068/p3164 [PubMed: 11515956]
- Beck DM, & Kastner S (2005). Stimulus context modulates competition in human extrastriate cortex. *Nature Neuroscience*, 8(8), 1110–1116. 10.1038/nn1501 [PubMed: 16007082]
- Beck DM, & Kastner S (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research*, 49(10), 1154–1165. 10.1016/j.visres.2008.07.012 [PubMed: 18694779]
- Benedek K, Janáky MR, Braunitzer GB, Rokszin A, Ká Ri S, & Benedek GR (2010). Parallel development of contour integration and visual contrast sensitivity at low spatial frequencies. *Neuroscience Letters*, 472(3), 175–178. 10.1016/j.neulet.2010.02.001 [PubMed: 20138967]
- Berkeley G (1996). *Philosophical works including the works on vision*. (Myers MR, Ed.). London: J. M. Dent.
- Berzhanskaya J, Grossberg S, & Mingolla E (2007). Laminar cortical dynamics of visual form and motion interactions during coherent object motion perception. *Spatial Vision*, 20(4), 337–395. 10.1163/156856807780919000 [PubMed: 17594799]
- Bex PJ, Simmers AJ, & Dakin SC (2001). Snakes and ladders: the role of temporal modulation in visual contour integration. *Vision Research*, 41(27), 3775–3782. [PubMed: 11712989]
- Biederman I (1987). *Recognition-by-Components - a Theory of Human Image Understanding*. *Psychological Review*, 94(2), 115–147. [PubMed: 3575582]
- Braun J (1999). On the detection of salient contours. *Spatial Vision*, 12(2), 211–225. [PubMed: 10221428]
- Bregman AS (1981). Asking the “what for” question in auditory perception In Kubovy M & Pomerantz JR (Eds.), *Perceptual organization* (pp. 99–118). Hillsdale, NJ: Earlbaum Associates.
- Carandini M, & Heeger DJ (2012). Normalization as a canonical neural computation. *Nature Reviews Neuroscience*, 13(1), 51–62. 10.1038/nrn3136

- Chen M, Yan Y, Gong X, Gilbert CD, Liang H, & Li W (2014). Incremental integration of global contours through interplay between visual cortical areas. *Neuron*, 82(3), 682–694. 10.1016/j.neuron.2014.03.023 [PubMed: 24811385]
- Ciaramelli E, Leo F, Del Viva MM, Burr DC, & Ladavas E (2007). The contribution of prefrontal cortex to global perception. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*, 181(3), 427–434. 10.1007/s00221-007-0939-7
- Clark A (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *The Behavioral and Brain Sciences*, 36(3), 181–204. 10.1017/S0140525X12000477 [PubMed: 23663408]
- Clune J, Mouret J-B, & Lipson H (2013). The evolutionary origins of modularity. *Proceedings of the Royal Society B: Biological Sciences*, 280(1755), 20122863 10.1098/rspb.2012.2863
- Cochran CF (1966). Letters. *Scientific American*, 214(8), 1–1.
- Coltheart M (1999). Modularity and cognition. *Trends in Cognitive Sciences*, 3(3), 115–120. [PubMed: 10322463]
- Coren S (1991). Retinal mechanisms in the perception of subjective contours: the contribution of lateral inhibition. *Perception*, 20(2), 181–191. [PubMed: 1745590]
- Cox MA, Schmid MC, Peters AJ, Saunders RC, Leopold DA, & Maier A (2013). Receptive field focus of visual area V4 neurons determines responses to illusory surfaces. *Proceedings of the National Academy of Sciences of the United States of America*, 110(42), 17095–17100. 10.1073/pnas.1310806110/-DCSupplemental [PubMed: 24085849]
- Dakin SC, & Baruch NJ (2009). Context influences contour integration. *Journal of Vision*, 9(2), 13–13. 10.1167/9.2.13
- Dakin SC, & Hess RF (1998). Spatial-frequency tuning of visual contour integration. *Journal of the Optical Society of America a, Optics, Image Science, and Vision*, 15(6), 1486–1499.
- Davis G, & Driver J (1994). Parallel detection of Kanizsa subjective figures in the human visual system. *Nature*, 371(6500), 791–793. 10.1038/371791a0 [PubMed: 7935838]
- Davis G, & Driver J (1998). Kanizsa subjective figures can act as occluding surfaces at parallel stages of visual search. *Journal of Experimental Psychology Human Perception and Performance*, 24(1), 169–184.
- Desimone R, & Duncan J (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18(1), 193–222.
- Doron R, Spierer A, & Polat U (2015). How crowding, masking, and contour interactions are related: A developmental approach. *Journal of Vision*, 15(8), 5 10.1167/15.8.5
- Elder JH, & Goldberg RM (2002). Ecological statistics of Gestalt laws for the perceptual organization of contours. *Journal of Vision*, 2(4), 324–353. [PubMed: 12678582]
- Elder J, & Zucker S (1993). The effect of contour closure on the rapid discrimination of twodimensional shapes. *Vision Research*, 33(7), 981–991. [PubMed: 8506640]
- Erlikhman G, & Kellman PJ (2015). Modeling spatiotemporal boundary formation. *Vision Research*. 10.1016/j.visres.2015.03.016
- Erlikhman G, Keane BP, Mettler E, Horowitz TS, & Kellman PJ (2013). Automatic Feature- Based Grouping During Multiple Object Tracking. *Journal of Experimental Psychology Human Perception and Performance*, 1–14. 10.1037/a0031750
- Fedorenko E, Behr MK, & Kanwisher N (2011). Functional specificity for high-level linguistic processing in the human brain. *Proceedings of the National Academy of Sciences*, 108(39), 16428–16433. 10.1073/pnas.1112937108
- Field DJ, Hayes A, & Hess RF (1993). Contour integration by the human visual system: evidence for a local “association field”. *Vision Research*, 33(2), 173–193. 10.1016/0042-6989(93)90156-Q [PubMed: 8447091]
- Field DJ, Hayes A, & Hess RF (2000). The roles of polarity and symmetry in the perceptual grouping of contour fragments. *Spatial Vision*, 13(1), 51–66. [PubMed: 10688229]
- Firestone C, & Scholl BJ (2015). Cognition does not affect perception: Evaluating the evidence for “top-down” effects. *The Behavioral and Brain Sciences*, 1–77. 10.1017/S0140525X15000965
- Fisher GH (1967). Preparation of ambiguous stimulus materials. *Perception and Psychophysics*.

