

A Century of Gestalt Psychology in Visual Perception: II. Conceptual and Theoretical Foundations

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Our first review article (Wagemans et al., 2012) on the occasion of the centennial anniversary of Gestalt psychology focused on perceptual grouping and figure–ground organization. It concluded that further progress requires a reconsideration of the conceptual and theoretical foundations of the Gestalt approach, which is provided here. In particular, we review contemporary formulations of holism within an information-processing framework, allowing for operational definitions (e.g., integral dimensions, emergent features, configural superiority, global precedence, primacy of holistic/configural properties) and a refined understanding of its psychological implications (e.g., at the level of attention, perception, and decision). We also review 4 lines of theoretical progress regarding the law of Prägnanz—the brain's tendency of being attracted towards states corresponding to the simplest possible organization, given the available stimulation. The first considers the brain as a complex adaptive system and explains how self-organization solves the conundrum of trading between robustness and flexibility of perceptual states. The second specifies the economy principle in terms of optimization of neural resources, showing that elementary sensors working independently to minimize uncertainty can respond optimally at the system level. The third considers how Gestalt percepts (e.g., groups, objects) are optimal given the available stimulation, with optimality specified in Bayesian terms. Fourth, structural information theory explains how a Gestaltist visual system that focuses on internal coding efficiency yields external veridicality as a side effect. To answer the fundamental question of why things look as they do, a further synthesis of these complementary perspectives is required.

Keywords: Gestalt, holism, simplicity versus likelihood, dynamical systems, information theory

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General Introduction

From the very beginning, the following ideas were central to Gestalt thinking. Phenomenal experience consists of part-whole structures, configurations, or *Gestalten*. A Gestalt is an integrated, coherent structure or form, a whole that is different from the sum of the parts. Gestalts emerge spontaneously from self-organizational processes in the brain. Gestalts result from global field forces that lead to the simplest possible organization, or minimum solution, given the available stimulation. With this simplicity or minimum principle (also known as the *law of Prägnanz*), the Gestaltists found themselves in opposition to the likelihood principle advanced by von Helmholtz: the idea that the visual system interprets, through some unconscious inference mechanism, incoming proximal stimuli in terms of the most likely distal source that might have given rise to these proximal stimuli.

In the first half of the 20th century, Gestalt psychology struggled with several foundational problems arising from vaguenesses in the research agenda: the inability to precisely define terms like emergence and *Prägnanz*, the inability to quantify the minimum principle and thus to make specific behavioral predictions, the lack of methodological tools for operationalizing these notions, and the difficulty of articulating testable theories or models of the underlying neural mechanisms. All of these shortcomings led to growing dissatisfaction with the Gestalt program of research in the 1950s and 1960s, and the subsequent decline of its impact on research in perception and the rest of psychology. In our first article on the occasion of 100 years of Gestalt psychology (Wagemans et al., 2012), we demonstrated how some of these shortcomings were already alleviated in more contemporary research, performed in the Gestalt spirit, on perceptual grouping and figure-ground organization. Specifically, it was shown that psychophysical and computational work on grouping, using carefully constructed stimuli, allowed for quantification of grouping principles. Furthermore, experiments with richer stimuli than previously used revealed new grouping and figure-ground principles, as well as their interactions with other aspects of visual processing (e.g., attention and shape perception). Finally, it was shown how grouping and figure-ground organization could be related to computational principles, ecological statistics, and neural mechanisms.

The present review complements the first one (Wagemans et al., 2012) by describing the progress made regarding the core notions from Gestalt theory—holism, emergence, the primacy of the whole, the minimum principle or law of *Prägnanz*, and self-organizing dynamics. First, we clarify the conceptual foundations of Gestalt thinking by refining notions such as holistic properties, emergent features, configural superiority, and global precedence—relying mainly on operational definitions fitting into a more contemporary information-processing framework (Section 2). Afterwards, we illustrate recent progress regarding the deeper theoretical foundations of the Gestalt framework by reviewing models that implement, and thereby explain, Gestalt principles as on-going dynamics (Section 3) and from three considerations of economy: in the use of neural sensors (Section 4), in terms of Bayes' theorem (Section 5), and in symbolic descriptions that allow for a dynamic implementation (Section 6). For a more detailed list of contents, see the Appendix.

Although the discussed models pertain to specific perceptual topics such as perceptual switching, apparent motion, object for-

mation, and visual regularity, Sections 3–6 focus on generic theoretical frameworks such as dynamical systems theory, complex adaptive systems, measurement theory, the Bayesian approach to perception, and neural networks. A review of these approaches might also be useful to psychologists who are not primarily interested in visual perception, but are intrigued by the Gestalt approach to psychological theory. We hope that casting a range of current perspectives on the issues raised in Gestalt psychology will contribute significantly towards a synthesis between previous oppositions (e.g., regarding flexibility vs. stability, intrinsic vs. extrinsic processes, simplicity vs. likelihood), but the current status of the field does not allow for such a synthesis yet. Only the first steps in this direction are taken in this article. In the main body of the article, we explicitly point out the interrelations between different theoretical notions and views, but a more integrative summary is provided only in the final, concluding section of the article. We start our review with a discussion of historical and contemporary views on holism, a fundamental notion of Gestalt psychology.

Holism

Holism in Traditional Gestalt Psychology

Gestalt psychologists argued that perceptual experiences are intrinsically holistic and organized. They forcefully rejected the proposal by structuralism (Wundt, Titchener)—rooted firmly in British empiricism—that perceptions are constructed from atoms of elementary, unrelated local sensations that are unified by associations due to spatial and temporal contiguity. The Gestalt theorists rejected both atomism and associationism, as well as any summative approach, as an account for the experience of structured wholes. This was most clearly visible in Wertheimer's (1912) phi motion, in which pure motion could be seen without actually seeing any object moving. In our first article (Wagemans et al., 2012), the historical significance of this discovery was discussed as the roots of the Berlin school of Gestalt psychology and its distinction from the Graz school. Here, we offer a brief description of the essential theoretical claims.

Wertheimer (1924/1938b, p. 2) described holism as the “fundamental formula” of traditional Gestalt psychology: “There are wholes, the behavior of which is not determined by that of their individual elements, but where the part-processes are themselves determined by the intrinsic nature of the whole.” A specific sensory whole is qualitatively different from what one might predict by considering only its individual parts, and the quality of a part depends upon the whole in which this part is embedded (e.g., Köhler, 1930/1971). The proposition most often stated as characterizing Gestalt theory, that the whole is more than the sum of its parts, is inaccurate. It is more correct to say, “The whole is something else than the sum of its parts, because summing is a meaningless procedure, whereas the whole-part relationship is meaningful” (Koffka, 1935, p. 176).