- Fodor JA (1983). *The Modularity of Mind*. Cambridge, MA: MIT Press.
- Fodor JA (2001). *The Mind Doesn't Work that Way*. Cambridge, MA: MIT Press.
- Foxe JJ, Murray MM, & Javitt DC (2005). Filling-in in schizophrenia: a high-density electrical mapping and source-analysis investigation of illusory contour processing. *Cerebral Cortex* (New York, NY : 1991), 15(12), 1914–1927. 10.1093/cercor/bhi069
- Freeman E, & Driver J (2005). Task-dependent modulation of target-flanker lateral interactions in vision. *Perception and Psychophysics*, 67(4), 624–637. [PubMed: 16134456]
- Freeman E, Sagi D, & Driver J (2001). Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers. *Nature Neuroscience*, 4(10), 1032–1036. 10.1038/nn728 [PubMed: 11559851]
- Friston K (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1456), 815–836. 10.1038/335311a0
- Fulvio JM, Singh M, & Maloney L (2006). Consistency of location and gradient judgments of visually-interpolated contours. *Computer Vision and Pattern Recognition Workshop, 2006 Conference on*, 186–186.
- Fuss T, Bleckmann H, & Schluessel V (2014). The brain creates illusions not just for us: sharks (*Chiloscyllium griseum*) can “see the magic” as well. *Frontiers in Neural Circuits*, 8, 24–24. 10.3389/fncir.2014.00024 [PubMed: 24688458]
- Gandhi T, Kalia A, Ganesh S, & Sinha P (2015). Immediate susceptibility to visual illusions after sight onset. *Current Biology: CB*, 25(9), R358–R359. 10.1016/j.cub.2015.03.005 [PubMed: 25942545]
- Geisler WS, & Perry JS (2009). Contour statistics in natural images: Grouping across occlusions. *Visual Neuroscience*, 26(01), 109. 10.1017/S0952523808080875 [PubMed: 19216819]
- Geisler WS, Perry J, Super B, & Gallogly D (2001). Edge co-occurrence in natural images predicts contour grouping performance. *Vision Research*, 41(6), 711–724. [PubMed: 11248261]
- Gerhardstein P, Tse J, Dickerson K, Hipp D, & Moser A (2012). The human visual system uses a global closure mechanism. *Vision Research*, 71, 18–27. 10.1016/j.visres.2012.08.011 [PubMed: 22940526]
- Gilaie-Dotan S, Bentin S, Harel M, Rees G, & Saygin AP (2011). Normal form from biological motion despite impaired ventral stream function. *Neuropsychologia*. 10.1016/j.neuropsychologia.2011.01.009
- Gilaie-Dotan S, Perry A, Bonneh Y, Malach R, & Bentin S (2009). Seeing with profoundly deactivated mid-level visual areas: non-hierarchical functioning in the human visual cortex. *Cerebral Cortex*, 19(7), 1687–1703. 10.1093/cercor/bhn205 [PubMed: 19015369]
- Gilbert CD, & Li W (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, 14(5), 350–363. 10.1038/nrn3476 [PubMed: 23595013]
- Gold JM, & Shubel E (2006). The spatiotemporal properties of visual completion measured by response classification. *Journal of Vision*, 6(4), 356–365. 10.1167/6.4.5 [PubMed: 16889474]
- Gold JM, Murray RF, Bennett PJ, & Sekuler AB (2000). Deriving behavioural receptive fields for visually completed contours. *Current Biology*, 10(11), 663–666. [PubMed: 10837252]
- Gosselin F, & Schyns PG (2001). Bubbles: a technique to reveal the use of information in recognition tasks. *Vision Research*, 41(17), 2261–2271. [PubMed: 11448718]
- Gosselin F, & Schyns PG (2003). Superstitious perceptions reveal properties of internal representations. *Psychological Science: a Journal of the American Psychological Society/APS*, 14(5), 505–509.
- Gregory RL (1970). *The Intelligent Eye*. London: Weidenfeld & Nicolson.
- Gregory RL (1972). Cognitive contours. *Nature*, 238(5358), 51–52. [PubMed: 12635278]
- Guttman SE, & Kellman PJ (2004). Contour interpolation revealed by a dot localization paradigm. *Vision Research*, 44(15), 1799–1815. 10.1016/j.visres.2004.02.008 [PubMed: 15135995]
- Guttman SE, Sekuler AB, & Kellman PJ (2003). Temporal Variations in Visual Completion: A Reflection of Spatial Limits? *Journal of Experimental Psychology Human Perception and Performance*, 29(6), 1211–1227. 10.1037/0096-1523.29.6.1211 [PubMed: 14640839]