The idea that sensory wholes possess properties that cannot be derived from the properties of their constituents was not the discovery of Gestalt psychology. Before the advent of Gestalt theory, Christian von Ehrenfels (1890/1988) called attention to the fact that perceptual experiences, such as perception of melody or the shape of a visual object, are more than the mere sum of their independent components. To account for such perceptual experi-

ences, von Ehrenfels postulated a new sort of element, which he termed Gestalt quality (*Gestaltqualität*). The Gestalt quality is superadded to our experiences of sensory elements. Gestalt qualities exist alongside or above the fundamental independent constituents with which they are associated.

The Berlin school's view of holism was more radical. Rejecting the premise that the sum of sensory elements constitutes the primary foundation of perceptual experience, Wertheimer (1922/1938a) objected to any summative account in which something is *added* to the sum of sensory elements, be it von Ehrenfels's (1890/1988) qualities, relations-between-elements, or higher mental operations imposed on the sensory elements to produce unity. Rather, he argued that we directly and immediately perceive Gestalten: integrated, structured wholes the properties of which are not derived from its individual parts or their simple sum and within which constituent parts are in dynamic interrelations, such that the specific functions and properties of the parts can only be defined in relation to the whole.

This formulation raises many deep questions regarding the functional relationships between parts and wholes and how they might continuously change through their dynamic interrelationships (e.g., Grelling & Oppenheim, 1938; Rausch, 1937; Smith, 1988). In general, it is useful to distinguish Gestalt parts (in a person's perception) from stimulus parts (in the environment). Gestalt parts evolve from an interaction among the representations of stimulus parts, even if the stimulus parts themselves do not change, so that the whole determines how a stimulus part is perceived and whether it becomes a Gestalt part.

Modern Approaches to Holism

The traditional Gestalt view on part-whole relations summarized above may appear somewhat fuzzy to modern readers, who are used to specific operational definitions. These have been offered by more recent researchers, working in an information-processing framework. We review four of these notions here: (a) Garner's dimensional integrality, (b) emergent features and configural superiority, (c) global precedence in hierarchical patterns, and (d) the primacy of holistic or configural properties.

Garner's dimensional integrality. One notion central to Gestalts is that whatever parts (features, elements), if any, they may contain, these parts are perceived holistically rather than separately or independently. Garner (1962, 1974; Garner, Hake, & Eriksen, 1956) looked for empirical support from converging operations, starting with elementary 2-D stimuli, in which each of the given dimensions A and B possess two levels, 1 and 2, resulting in four stimuli: A_1B_1 , A_1B_2 , A_2B_1 , and A_2B_2 . If Dimension A were color with 1 = red and 2 = green, and B were shape with 1 = circle and 2 = square, the four stimuli would be red circle, green circle, red square, green square. The first converging operations tested whether perceivers could make speeded judgments of (say) color without experiencing interference from uncorrelated variation on shape in a sequence of stimuli; if not, they would experience what is now called *Garner interference*, meaning that one dimension was not being perceived independently from the other. A second convergence tested whether two stimuli that differed (redundantly) in both dimensions could be discriminated from each other more quickly than could two stimuli differing in just one dimension. If so, and if the magnitude of that

redundancy gain exceeded what would be created by mere horse-race statistics, that too would indicate that the dimensions were not being perceived separately or sequentially but were instead perceived jointly. A third convergence tested performance in divided attention tasks: If perceivers could make classification judgments that required perceiving both dimensions as well as or better than judgments based on only one, that would indicate they could divide their attention across both dimensions simultaneously (Garner, 1974).

The results showed that some stimulus dimensions, such as shape and color, are perceived separately: They show no Garner interference, no significant gains from redundancy, and worse performance in divided attention tasks than in selective attention tasks. Such dimensions further showed city-block metrics on similarity judgments (the perceived dissimilarity of two stimuli is the simple sum of their dissimilarities on the two dimensions). Garner (1974) called these dimensions *separable*; for them, the whole does indeed resemble the sum of its parts.

Other stimulus dimensions, such as the hue and saturation of a single color chip, revealed a pattern of results he called *integral*: They show both Garner interference and redundancy gains, but again they show poor performance on divided attention tasks relative to selective attention. In addition, integral dimensions show Euclidean metrics on similarity judgments: The similarity of two stimuli is determined by the length of the diagonal connecting them in 2-D space. The interpretation is that integral dimensions are perceived together, simultaneously, in a way in which the separate dimensions have no psychological primacy. Shape dimensions, such as curvature and elongation, are often perceived as integral dimensions, even though they can be defined mathematically in independent terms, but one can use Garner's procedure to psychophysically calibrate the dimensions and make them as separable as possible (Ons, De Baene, & Wagemans, 2011).

For some stimuli, Dimension A is integral with respect to B, but B is separable with respect to A. Garner called these *asymmetrically integral* dimensions. Still other stimulus dimensions are called *configural* when they show Garner interference, no redundancy gains, but better performance on divided attention than on selective attention tasks. An example would be the four stimuli generated from pairs of parentheses: ((, (),), and)). Such stimuli seem to be perceived via neither integral nor separable processing of their individual curved segments but rather via emergent features such as bilateral symmetry, parallelism, and closure (Pomerantz & Garner, 1973).

Emergent features and configural superiority. *Emergent features* or EFs are features that are possessed by wholes—groups of parts—but not by any individual part nor by any single group of parts. Thus, they emerge when parts combine into wholes. Wholes can have fewer or more Gestalt qualities because they possess fewer or more EFs. If a set of trees is closely spaced, proximity and similarity lead them to be grouped visually into a whole forest, and that forest has properties (such as density) not possessed by any individual tree. If the trees are planted into regularly spaced rows, however, they now gain EFs such as collinearity and symmetry that go beyond the mere clumping of parts into bunches. Wholes with yet stronger Gestalt qualities show EFs that are unpredictable and even *surprising*, characteristics central to the notion of emergence itself (e.g., the Dalmatian dog once it is seen to stand out

from the rest of the scene; see Figure 13 in Gallace & Spence, 2011).

Let us start with the simplest of all stimuli, a single dot, and assume that its only distinguishing feature is its location. If we add a second such dot, we then add its location as a second feature, but we also add interdot distance and angle as two EFs not possessed by either individual dot, though they are derivable from the dots' positions. We can also start with a single line segment as a stimulus, with length and orientation as distinctive features in addition to its location. If we add a second segment, we add its location, length, and orientation, but we also gain EFs such as the distance and angle between the two lines and further EFs such as the type of intersection they form if they touch (T, L, X, etc.) and possibly forms of parallelism, collinearity, and symmetry as well.

With stimuli of greater complexity, there are an infinite number of logically possible EFs that can be imagined. With a face, for example, the ratio of the diameter of the left pupil to the width of the mouth is an EF not possessed by the eye or the mouth alone, but it is unlikely that perceivers would attend to such an EF, so only a subset of EFs is likely to be perceived (i.e., have psychological reality). For instance, two line segments always create a specific angle, but only certain angles are particularly salient, such as zero degrees, which denotes that the lines are either parallel or collinear. Research has shown that humans and some lower animals are exquisitely sensitive to parallelism and collinearity, which also serve as quasi regularities in the case of small deviations from zero degrees (e.g., Kukkonen, Foster, Wood, Wagemans, & Van Gool, 1996; Wagemans, Van Gool, Lamote, & Foster, 2000). When a third line segment is added, new EFs become possible, such as closure, to which visual systems are also quite sensitive (Chen, 2005; Wagemans et al., 2012, Section 4). Importantly, no matter how many relational properties are added to the originally local and basic features, these EFs may be merely sufficient for perceiving a global Gestalt, not necessary: They may form the basis for it, but they cannot be the cause of it.

Only some of these EFs also give rise to *configural superiority effects* or CSEs (Pomerantz, Sager, & Stoever, 1977), which can be used as an index to indicate when wholes are perceived before parts (forest before trees). The easiest test for CSEs starts with benchmarking performance in a baseline task of localizing a singleton (or odd one out) in a search display, for example, finding a single B in a display otherwise consisting of As. Then an identical-context stimulus C is added to each element so the task is now to locate the sole BC in a field of ACs. Normally, adding identical, noninformative context hurts performance because it makes the stimuli more similar (in addition to increasing overall processing load and possibly introducing masking or crowding). That is the case with these letter stimuli: Participants take longer to find the BC in a field of ACs than to find the B in a field of As.

With other parts substituted for A, B, and C, however, the opposite result can arise, which constitutes evidence for configural superiority. If diagonal line segments and an L-shaped corner are used for A, B, and C so that the diagonals combine with the Ls to form arrows and triangles, perceivers are more than twice as fast to spot the target (see Figure 1A). When these same parts are shifted just slightly in position, however, the CSE is lost (see Figure 1B). Similar effects arise with pairs of parentheses (see Figures 1C and 1D).

The key factor in obtaining a CSE appears to be the creation of salient emergent features when the context C is added to the base elements A and B. With the arrows and triangles of Figure 1A, those EFs appear to be closure, number of terminators, and type of intersection. Some of the strongest, most robust CSEs discovered involve topological EFs such as presence versus absence of holes, connectivity, and inside–outside relationships (Chen, 2005). (For more CSEs and a new framework called the *theory of basic Gestalts*, see Pomerantz & Portillo, 2011.)

Global precedence. Navon's (1977) *global precedence hypothesis* states that processing proceeds from global structures towards analysis of local properties. This hypothesis was formulated within a framework that views a visual object as represented by a hierarchical network with nested relationships. The globality of a visual property corresponds to the level it occupies within the hierarchy: Properties at the top of the hierarchy are more global than those at the bottom, which are in turn more local. Consider a face defined by spatial relationship between facial components (e.g., eyes, nose, mouth), which are, in turn, defined by relationships among their subparts. The spatial relationship between the components is more global than the specific shapes of the components, and in turn, the relationship between the subparts of a component is more global than the specific properties of the subparts. The global precedence hypothesis claims that the order of processing of an object is from global to local: Global properties of a visual object are processed first, followed by analysis of local properties. It has been tested with hierarchical patterns, in which larger figures are constructed from smaller figures (first introduced by Asch, 1962, and later by Kinchla, 1974, 1977). An example is a set of hierarchical letters: large letters constructed from the same set of smaller letters having either the same identity as the larger letter or a different identity. Hierarchical patterns like these satisfy two conditions, which are critical for testing the hypothesis (Navon, 1977): First, the global and local structures can be equated in familiarity, complexity, codability, and identifiability, so they differ only in level of globality, and second, the two structures can be independent, so that one structure cannot be predicted from the other.

In a popular paradigm, observers are presented with hierarchical stimuli and are required to identify the larger (global) or the smaller (local) letter, in separate blocks of trials. Findings of *global advantage*—faster identification of the global letter than the local letter and disruptive influence from irrelevant global conflicting information on local identification (global-to-local interference)—are taken as support for global precedence (e.g., Navon, 1977, Experiment 3). Much subsequent research has concentrated on delineating the boundary conditions of the global advantage effect and examining whether its locus is perceptual or postperceptual (for reviews, see Kimchi, 1992; Navon, 2003). Several factors can modulate the effect, including overall size, eccentricity, spatial uncertainty, elements' sparseness, number of elements, relative size of elements, figural goodness, exposure duration, and attention allocation. Research indicates that the global advantage—when it occurs—arises at the perceptual level, although the effect can be magnified by postperceptual, response-related processes.

Overall, global advantage is normally observed with the typical hierarchical stimuli used in the global–local paradigm to the limits of visibility and visual acuity. Nonetheless, to the extent that