- Hadad B-S, Maurer D, & Lewis TL (2010). The development of contour interpolation: Evidence from subjective contours. *Journal of Experimental Child Psychology*, 106(2–3), 163–176. 10.1016/j.jecp.2010.02.003 [PubMed: 20227089]
- Hadad B-S, Maurer D, & Lewis TL (2016). The role of early visual input in the development of contour interpolation: the case of subjective contours. *Developmental Science*, n/a–n/a. 10.1111/desc.12379
- Hafed ZM, & Krauzlis RJ (2006). Ongoing eye movements constrain visual perception. *Nature Neuroscience*, 9(11), 1449–1457. 10.1038/nn1782 [PubMed: 17028586]
- Haidt J, & Joseph C (2007). The moral mind: How five sets of innate intuitions guide the development of many culture-specific virtues, and perhaps even modules In Carruthers P, Laurence S, & Stich S (Eds.), *The Innate Mind*, Vol. 3: Foundations and the future (pp. 367–392). New York: Oxford University Press.
- Halgren E, Mendola J, Chong CDR, & Dale AM (2003). Cortical activation to illusory shapes as measured with magnetoencephalography. *NeuroImage*, 18(4), 1001–1009. [PubMed: 12725774]
- Halko MA, Mingolla E, & Somers DC (2008). Multiple mechanisms of illusory contour perception. *Journal of Vision*, 8(11), 17.1–17. 10.1167/8.11.17
- Hanson SJ, & Schmidt A (2011). High-resolution imaging of the fusiform face area (FFA) using multivariate non-linear classifiers shows diagnosticity for non-face categories. *NeuroImage*, 54(2), 1715–1734. 10.1016/j.neuroimage.2010.08.028 [PubMed: 20736071]
- He Z, & Nakayama K (1992). Surfaces versus features in visual search. *Nature*, 359(6392), 231–233. [PubMed: 1528263]
- Hess RF, Hayes A, & Field DJ (2003). Contour integration and cortical processing. *Journal of Physiology, Paris*, 97(2–3), 105–119. 10.1016/j.jphysparis.2003.09.013
- Hess RF, May KA, & Dumoulin SO (2013). Contour integration: Psychophysical, neurophysiological and computational perspectives. *Oxford Handbook of Perceptual Organization*.
- Heydt, Von der R, Peterhans E, & Baumgartner G (1984). Illusory contours and cortical neuron responses. *Science (New York, NY)*, 224(4654), 1260–1262.
- Huang P-C, Hess RF, & Dakin SC (2006). Flank facilitation and contour integration: different sites. *Vision Research*, 46(21), 3699–3706. 10.1016/j.visres.2006.04.025 [PubMed: 16806389]
- Huxlin KR, Saunders RC, Marchionini D, Pham HA, & Merigan WH (2000). Perceptual deficits after lesions of inferotemporal cortex in macaques. *Cerebral Cortex (New York, NY : 1991)*, 10(7), 671–683. 10.1093/cercor/10.7.671
- Iacaruso MF, Gasler IT, & Hofer SB (2017). Synaptic organization of visual space in primary visual cortex. *Nature*, 547(7664), 449–452. 10.1038/nature23019 [PubMed: 28700575]
- Imamoglu F, Kahnt T, Koch C, & Haynes J-D (2012). Changes in functional connectivity support conscious object recognition. *NeuroImage*, 63(4), 1909–1917. 10.1016/j.neuroimage.2012.07.056 [PubMed: 22877578]
- Ito M, & Gilbert C (1999). Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron-Cambridge Ma-*, 22, 593–604.
- Johnson SP, & Aslin RN (1996). Perception of object unity in young infants: The roles of motion, depth, and orientation. *Cognitive Development*, 11(2), 161–180. 10.1016/S0885-2014(96)90001-5
- Kahn RS, & Keefe RSE (2013). Schizophrenia is a cognitive illness. *JAMA Psychiatry*, 70(10), 1107–1108. 10.1001/jamapsychiatry.2013.155 [PubMed: 23925787]
- Kahneman D (2011). *Thinking, Fast and Slow*. New York, NY: Farrar, Straus and Giroux.
- Kalar DJ, Garrigan P, Wickens TD, Hilger JD, & Kellman PJ (2009). A unified model of illusory and occluded contour interpolation. *Vision Research*, 1–16. 10.1016/j.visres.2009.10.011 [PubMed: 18848956]
- Kanizsa G (1955). Margini quasi-percettivi in campi con stimolazione omogenea. *Rivista Di Psicologia*, 49(1), 7–30.
- Kanizsa G (1976). Subjective contours. *Scientific American*, 234(4), 48–52. 10.1038/scientificamerican0476-48 [PubMed: 1257734]
- Kanizsa G (1979). *Organization in Vision*. New York: Praeger.
- Kanizsa G (1985). Seeing and thinking. *Acta Psychologica*, 59(1), 23–33. [PubMed: 4024981]