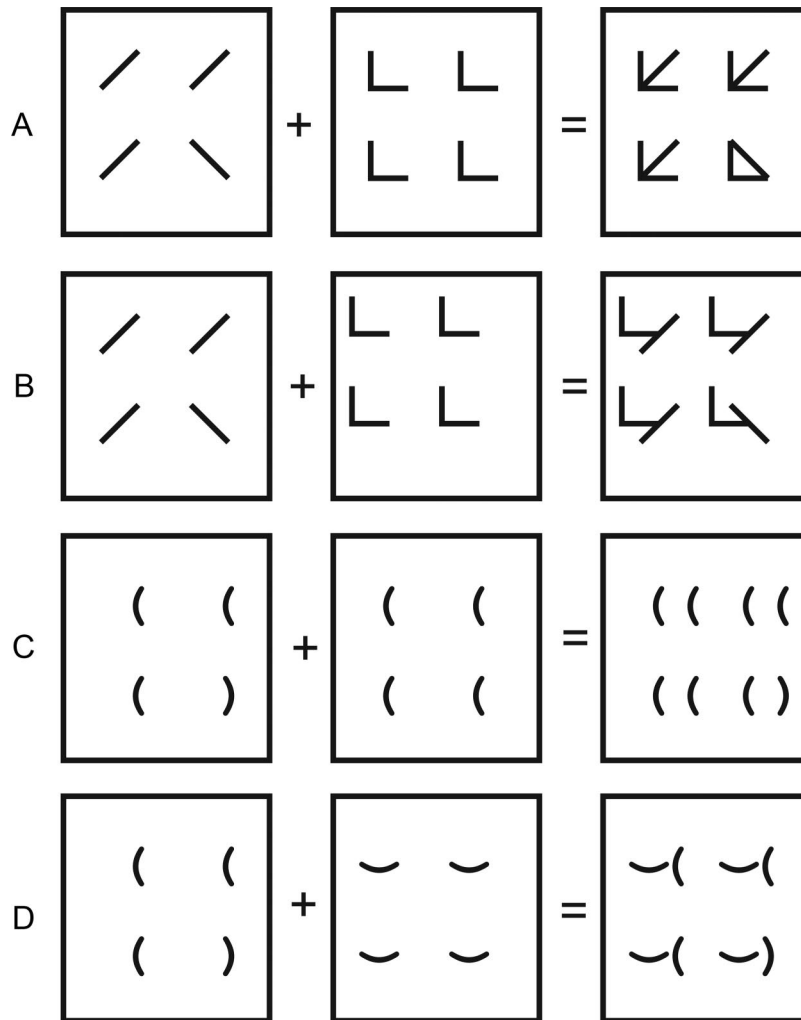


Figure 1. Emergent features in visual search, demonstrating configural superiority. Adding redundant elements to each of the stimuli improves detection of the odd element in the display, but only when certain emergent features arise (such as closure in Row A or symmetry in Row C). Adapted from "Perception of Wholes and Their Component Parts: Some Configural Superiority Effects," by J. R. Pomerantz, L. C. Sager, and R. J. Stoeber, 1977, *Journal of Experimental Psychology: Human Perception and Performance*, 3, pp. 427–428. Copyright 1977 by the American Psychological Association.

global advantage implies global precedence, the fact that global advantage is obtained only under certain conditions suggests that global precedence is not a universal law. Two main issues have been raised concerning the interpretation of global advantage. One issue concerns the hierarchical patterns that are the cornerstone of the global–local paradigm. Hierarchical patterns provide an elegant control for many intervening variables while keeping the hierarchical structure transparent, but the local elements of the hierarchical patterns do not really form the parts of the whole (Kimchi, 1992; Navon, 2003). Furthermore, it has been argued that the local elements in the Navon type of hierarchical patterns function merely as placeholders (Pomerantz, 1983) or serve just to define texture (Kimchi & Palmer, 1982; Pomerantz, 1983; but see Navon, 2003). If so, the local elements may not be represented as figural units, and consequently, faster identification of the global form may be accounted for not by its level of globality but by a

qualitative difference in identification of a figural unit versus a texture element. However, a study of the development over time or microgenesis of the perception of hierarchical stimuli using a primed matching paradigm (Kimchi, 1998) showed that the global form was primed at brief exposures, whereas the local elements were primed only at longer exposures, suggesting that the global form is effective already early in the perceptual process, followed by the individuation of the local elements.

The second issue is that relative size alone rather than globality could explain the global advantage (e.g., Kinchla & Wolfe, 1979; Navon & Norman, 1983). Navon (2003, p. 290) argued that globality is inherently confounded with relative size—it is a fact of nature that relative size is "an inherent concomitant of part–whole relationship." This is indeed the case if global properties are properties of a higher level unit. Yet, if global properties depend on the relationship between the elements, as the theoretical moti-

vation for the global precedence hypothesis implies (e.g., Navon, 1977, 2003), then the essential difference between global properties and component properties is not in their relative size. For example, to distinguish squareness from its component vertical and horizontal lines or faceness from its facial components based only on their relative sizes would miss the point.

The vast majority of results demonstrate that perceptual processing can proceed from global structuring towards analysis of local properties under certain conditions (hence, global precedence). Further findings also suggest that there are different kinds of wholes with different kinds of parts and part-whole relationships. Consider a face with its eyes, nose, and mouth, versus a wall of bricks. Both are complex visual objects—wholes—but the eyes, nose, and mouth of a face are its parts, whereas the bricks in the wall are mere constituents. It is therefore possible that global precedence characterizes the course of processing of some wholes but not of others. This cries out for a refinement of the terminology (e.g., global vs. holistic/configural properties) and a reconsideration of the primacy of holistic properties, which may not necessarily reside strictly in temporal precedence. These are provided in the next section.

The primacy of holistic properties. The Gestaltists' claim that wholes have properties that cannot be derived from the properties of their constituents is captured in modern cognitive psychology by the notion of *holistic* or *configural properties*. Holistic properties are emergent properties that cannot be predicted by considering only the individual component parts or their simple sum. Rather, they arise from the *interrelations* between the parts comprising strong configurations. Examples are symmetry, regularity, and closure (Garner, 1978; Kimchi, 1992, 1994; Pomerantz, 1981; Rock, 1986; Wagemans, 1995, 1997). Thus, for example, four line segments that vary in orientation can configure into a square—with a configural property of closure—or into a cross—with a configural property of intersection. Holistic properties exist along with, not instead of, component properties, and are a different aspect of a stimulus (Garner, 1978). The Gestaltists' claim that wholes dominate parts finds its modern counterpart in the hypothesis about the primacy of holistic properties, which states that holistic properties dominate component properties in information processing.

Empirical research pitting holistic against component properties (with proper controls for differences in discriminability) provides converging evidence for the primacy of holistic properties (see Kimchi, 2003, for a review). For example, holistic properties have been found to dominate speeded classification and discrimination performance regardless of the discriminability of the components (Kimchi, 1994), to be accessible to rapid search (Rensink & Enns, 1995), and to be available for priming under very short exposure durations (Kimchi, 2000). Also related is the CSE (Pomerantz et al., 1977), described above. In light of this, it is hardly tenable that the whole is perceived just by assembling components. However, several findings suggest that positing holistic primacy as a rigid perceptual law is hardly tenable either. Configural dominance has been found with some configurations but not others (e.g., Pomerantz, 1981), and the relative dominance of configural properties versus component properties has been found to depend on its relevance to the task at hand (e.g., Han, Humphreys, & Chen, 1999; Pomerantz & Pristach, 1989).

Furthermore, the description of holistic/configural properties as emergent is only supported as a description of the stimulus. There is no necessity that emergent properties be derived perceptually because they may be directly detected by the perceptual system rather than being computed from relevant properties of the components. Thus, both component and holistic properties (whether emergent or not) must be treated as stimulus aspects. Whether holistic properties dominate component properties at a certain level of processing or are extracted earlier than component properties is ultimately an empirical question, as long as the concepts are clearly defined and the methods are available to address them. For instance, phenomenological notions such as configural superiority and dominance of the whole over the parts suggest that perceptual processing is guided by the quality of wholes, which does not imply a specific processing order, but which does suggest that attentional processing proceeds from wholes to parts.

Although the terms are often used interchangeably, global and holistic properties can be distinguished on theoretical and empirical grounds. *Global properties* are defined by the level they occupy within the hierarchical structure of the stimulus. The difference between global and local properties (as operationally defined in the global-local paradigm) involves size: Global properties are by definition larger than local properties because the global configuration is necessarily larger than the local elements of which it is composed. The critical difference between holistic properties and component properties, however, is not their relative size. *Holistic properties* are relational properties that arise from the interrelations among the component properties of the stimulus.

To examine whether the distinction between global and holistic properties has psychological reality, we must dissociate level of globality (global vs. local) from type of property (holistic vs. nonholistic). With hierarchical stimuli, different types of properties may be present at the global and the local levels. Accordingly, Kimchi (1994) employed hierarchical stimuli that varied in configural properties (e.g., closure) and basic, nonconfigural properties (e.g., line orientation) at the global or the local level. The orthogonal combination of type of property and level of structure produced four sets of four stimuli each (see Figure 2). Participants classified a set of four stimuli on the basis of the variation at either the global or the local level of the stimuli (global or local classification task). Depending on the stimulus set, classification (global or local) was based on closure or on line orientation. The results showed that global classification was faster than local classification (i.e., there was a global advantage) only when the local classification was based on line orientation, not on closure.

Han et al. (1999) used arrows and triangles in the typical global-local task. They found faster reaction times for global than for local identification and global-to-local interference for both orientation discrimination and closure discrimination, but the global advantage was much weaker for the closure discrimination task than for the orientation discrimination task. Under divided attention conditions, there was a global advantage for orientation but not for closure discrimination tasks. Thus, both Kimchi's (1994) and Han et al.'s results indicate that global or local advantage for many-element hierarchical patterns depends on whether discrimination at each level involves holistic or basic properties. When local discrimination involves a configural property like closure, the global advantage markedly decreases or even disap-

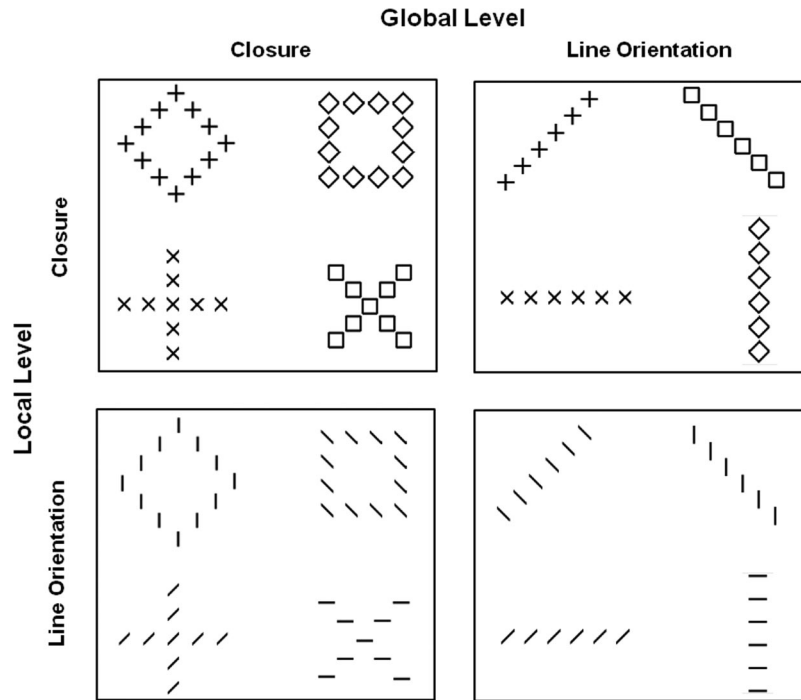


Figure 2. Four sets of four stimuli each, produced by the orthogonal combination of type of property and level of structure. Adapted from "The Role of Wholistic/Configural Properties Versus Global Properties in Visual Form Perception," by R. Kimchi, 1994, *Perception*, 23, p. 498. Copyright 1994 by Pion Ltd.

pears relative to the case in which discrimination at that level involves a basic property like orientation.

These findings converge with others showing a relative perceptual dominance of holistic properties. They also suggest that holistic properties are not necessarily global or larger. Using a different approach, Leeuwenberg and van der Helm (1991) also claimed that holistic properties that dominate classification and discrimination of visual forms are not always global. According to their descriptive minimum principle approach (see Section 6, below), the specification of dominant properties can be derived from the simplest pattern representations, and it is the highest hierarchical level in the simplest pattern representation, the *superstructure*, that dominates classification and discrimination of visual forms. The superstructure is not necessarily global or larger.

It is important to notice that there are logical asymmetries in the relations between parts and wholes, or between components and configurations: Components can exist without a global configuration, but a configuration cannot exist without components. Therefore, components are logically prior to the configuration of which they are part. Similarly, if holistic/configural properties do not reside in the component properties but rather emerge from the interrelations among components, then logic dictates the priority of the components. This issue received considerable attention in the old Gestalt literature (e.g., Rausch, 1937). The point is that the logical structure of a stimulus does not imply one fixed processing order at all levels of processing (Garner, 1983; Kimchi, 1992; Kimchi & Palmer, 1985). One possible solution is to assume that nonconscious, bottom-up, stimulus-driven perceptual processing proceeds from components to configurations, whereas conscious,

top-down, task-driven attentional processing generally starts with configural properties and then descends to component properties if required by the task (e.g., Hochstein & Ahissar, 2002).

In sum, the empirical evidence reviewed in these subsections converges towards the idea that wholes dominate parts in attentional and perceptual processing. As for perceptual processing, however, this dominance does not imply a specific processing order. In fact, the central Gestalt idea is that the dominance in perceptual processing is not so much due to a specific processing order but rather emerges from interactions between stimulus parts resulting in perceived wholes. As we discuss next, this raises the question of how perceptual processing might be modeled such that it complies with the empirical evidence.