- Kanwisher N (2010). Inaugural Article: Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences*, 107(25), 11163–11170. 10.1073/pnas.1005062107
- Kapadia MK, Ito M, Gilbert CD, & Westheimer G (1995). Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. *Neuron*, 15(4), 843–856. [PubMed: 7576633]
- Keane BP, Erlikhman G, Kastner S, Paterno D, & Silverstein SM (2014a). Multiple forms of contour grouping deficits in schizophrenia: What is the role of spatial frequency? *Neuropsychologia*, 65, 221–233. 10.1016/j.neuropsychologia.2014.10.031 [PubMed: 25446968]
- Keane BP, Joseph J, & Silverstein SM (2014b). Late, not early, stages of Kanizsa shape perception are compromised in schizophrenia. *Neuropsychologia*, 56, 302–311. 10.1016/j.neuropsychologia.2014.02.001 [PubMed: 24513023]
- Keane BP, Lu H, & Kellman PJ (2007). Classification images reveal spatiotemporal contour interpolation. *Vision Research*, 47(28), 3460–3475. 10.1016/j.visres.2007.10.003 [PubMed: 18053850]
- Keane BP, Lu H, Papathomas TV, Silverstein SM, & Kellman PJ (2012). Is interpolation cognitively encapsulated? Measuring the effects of belief on Kanizsa shape discrimination and illusory contour formation. *Cognition*, 123(3), 404–418. 10.1016/j.cognition.2012.02.004 [PubMed: 22440789]
- Keane BP, Lu H, Papatomas TV, Silverstein SM, & Kellman PJ (2013). Reinterpreting behavioral receptive fields: Lightness induction alters visually completed shape. *Plos One*, 8(6), e62505 10.1371/journal.pone.0062505.s021 [PubMed: 23750200]
- Keane BP, Mettler E, Tsoi V, & Kellman PJ (2011). Attentional signatures of perception: Multiple object tracking reveals the automaticity of contour interpolation. *Journal of Experimental Psychology Human Perception and Performance*, 37(3), 685–698. 10.1037/a0020674 [PubMed: 21038997]
- Kellman PJ, & Shipley T (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, 23(2), 141. [PubMed: 2055000]
- Kellman PJ, & Spelke ES (1983). Perception of partly occluded objects in infancy. *Cognitive Psychology*, 15(4), 483–524. [PubMed: 6641127]
- Kellman PJ, Garrigan P, & Shipley TF (2005). Object interpolation in three dimensions. *Psychological Review*, 112(3), 586–609. 10.1037/0033-295X.112.3.586 [PubMed: 16060752]
- Kellman PJ, Garrigan P, Shipley TF, & Keane BP (2007). Interpolation processes in object perception: Reply to Anderson (2007). *Psychological Review*, 114(2), 488–502. 10.1037/0033-295X.114.2.488 [PubMed: 17500638]
- Kellman PJ, Guttman SE, & Wickens TD (2001). Geometric and neural models of object perception In Shipley TF & Kellman PJ (Eds.), *From fragments to objects: Segmentation and grouping in vision*. Oxford, UK: Elsevier Science Publishers.
- Kogo N, & Wagemans J (2013). The emergent property of border-ownership and the perception of illusory surfaces in a dynamic hierarchical system. *Cognitive Neuroscience*, 279(1737), 2386–2390. 10.1126/science.6539501
- Kogo N, Strecha C, Van Gool L, & Wagemans J (2010). Surface construction by a 2-D differentiation-integration process: A neurocomputational model for perceived border ownership, depth, and lightness in Kanizsa figures. *Psychological Review*, 117(2), 406–439. 10.1037/a0019076 [PubMed: 20438232]
- Kovács I (2000). Human development of perceptual organization. *Vision Research*, 40(10–12), 1301–1310. [PubMed: 10788641]
- Kovács I, & Julesz B (1993). A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. *Proceedings of the National Academy of Sciences of the United States of America*, 90(16), 7495–7497. [PubMed: 8356044]
- Kovács I, Kozma P, Fehér A, & Benedek G (1999). Late maturation of visual spatial integration in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 96(21), 12204–12209. [PubMed: 10518600]
- Kurzban R (2011). *Why Everyone (Else) Is a Hypocrite*. Princeton, NJ: Princeton University Press.

- Ledgeway T, & Smith AT (1994). Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Research*, 34(20), 2727–2740. [PubMed: 7975310]
- Lee T, & Nguyen M (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences*, 98(4), 1907–1911. 10.1073/pnas.031579998
- Leshner G (1995). Illusory contours: Toward a neurally based perceptual theory. *Psychonomic Bulletin and Review*, 2(3), 279–321. [PubMed: 24203713]
- Li W, & Gilbert CD (2002). Global contour saliency and local colinear interactions. *Journal of Neurophysiology*, 88(5), 2846–2856. 10.1152/jn.00289.2002 [PubMed: 12424317]
- Li W, Piëch V, & Gilbert C (2008a). Learning to link visual contours. *Neuron*, 57(3), 442–451. [PubMed: 18255036]
- Li W, Piëch V, & Gilbert CD (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, 7(6), 651–657. 10.1038/nn1255 [PubMed: 15156149]
- Li W, Piëch V, & Gilbert CD (2006). Contour saliency in primary visual cortex. *Neuron*, 50(6), 951–962. 10.1016/j.neuron.2006.04.035 [PubMed: 16772175]
- Li X, Cave KR, & Wolfe JM (2008b). Kanizsa-type subjective contours do not guide attentional deployment in visual search but line termination contours do. *Perception and Psychophysics*, 70(3), 477–488. 10.3758/PP.70.3.477 [PubMed: 18459258]
- Liang H, Gong X, Chen M, Yan Y, Li W, & Gilbert CD (2017). Interactions between feedback and lateral connections in the primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 114(32), 8637–8642. 10.1137/0123044
- Lorenceau J, & Alais D (2001). Form constraints in motion binding. *Nature Neuroscience*, 4(7), 745–751. [PubMed: 11426232]
- Lorenceau J, & Shiffrar M (1992). The influence of terminators on motion integration across space. *Vision Research*, 32(2), 263–273. [PubMed: 1574843]
- Lorenceau J, & Shiffrar M (1999). The linkage of visual motion signals. *Visual Cognition*, 6(3), 431–460.
- Maertens M, & Shapley R (2008). Local determinants of contour interpolation. *Journal of Vision*, 8(7), 3.
- Mandon S, & Kreiter AK (2005). Rapid contour integration in macaque monkeys. *Vision Research*, 45(3), 291–300. 10.1016/j.visres.2004.08.010 [PubMed: 15607346]
- Marr D (1982). *Vision*. New York: W. H. Freeman & Company.
- Mattingley JB, Davis G, & Driver J (1997). Preattentive Filling-in of Visual Surfaces in Parietal Extinction. *Science (New York, NY)*, 275(5300), 671–674. 10.1126/science.275.5300.671
- McDermott J, Weiss Y, & Adelson EH (2001). Beyond junctions: nonlocal form constraints on motion interpretation. *Perception*, 30(8), 905–923. 10.1068/p3219 [PubMed: 11578077]
- McMains SA, & Kastner S (2010). Defining the units of competition: influences of perceptual organization on competitive interactions in human visual cortex. *Journal of Cognitive Neuroscience*, 22(11), 2417–2426. 10.1162/jocn.2009.21391 [PubMed: 19925189]
- McMains SA, & Kastner S (2011). Interactions of Top-Down and Bottom-Up Mechanisms in Human Visual Cortex. *Journal of Neuroscience*, 31(2), 587–597. 10.1523/JNEUROSCI.3766-10.2011 [PubMed: 21228167]
- McManus JNJ, Li W, & Gilbert CD (2011). Inaugural Article: Adaptive shape processing in primary visual cortex. *Proceedings of the National Academy of Sciences*, 108(24), 9739–9746. 10.1073/pnas.1105855108
- Michotte A, Thinès A, & Crabbé G (1964). Les compléments amodaux des structures perceptives [Amodal completion of perceptual structures] In Thinès G, Costall A, & Butterworth G (Eds.), *Michotte's experimental phenomenology of perception*. New York: Routledge.
- Mitchell JF, Sundberg KA, & Reynolds JH (2007). Differential Attention-Dependent Response Modulation across Cell Classes in Macaque Visual Area V4. *Neuron*, 55(1), 131–141. 10.1016/j.neuron.2007.06.018 [PubMed: 17610822]
- Mooney CM, & Ferguson GA (1951). A new closure test. *Canadian Journal of Psychology/Revue Canadienne De Psychologie*, 5(3), 129–133.

- Mullen KT, Beaudot WH, & McIlhagga WH (2000). Contour integration in color vision: a common process for the blue-yellow, red-green and luminance mechanisms? *Vision Research*, 40(6), 639–655. [PubMed: 10824267]
- Murray MM, Imber ML, Javitt DC, & Foxe JJ (2006). Boundary Completion Is Automatic and Dissociable from Shape Discrimination. *Journal of Neuroscience*, 26(46), 12043–12054. 10.1523/JNEUROSCI.3225-06.2006 [PubMed: 17108178]
- Murray MM, Matusz PJ, & Amedi A (2015). Neuroplasticity: Unexpected consequences of early blindness. *Current Biology : CB*, 25(20), R998–R1001. 10.1016/j.cub.2015.08.054 [PubMed: 26485377]
- Murray M, Wylie G, Higgins B, Javitt D, Schroeder C, & Foxe J (2002). The spatiotemporal dynamics of illusory contour processing: combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *Journal of Neuroscience*, 22(12), 5055. [PubMed: 12077201]
- Murray RF (2011). Classification images: A review. *Journal of Vision*, 11(5), 2–2. 10.1167/11.5.2
- Ni R, Wang Z, Wu X, Wang Y, & Li D (2003). Perception of illusory contours enhanced in motion. *Science in China. Series C, Life Sciences / Chinese Academy of Sciences*, 46(6), 570–583. 10.1360/03yc0106
- Nieder A (2002). Seeing more than meets the eye: processing of illusory contours in animals. *Journal of Comparative Physiology a, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 188(4), 249–260. 10.1007/s00359-002-0306-x
- Nieder A, & Wagner H (1999). Perception and neuronal coding of subjective contours in the owl. *Nature Neuroscience*, 2(7), 660–663. 10.1038/10217 [PubMed: 10404200]
- Nugent AK, Keswani RN, Woods RL, & Peli E (2003). Contour integration in peripheral vision reduces gradually with eccentricity. *Vision Research*, 43(23), 2427–2437. [PubMed: 12972393]
- Ostrovsky Y, Meyers E, Ganesh S, Mathur U, & Sinha P (2009). Visual parsing after recovery from blindness. *Psychological Science: a Journal of the American Psychological Society/APS*, 20(12), 1484–1491. 10.1111/j.1467-9280.2009.02471.x
- Otsuka Y, Kanazawa S, & Yamaguchi MK (2004). The effect of support ratio on infants' perception of illusory contours. *Perception*, 33(7), 807–816. 10.1068/p5129 [PubMed: 15460508]
- Palmer EM, Kellman PJ, & Shipley TF (2006). A theory of dynamic occluded and illusory object perception. *Journal of Experimental Psychology: General*, 135(4), 513–541. 10.1037/0096-3445.135.4.513 [PubMed: 17087570]
- Palmer SE (1999). *Vision Science*. Cambridge: MIT Press / Bradford Books.
- Pessoa L, Thompson E, & Noë A (1998). Finding out about filling-in: A guide to perceptual completion for visual science and the philosophy of perception. *Behavioral and Brain Sciences*, 21(06), 723–748. [PubMed: 10191878]
- Peterhans E, & Heydt, Von der R (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *Journal of Neuroscience*, 9(5), 1749–1763. [PubMed: 2723748]
- Pettet MW (1999). Shape and contour detection. *Vision Research*, 39(3), 551–557. 10.1016/S0042-6989(98)00130-8 [PubMed: 10341983]
- Pillow J, & Rubin N (2002). Perceptual completion across the vertical meridian and the role of early visual cortex. *Neuron*, 33(5), 805–813. [PubMed: 11879656]
- Pinker S (2009). *How the Mind Works*. New York: W. W. Norton & Company.
- Pitcher D, Charles L, Devlin JT, Walsh V, & Duchaine B (2009). Triple Dissociation of Faces, Bodies, and Objects in Extrastriate Cortex. *Current Biology : CB*, 19(4), 319–324. 10.1016/j.cub.2009.01.007 [PubMed: 19200723]
- Polat U, & Sagi D (1994a). Spatial interactions in human vision: from near to far via experience-dependent cascades of connections. *Proceedings of the National Academy of Sciences of the United States of America*, 91(4), 1206–1209. [PubMed: 8108388]
- Polat U, & Sagi D (1994b). The architecture of perceptual spatial interactions. *Vision Research*, 34(1), 73–78. [PubMed: 8116270]
- Polat U, Mizobe K, Pettet MW, Kasamatsu T, & Norcia AM (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature*, 391(6667), 580–584. 10.1038/35372 [PubMed: 9468134]