Interim Evaluation: New Foundations Needed

The conceptual clarifications and operational definitions of key Gestalt notions—such as holism, emergence, dominance of the whole over the parts, global precedence, and configural superiority—have been useful in making further theoretical and empirical progress. For instance, the distinctions between global versus local in terms of relative size and levels of representation in a hierarchical context and between holistic/configural versus simple/component properties—the former depending on relations between the latter but not vice versa—have been important in shedding light on an extensive and muddled literature. Extending this work significantly, Townsend and colleagues have developed a rigorous framework for the investigation of holistic perception (e.g., perceptual dependence of parts on wholes) in terms of information

processing, making use of systems factorial technology (e.g., Fific & Townsend, 2010; Townsend & Wenger, 2004). Moreover, the distinction between characteristics of stimulus properties and their representations, on the one hand, and temporal relationships in their course of processing has allowed for innovative ideas about possible neural mechanisms. For instance, Hochstein and Ahissar (2002) proposed *reverse hierarchy theory*, in which they argued that a fast feedforward sweep quickly activates global percepts (e.g., the overall gist of a scene) in high-level areas with large receptive fields, whereas feedback from these higher areas to lower areas and recurrent processing in the low-level areas with small receptive fields is necessary for fine-grained processing of local details. Hence, this theory distinguishes the anatomical, structural aspects of the hierarchy of the visual system (low- vs. high-level representations) from the temporal, functional aspects of it (early vs. late stages of processing). In this context, it is not unusual to find that some Gestalts might emerge gradually along the visual system's hierarchy, for instance, CSEs being reflected in neural activity in early retinotopic regions (Alexander & van Leeuwen, 2010), as well as high-level object areas (Kubilius, Wagemans, & Op de Beeck, 2011; Liu, Plomp, van Leeuwen, & Ioannides, 2006), whereas other Gestalts seem to be encoded in low-level areas based on feedback from higher order regions (e.g., Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003; Murray, Boyaci, & Kersten, 2006).

Despite this progress on the conceptual and empirical front, we are still in need of stronger theoretical frameworks to provide solid foundations to the Gestalt approach's major principles. Gestalt psychology led to a proliferation of hundreds of laws (or, more accurately, principles) of perceptual organization, such as grouping by proximity, similarity, and good continuation. Thus, concerns arose that there were more explanations being proposed than the number of phenomena they could explain. Could these highly specific principles be reduced to just one or two? Two such general explanations emerged: *Prägnanz* (also known as the *simplicity* or the *minimum principle*), which holds that perceptions are structured into the simplest organizations possible, and the *likelihood principle*, which holds that percepts are structured to conform to the most likely stimulus that could have given rise to the sensory information registered on the retina (Pomerantz & Kubovy, 1986). Consider Necker's (1832) well-known wire-frame image of a cube, its parallel edges drawn as 12 parallel lines of the same length allowing for two alternative in-depth interpretations. Do we see it as a cube because doing so simplifies the percept or because a cube is the most likely distal stimulus consistent with the retinal image resulting from this stimulus? Similarly, do we perceive the trapezoidal Ames window as rectangular because this is simpler or because it is more likely?

The simplicity principle is most closely associated with the Gestalt school. The core idea was that percepts are organized automatically into simple, global structures, perhaps through processes analogous to physical mechanisms at work with magnetic fields and soap bubbles. In the absence of complicating factors such as wind or acceleration, a soap bubble will shape itself into a sphere, which is the simplest of all 3-D shapes in that it is fully described by one parameter (its diameter). Correspondingly, the 12 line segments constituting the Necker cube pattern are seen as a cube because a cube has only one parameter (edge length). In doing so, all its edge lengths become the same and all angles

become 90°. The likelihood principle is most closely associated with von Helmholtz (see also Rock, 1983). It holds that the perceptual system determines the most likely distal stimulus that could have given rise to the proximal stimulus (the retinal image). It holds that we see the 12 line segments as a cube because historically (in either phylogenetic or ontogenetic terms) a cube has been the most frequent distal stimulus consistent with the proximal stimulus of the Necker cube image.

Distinguishing between the simplicity and likelihood principles has proven challenging because of difficulty unconfounding the simplicity and the likelihood of test stimuli. Controlled rearing studies might answer this question but they are not feasible. Kanizsa (1979) created demonstrations arguing forcefully against simplicity but there is a complication here too: Simplicity usually only refers to the perceived objects as such, whereas his demonstrations also required the inclusion of positional complexity in terms of coincidence avoidance (see Rock, 1983, and below, particularly Figure 8).

From a functional, evolutionary viewpoint, the likelihood principle would be more appealing because the veridicality of perception is a primary factor in determining natural selection: An organism is less likely to survive and reproduce if its perception of the physical environment is erroneous in important respects. A potentially serious problem for the likelihood framework, however, is that the organism does not actually have access to veridical properties of the physical world, but only to its imperfect sensory information about them (i.e., the brain-in-a-vat argument). How can the organism compute likelihoods of external circumstances without knowing their prior probabilities? The simplicity hypothesis suggests an answer: Perhaps evolution has built into the organism's perceptual system a surrogate for likelihood via simplicity, which is internally accessible (Palmer, 2003). Mach (1906/1959) and Attneave (1982), therefore, suggested that both principles may be two sides of the same coin.

In the next four sections, we review recent progress regarding simplicity and likelihood, extending these principles far beyond the sterile conflict between the Gestaltists and the Helmholtzians. First, we show how the intuitive notion of *Prägnanz* or simplicity can be further substantiated in terms of the intrinsic dynamics of the brain as a self-organizing, adaptive system. Then, in three consecutive sections, we discuss how simplicity and likelihood may be connected in a deep and meaningful way, in views derived from (a) measurement principles in a system of sensors, (b) a Bayesian approach, and (c) structural information theory.

A Dynamical Systems Approach

Introduction

As noted above, traditional Gestalt psychology envisaged the many laws of perceptual organization to be manifestations of a common principle: the law of *Prägnanz*. Persistently, the Gestaltists sought to elucidate this principle by relying on metaphors involving static equilibria of field forces. But equilibrium field forces are inert; they change only when external conditions change. At the same time, Gestaltists emphasized the active, spontaneous character of perceptual organization. The tension between inert and active aspects of perception constitutes a puzzle that is pervasive beyond Gestalt psychology, and has persisted to date.

Here, we discuss how more recent developments in nonlinear dynamical systems theory may eventually resolve this conundrum.

Dynamical systems theory describes equilibria in terms of *attractors* (e.g., Hopfield, 1982). The strength of attractors could be equated with a measure of *Prägnanz* (van Leeuwen, 1990). Attractors are a desirable concept for perception, as they offer robustness against variation in stimulation. For instance, Luccio (1999, p. 91) wrote,

The principle of organization acts as precise laws to which the process is forced to obey, overall in the sense of maximum economy and simplicity. Its result is a perfect balance of the forces at play and thus has also a *maximum of stability and resistance to change*.

However, this comment emphasizes only the inert aspect of dynamics.