- Pratte MS, Ling S, Swisher JD, & Tong F (2013). How attention extracts objects from noise. *Journal of Neurophysiology*, 110(6), 1346–1356. 10.1152/jn.00127.2013 [PubMed: 23803331]
- Prinz JJ (2006). Is the mind really modular. *Contemporary Debates in Cognitive Science*, 22–36.
- Purghé F, & Coren S (1992). Subjective contours 1900–1990: research trends and bibliography. *Perception and Psychophysics* (Vol. 51, pp. 291–304). [PubMed: 1561054]
- Pylyshyn Z (1999). Is vision continuous with cognition?: The case for cognitive impenetrability of visual perception. *Behavioral and Brain Sciences*, 22(03), 341–365. [PubMed: 11301517]
- Pylyshyn ZW, & Storm RW (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spatial Vision*, 3(3), 179–197. [PubMed: 3153671]
- Qiu FT, Sugihara T, & Heydt, von der R (2007). Figure-ground mechanisms provide structure for selective attention. *Nature Neuroscience*, 10(11), 1492–1499. 10.1038/nn1989 [PubMed: 17922006]
- Ramachandran V, Ruskin D, Cobb S, Rogers-Ramachandran D, & Tyler C (1994). On the perception of illusory contours. *Vision Research*, 34(23), 3145–3152. [PubMed: 7975347]
- Ramalingam N, McManus JNJ, Li W, & Gilbert CD (2013). Top-down modulation of lateral interactions in visual cortex. *The Journal of Neuroscience : the Official Journal of the Society for Neuroscience*, 33(5), 1773–1789. 10.1523/JNEUROSCI.3825-12.2013 [PubMed: 23365217]
- Rao RP, & Ballard DH (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1), 79–87. 10.1038/4580 [PubMed: 10195184]
- Regolin L, & Vallortigara G (1995). Perception of partly occluded objects by young chicks. *Perception and Psychophysics*, 57(7), 971–976. [PubMed: 8532500]
- Reynolds JH, Chelazzi L, & Desimone R (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *The Journal of Neuroscience*, 19(5), 1736–1753. [PubMed: 10024360]
- Reynolds RI (1981). Perception of an illusory contour as a function of processing time. *Perception*, 10(1), 107–115. [PubMed: 7255079]
- Ringach D, & Shapley R (1996). Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Research*, 36(19), 3037–3050. [PubMed: 8917767]
- Ritzl A, Marshall JC, Weiss PH, Zafiris O, Shah NJ, Zilles K, & Fink GR (2003). Functional anatomy and differential time courses of neural processing for explicit, inferred, and illusory contours. An event-related fMRI study. *NeuroImage*, 19(4), 1567–1577. [PubMed: 12948712]
- Rock I (1983). *The Logic of Perception*. Cambridge, MA: MIT Press/Bradford Books.
- Rorschach H (1921). *Pscyodiagnostik*. Bern (Switzerland): Bircher.
- Rubin N (2001). The role of junctions in surface completion and contour matching. *Perception*, 30(3), 339–366. 10.1068/p3173 [PubMed: 11374204]
- Rubin N, Nakayama K, & Shapley R (1997). Abrupt learning and retinal size specificity in illusory-contour perception. *Current Biology : CB*, 7(7), 461–467. [PubMed: 9210373]
- Runeson S (1977). On the possibility of “smart” perceptual mechanisms. *Scandinavian Journal of Psychology*, 18(3), 172–179. [PubMed: 897593]
- Scholl BJ, & Leslie AM (1999). Modularity, Development and “Theory of Mind.” *Mind & Language*, 14(1), 131–153.
- Seghier ML, & Vuilleumier P (2006). Functional neuroimaging findings on the human perception of illusory contours. *Neuroscience and Biobehavioral Reviews*, 30(5), 595–612. 10.1016/j.neubiorev.2005.11.002 [PubMed: 16457887]
- Seghier M, Dojat M, Delon-Martin C, Rubin C, Warnking J, Segebarth C, & Bullier J (2000). Moving illusory contours activate primary visual cortex: an fMRI study. *Cerebral Cortex* (New York, NY : 1991), 10(7), 663–670.
- Sehatpour P, Molholm S, Javitt DC, & Foxe JJ (2006). Spatiotemporal dynamics of human object recognition processing: An integrated high-density electrical mapping and functional imaging study of “closure” processes. *NeuroImage*, 29(2), 605–618. 10.1016/j.neuroimage.2005.07.049 [PubMed: 16168676]

- Sehatpour P, Molholm S, Schwartz TH, Mahoney JR, Mehta AD, Javitt DC, et al. (2008). A human intracranial study of long-range oscillatory coherence across a frontal-occipital-hippocampal brain network during visual object processing. *Proceedings of the National Academy of Sciences of the United States of America*, 105(11), 4399–4404. [PubMed: 18334648]
- Sekuler AB, Palmer SE, & Flynn C (1994). Local and global processes in visual completion. *Psychological Science*, 5(5), 260–267. 10.2307/40063115?ref=search-gateway:dcbf2590212b47d53073a0d40181f841
- Shipley TF, & Kellman PJ (1992). Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Perception and Psychophysics*, 52(1), 97–106. [PubMed: 1635860]
- Shipley TF, & Kellman PJ (1993). Optical tearing in spatiotemporal boundary formation: when do local element motions produce boundaries, form, and global motion? *Spatial Vision*, 7(4), 323–339. [PubMed: 8110632]
- Shore DI, & Enns JT (1997). Shape completion time depends on the size of the occluded region. *J Exp Psychol Hum Percept Perform*, 23(4), 980–998. [PubMed: 9269724]
- Shpaner M, Murray MM, & Foxe JJ (2009). Early processing in the human lateral occipital complex is highly responsive to illusory contours but not to salient regions. *European Journal of Neuroscience*, 30(10), 2018–2028. 10.1111/j.1460-9568.2009.06981.x [PubMed: 19895562]
- Silverstein SM, & Keane BP (2011). Perceptual organization impairment in schizophrenia and associated brain mechanisms: Review of research from 2005 to 2010. *Schizophrenia Bulletin*, 37(4), 690–699. 10.1093/schbul/sbr052 [PubMed: 21700589]
- Singh M, & Fulvio JM (2005). Visual extrapolation of contour geometry. *Proceedings of the National Academy of Sciences of the United States of America*, 102(3), 939–944. 10.1073/pnas.0408444102 [PubMed: 15647347]
- Soriano M, Spillmann L, & Bach M (1996). The abutting grating illusion. *Vision Research*, 36(1), 109–116. 10.1016/0042-6989(95)00107-B [PubMed: 8746248]
- Spehar B, & Clifford CWG (2003). When does illusory contour formation depend on contrast polarity? *Vision Research*, 43(18), 1915–1919. [PubMed: 12831754]
- Stanley DA, & Rubin N (2003). fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron*, 37(2), 323–331. [PubMed: 12546826]
- Sun L, Grützner C, Bölte S, Wibral M, Tozman T, Schlitt S, et al. (2012). Impaired Gamma-Band Activity during Perceptual Organization in Adults with Autism Spectrum Disorders: Evidence for Dysfunctional Network Activity in Frontal-Posterior Cortices. *The Journal of Neuroscience*, 32(28), 9563–9573. 10.1523/JNEUROSCI.1073-12.2012 [PubMed: 22787042]
- Valenza E, & Bulf H (2007). The role of kinetic information in newborns' perception of illusory contours. *Developmental Science*, 10(4), 492–501. 10.1111/j.1467-7687.2007.00602.x [PubMed: 17552938]
- Valenza E, & Bulf H (2010). Early development of object unity: evidence for perceptual completion in newborns. *Developmental Science*, 1–10. 10.1111/j.1467-7687.2010.01026.x [PubMed: 20121858]
- Valenza E, Leo I, Gava L, & Simion F (2006). Perceptual completion in newborn human infants. *Child Development*, 77(6), 1810–1821. [PubMed: 17107462]
- van Lier R, van der Helm P, & Leeuwenberg E (1994). Integrating global and local aspects of visual occlusion. *Perception*, 23(8), 883–903. 10.1068/p230883 [PubMed: 7870565]
- Vancleef K, Wagemans J, & Humphreys GW (2013). Impaired texture segregation but spared contour integration following damage to right posterior parietal cortex. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale*. 10.1007/s00221-013-3629-7
- Vandenbroucke ARE, Fahrenfort JJ, Sligte IG, & Lamme VAF (2014). Seeing without Knowing: Neural Signatures of Perceptual Inference in the Absence of Report. *Journal of Cognitive Neuroscience*, 26(5), 955–969. 10.1038/nn1294 [PubMed: 24283494]
- Varin D (1971). Fenomeni di contrasto e diffusione cromatica nell'organizzazione spaziale del campo percettivo. *Revista Di Psicologia*, 101–128.
- Volberg G, Wutz A, & Greenlee MW (2013). Top-Down Control in Contour Grouping. *Plos One*, 8(1), e54085 10.1371/journal.pone.0054085.g005 [PubMed: 23326575]

- Voss JL, Federmeier KD, & Paller KA (2012). The Potato Chip Really Does Look Like Elvis! Neural Hallmarks of Conceptual Processing Associated with Finding Novel Shapes Subjectively Meaningful. *Cerebral Cortex*, 22(10), 2354–2364. 10.1093/cercor/bhr315 [PubMed: 22079921]
- Vuilleumier P, Valenza N, & Landis T (2001). Explicit and implicit perception of illusory contours in unilateral spatial neglect: behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia*, 39(6), 597–610. [PubMed: 11257285]
- Wagemans JP (1988). Modules in vision: a case study of interdisciplinarity in cognitive science. *Acta Psychologica*, 67(1), 59–93. [PubMed: 3369311]
- Wagemans J, van Lier R, & Scholl BJ (2006). Introduction to Michotte's heritage in perception and cognition research. *Acta psychologica* (Vol. 123, pp. 1–19). 10.1016/j.actpsy.2006.06.003
- Wattam-Bell J (1991). Development of motion-specific cortical responses in infancy. *Vision Research*, 31(2), 287–297. 10.1016/0042-6989(91)90119-P [PubMed: 2017889]
- Wattam-Bell J (1996). Visual motion processing in one-month-old infants: preferential looking experiments. *Vision Research*, 36(11), 1671–1677. 10.1016/0042-6989(95)00236-7 [PubMed: 8759467]
- Wertheimer M (1923). Untersuchungen zur Lehre von der Gestalt, II. *Psychologische Forschung*, 4, 301–350 (Translated as “Investigations on Gestalt principles.” In Spillmann L (Ed.), (2012). Max Wertheimer. On perceived motion and figural organization (pp. 127–182). Cambridge, MA: M.I.T. Press.)
- Wokke ME, Vandenbroucke ARE, Scholte HS, & Lamme VAF (2013). Confuse your illusion: feedback to early visual cortex contributes to perceptual completion. *Psychological Science*, 24(1), 63–71. 10.1177/0956797612449175 [PubMed: 23228938]
- Zhou J, Tjan B, Zhou Y, & Liu Z (2008). Better discrimination for illusory than for occluded perceptual completions. *Journal of Vision*, 8(7), 26.

Fig. 1. Nine varieties of contour interpolation.

Interpolation is defined broadly so as to include: (A, B) modal and amodal completion, where contours appear in front of or behind a surface, respectively (Kanizsa, 1955); (C,D) Varin figures and abutting line gratings, in which line endings (also known as terminators) induce the appearance of a single well-defined contour (Varin, 1971); (E,F) contour integration, where interpolation sprouts between co-aligned edge elements (Field, Hayes, & Hess, 1993; Kapadia, Ito, Gilbert, & Westheimer, 1995); (G) motion linking, where four line segments coalesce into a partly occluded diamond that orbits upright about a central point (Lorenceanu & Shiffrar, 1992); (H) spatiotemporal interpolation, in which different parts of an interpolated contour appear at different points in time (Adapted from E. M. Palmer, Kellman, & Shipley, 2006); and (I) three-dimensional interpolation, where a single contour can stereoscopically float in front of or slant behind another surface despite not being physically specified in either retinal image (the percept is achieved via crossing of the eyes) (Adapted from Kellman, Garrigan, & Shipley, 2005).