Resistance to change may not adequately characterize the visual system. Consider the two alternative in-depth interpretations of the Necker cube. Prolonged exposure typically leads to *switching* between these interpretations (e.g., Attneave, 1971; Einhäuser, Martin, & König, 2004; Nakatani & van Leeuwen, 2005, 2006; Peterson & Gibson, 1991; van Dam & van Ee, 2006; for a review, see Long & Toppino, 2004). To a large extent, this behavior is involuntary. We can try to deliberately hold on to an orientation; this will reduce the overall switching rate, but does not stop our perception from switching (Strüber & Stadler, 1999; Toppino, 2003). Interference with the organism's activity, such as focusing attention on a biased region (Peterson & Gibson, 1991; Toppino, 2003) or eliminating eye movements by retinally stabilizing the image (Pritchard, 1958) cannot prevent it either. Switching occurs even in the afterimage, when the stimulus has been removed (McDougall, 1903). Perceptual switching, therefore, is illustrative of an intrinsic tendency to actively move on from established interpretations (Leopold & Logothetis, 1999). We must conclude that there are mechanisms within the visual system that provide a degree of flexibility. These mechanisms involve spontaneous activity that offsets the resistance to change, which is a by-product of the system's robustness.

Noise-Driven Models

A classical Gaussian noise component added to its activity can drive the system out of an otherwise stable attractor. An accumulation of noise events can drive it sufficiently far away to enable a transition to another one. Consider a system with two roughly equivalent attractors (a *double-well* model). Let these correspond to two alternative interpretations of an ambiguous figure. Noise could be effectuating the switching back and forth between them. The concept of an internal noise source has gained wide acceptance in the study of sensory processes due to signal detection theory (Green & Swets, 1966). Empirical evidence suggesting that noise is responsible for perceptual switching is found in the observed distributions of *dwell times* (Levelt, 1967). These are the durations with which a certain interpretation is maintained. Dwell times are believed to follow a positively skewed distribution called gamma distribution (Borsellino, Marco, Allazetta, Rinesi, & Bartolini, 1972). These distributions are characterized by a parameter that can take real values. In dwell-time distributions, however, it typically takes whole values, consistent with models in which switching depends on a whole number of independent chance

events (Taylor & Aldridge, 1974). Although these models produce the right kind of distribution, other models, including ones that have no stochastic noise component whatsoever, can produce such a distribution just as well (van Leeuwen, Steyvers, & Nooter, 1997). Moreover, noise-based models predict zero correlation between subsequent dwell times. In fact, the correlations are consistently above zero and decrease with lag (Bassingthwaite, Liebovitch, & West, 1994; van Ee, 2009). Such sequential dependencies suggest that dynamics are contributing to the behavior.

As an alternative, therefore, we might consider systems far from equilibrium (Maturana & Varela, 1980), in which a small perturbation may have large consequences over time (the butterfly effect). Such systems would show the observed patterns of correlation but they would clash with the desirability of stable, robust perceptual representations. We can solve this problem if we consider systems that cycle between approach and avoidance of equilibria, in other words, between being governed by stability and flexibility. In olfactory perception, Skarda and Freeman (1987) described transitions between stability and flexibility as coordinated with the breathing cycle; upon inhalation the system is geared towards attracting states and thereby responsive to incoming odor, upon exhalation the attractors are annihilated for the system to be optimally sensitive to new information. Freeman and van Dijk (1987) envisaged a similar system for visual perception; we might consider a system becoming instable and thus ready to anticipate new information in preparation for what was dubbed a *visual sniff* (Freeman, 1991). We may envisage taking a visual sniff whenever new information is expected, for instance, when moving our eyes to a new location.

Dynamical Models

Cycles of approach and avoidance of equilibria provide double-well models with an internal, driving force of change. Suppose that the well in which the system is residing becomes gradually shallower due to mechanisms such as adaptation or competition. This means that fewer noise events suffice to drive the system out of its state. This assumption has been embedded into macroscopic models of the dynamics of switching behavior as a *phase transition* (Ditzinger & Haken, 1989, 1990). In such models, the fast noise and a slow dynamic cycle work together to produce switching and its characteristic gamma distributions.

Köhler and Wallach (1944) proposed this slow mechanism to be neural fatigue or satiation. There is no direct evidence of neural fatigue of active configurations, as Köhler (1940) envisaged it. There is, of course, the well-established phenomenon of neural adaptation—the reduced neural response to prolonged or repeated stimulation, for instance, to light intensities in the retina of the rat (Dowling, 1963) or to patterned stimuli in the retina (for a review, see Graham, 1989) or in the ventral visual system responsible for human form perception (Noguchi, Inui, & Kakigi, 2004). However, neural adaptation takes place at the *local* level of ion currents conductivity in the membrane of the neuron (Sanchez-Vives, Nowak, & McCormick, 2000), and is therefore unable to provide selectivity in adaptation at the level of *global* perceptual patterns (Barlow & Földiák, 1989). According to these authors, adaptation to patterns occurs through a mechanism of anti-Hebbian decoupling between cells that are simultaneously active; this generally serves to make neural population codes sparser with extended

presentation. It might thus be supposed that there is a continuous sparsification in population activity selective to patterns.

This slow mechanism could be useful to explain the steady, continuous increase in switching rate with prolonged presentation of a stimulus. Correlations between subsequent dwell times could be explained by fluctuations in adaptation rate (van Ee, 2009). Kim, Grabowecy, and Suzuki (2006) induced stochastic resonance in switching by periodically alternating the stimulus, thereby demonstrating the presence of macroscopic noise in the system. This means there are at least two switching mechanisms possible according to the double-well model: One is high-frequency, microscopic noise in sensory channels and the other is macroscopic noise in adaptation rates.

Can we attribute these two mechanisms to brain regions? Functional magnetic resonance imaging reveals that switching is accompanied by activation in ventral occipital and intraparietal higher order visual areas, and deactivation in primary visual cortex and the pulvinar (Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998). Electrocortical activity recording (electroencephalography [EEG]) shows transient synchronizations of activity between frontal and parietal areas, sometimes accompanied by occipital activity (Nakatani & van Leeuwen, 2006). On the other hand, suppression of frontal activity using transcranial magnetic stimulation did not eliminate switching (de Graaf, de Jong, Goebel, van Ee, & Sack, 2011). This leaves us with occipital areas as the (noise) source of switching and parietal areas as the putative locus of adaptation, responsible for sequential dependencies in switching.