Fig. 2. Interpolation is fast and spatially specific.

(A) Cells in superficial layers of monkey V2 responded differentially to interpolated contours within 50 ms and most strongly within the following 100 ms (Adapted from Lee & Nguyen, 2001). (B) V1 cells in the same study responded to real and interpolated contours, but the effect diminished dramatically when the contours were shifted slightly away from the receptive field centers (Adapted from Lee & Nguyen, 2001). (C) Subjects who judged whether a briefly appearing dot fell within or outside of a backward-masked Kanizsa square reached an impressive level of accuracy (2.5 arcmin) with only ~120 ms of presentation time. This duration was significantly faster than that required for an “arrow” control condition (173 ms) (Adapted from Guttman & Kellman, 2004) but slower than that needed for a real contour stimulus (80 ms). A Kanizsa square (D) becomes more salient when seemingly irrelevant background texture perfectly aligns with the contours (E), but less so if the texture is nudged out of alignment (F) (Adapted from Ramachandran et al., 1994).

Fig. 3. Contour interpolation is mandatory.

(A) On each trial of a multiple vertex tracking task, a distractor and an initially-flashed target disk (T) appeared within each screen quadrant. The disks transformed into pac-men, orbited within their respective quadrants for several seconds, and then transitioned back into undifferentiated disks. When the trial ended, subjects attempted to identify the originally flashed targets. On some trials, each target periodically interpolated with two nearby distractors (top panel in A), on other trials, the same objects were flipped 180 degrees to prevent interpolation (bottom panel in A). (B) Target-distractor interpolation worsened tracking; the effect could be released by (C) increasing the pac-man rotation angle or (D) decreasing the pac-man size (the dotted lines are shown for illustration only). (E, F, G) In visual search, subjects were forced to engage in a slow, serial search if amodal completion could transform the target (a notched circle) into a distractor look-alike (full circle; Adapted from Davis & Driver, 1998). (H, I) However, visual search proceeded quickly and without regard to distractor set size when the target hovered stereoscopically in front of the illusory square to prevent amodal completion (Adapted from Davis & Driver, 1998).

Fig. 4. Evidence that interpolation is cognitively encapsulated.

(A) Cross-fusing the two images produces a curved illusory contour even though the surrounding context would suggest a fourth camouflaged lobe (Adapted from Kellman et al., 2005). (B) Context and past experience should incline us to see a central octagon, but right angles are perceived behind each occluder (Adapted from Kanizsa, 1985). (C) Humans do not have seven-foot arms, but the geometry of the surrounding segments impels such a perception. (D) When the fragmented cube on the left is viewed from a specific angle, amodal completion necessitates the perception of the physically impossible cube on the right (Cochran, 1966). (E) Priming subjects with a completed shape before each trial did not improve the ability to discern whether partly occluded versions of those shapes orbited clockwise or counterclockwise (Adapted from Lorenceau & Alais, 2001).

Fig. 5. Contour abstraction versus contour interpolation.

(A) The classic Dalmatian dog photograph (by R. C. James) is initially difficult to see because interpolation is mostly absent, and the shape must be cognitively inferred (or “abstracted”) from a few local elements. (B) When the shape contours are relatable and have sufficient support ratio, interpolation is robust and a rabbit figure pops out. Global shape contours of (C) Mooney figures, (D) pareidolia figures, or (E) largely occluded objects cannot be interpolated, but must be imagined or inferred based on background knowledge or biases. (F) The central image of the trio is ambiguous between a man’s face and woman’s body (left and right image, respectively). Alternating between the two interpretations adds different contours to the image (e. g., parts of the woman’s arm, or parts of the man’s eye) so as to render it subjectively unambiguous (Fisher, 1967). (G) In certain psychophysical paradigms such as the “bubble” method shown here, objects are shown in a randomly degraded fashion (adapted from Gosselin & Schyns, 2001) such that some of the contours will interpolate (e.g., the face outline) while others must be abstracted (the entire mouth outline). (H) Recognizing the object depicted in partly visible line drawings is easy when the remaining segments are relatable (center image), but very hard when they are not (right image) (Adapted from Biederman, 1987).

Fig. 6. Cognitive expectation alters illusory shape discrimination but not contour filling-in.

(A) Subjects discriminated fat and thin shapes, the visible edges of which were positioned to induce or block illusory contours (relatable and unrelatable condition, respectively). Half of the trials incorporated distractor lines, which are known to disrupt the formation of illusory contours. (B) Across two experiments, half of the subjects ($N=45$) were cognitively biased to adopt a "group" strategy via pictures and instructions; the remaining subjects ($N=45$) were biased to adopt an "ungroup" strategy, which entailed treating the visible edge fragments as disconnected. (C, D) Applying an ungroup strategy neither worsened performance on the unrelatable condition ($p=.14$) nor altered the distractor line interaction ($p=.49$), but did worsen overall relatable performance ($p<.001$). Figure adapted from Keane et al. (2012).

Fig. 7. Ways to weaken/strengthen contour salience so as to decrease/increase the chances of observing modularity features.

Relative to the contour in A, edge elements less strongly interpolate when: (B, C) they connect via a sharply turned or misaligned path; (D, E) the junction structure or border ownership cues are inconsistent with occlusion or camouflage; or (F) additional (“noise”) edge segments compete to interpolate with a given segment. Relative to the contour in A, two edge elements *more* strongly interpolate when: (G, H) they move cohesively or appear abruptly behind an occluder; (I) the occlusion is distributed more evenly throughout the entire contour; (J) the support ratio is larger; or (K) the contour is closed. See text for supporting references.