Still, in these models, robustness and flexibility remain opposing regimes. Is it possible for a system to be robust at one time and flexible at another without having to cycle through a macroscopic loop? Consider the property called *meta-stability* as illustrated in Figure 3 (loosely based on the theory of Kelso et al., 1995), which shows a *return plot* of a system. On the x -axis the state of the

system is specified by the value of a single variable x at time t (x_t). The system evolves in time, according to a function F , the red curve. Follow the arrows to see how the system evolves over time. For simplicity, the system depicted here evolves in discrete time, such that $x_{t+1} = F(x_t)$. The y -axis plots x_{t+1} against x_t . The green line specifies the values where $x_t = x_{t+1}$. Should the system reach the green line, all changes would come to a halt. However, for the current F it will never reach such states. There are two intervals of x , $\langle A \rangle$ and $\langle B \rangle$, where the red line almost touches the green line. Here, changes to system state x are minimal. Thus, it can dwell in the neighborhood of A or B for a certain time interval. When approaching these states, the system is apparently stable. The system will get caught in one of these states, and free itself only to get caught after a while in the other one. In this manner, the system continues to swing back and forth between A and B. This simple model would perform perceptual switching, for instance, if the apparent stability in approaching A or B corresponds to reaching an alternative orientation of the Necker cube.

Were F actually to touch the green line in A and B, the system approaching A or B would actually stay there. This is where noise would come back into the picture. Small fluctuations could move the system beyond these points, such that x is allowed to roam until it eventually gets caught again. The difference with Figure 3 is that small-scale fluctuation, rather than fine tuning of the function to obtain a gap with the green line, is responsible for corrupting the attractor. The difference is moot. In both cases, we are dealing with a *corrupted fragile attractor*—that is, an attractor with a built-in escape route. Corrupted fragile attractors thus have built-in flexibility.

Dynamic Synchronization and Complex Adaptive Systems

Fragile attractor models of switching are generically in accordance with the empirical distributions of dwell times, and their dynamical character leads readily to the prediction of nonzero serial correlations in the dwell times (Fürstenau, 2010; van Leeuwen et al., 1997). To distinguish the two, we should look at long-range dependencies between dwell times (Wagenmakers, Grünwald, & Steyvers, 2006). Consider a series of dwell times: Clearly they fluctuate irregularly from one time to the next. With long-range dependency, nonoverlapping running means of these data fluctuate in a similarly irregular manner (Beran, 1992; Mandelbrot & Wallis, 1969). Because of these similarities across scales, these data are said to have fractal characteristics. Recently, Gao et al. (2006) presented experimental evidence for the fractal nature of dwell times in the Necker cube. This suggests that switching is best considered as a process governed by fragile attractors. These naturally occur in *complex adaptive systems consisting of coupled oscillators*. As the number of oscillators grows large, corrupted fragile attractors increasingly become predominant in their dynamics, due to a phenomenon called *attractor crowding* (Tsang & Wiesenfeld, 1990; Wiesenfeld & Hadley, 1989). This may be nature's solution to the problem of how to combine flexibility and robustness in a perceptual system.

This perspective was embodied in an early model of perceptual organization, in which meta-stability along the lines of Figure 3 of the system's synchronized activity is responsible for switching in ambiguous figures (van Leeuwen et al., 1997). The model consists

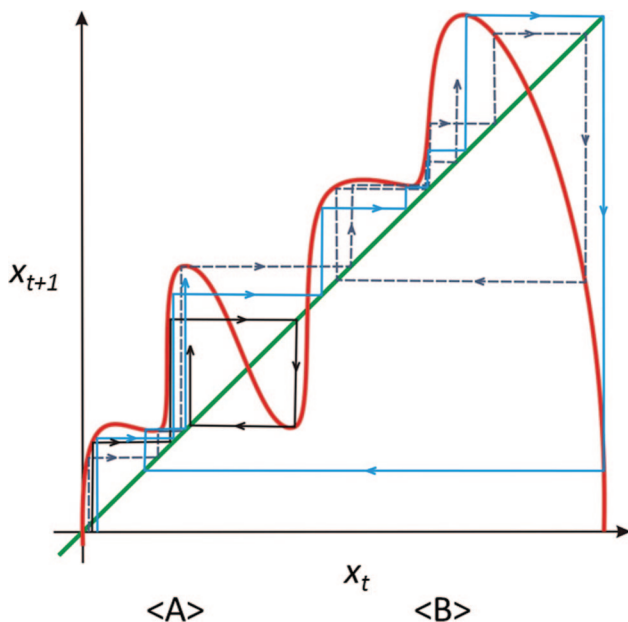


Figure 3. A simple dynamical system model for perceptual switching characterized by two meta-stable states.

of several layers of nonlinear neural mass oscillators. Ongoing activity in this model synchronizes and breaks down spontaneously; the patterns of synchronization are modulated by stimulation. For ambiguous stimuli, the system shows two alternative patterns of synchrony, and switches rapidly between them. This model was never tuned to empirical data and lacks a plausible large-scale neural architecture. Despite these shortcomings, the model may still have some theoretical value to date as an early application of complex adaptive systems in psychology. More recent applications of the model have addressed the self-organization of modular, connected networks in functional architecture (Gong & van Leeuwen, 2003; Rubinov, Sporns, van Leeuwen, & Breakspear, 2009). Further along these lines, the more recent model by Fürstner (2010) has a layered structure that takes into account the global architecture of the thalamo-cortical loop, and it accommodates the fractal nature of dwell times in accordance with Gao et al.'s (2006) observations.

Complex adaptive systems show long-term dependencies because their behavior exhibits *self-organized criticality*. Self-organized criticality has been observed in the spontaneous synchronization and desynchronization of EEG activity (Gong, Nikolaev, & van Leeuwen, 2007). Long-term dependencies are found in a large variety of tasks, such as mental rotation, lexical decision, speeded visual search, estimation of distance, estimation of rotation, estimation of force, estimation of time, simple reaction time, and word naming (Gilden, 1997, 2001; Gilden, Thornton, & Mallon, 1995; Van Orden, Holden, & Turvey, 2003), as well as in recordings of human EEG (Ito, Nikolaev, & van Leeuwen, 2007). It seems, therefore, that a dynamic characterization is appropriate for a much wider range of behaviors other than switching. This underlines the general relevance of dynamic models for psychology and the illustrative value of switching for understanding perception and cognition.

Complex adaptive systems imply a new perspective on the perceptual sniff. Generally, more stable and instable periods like those in Figure 3 (Ito et al., 2007) alternate in the brain. Unstable periods are characterized by transient patterns of synchrony in short-range, high-frequency activity. According to an influential point of view, this is when collective representations are bound together through synchronization of oscillatory activity (Milner, 1974; von der Malsburg, 1981). Binding-related neural oscillations have been observed in the gamma range (roughly 40–70 Hz) within as well as between local brain regions (Eckhorn et al., 1988; Gray, König, Engel, & Singer, 1989; Singer & Gray, 1995). It is possible that these episodes do not necessarily reflect binding, but rather the breakdown of global stability of interpretation in a stage in which the system is exploring competing new representations. Accordingly, brief episodes of synchronous activity in the gamma band occur prior to perceptual switching (Nakatani & van Leeuwen, 2006).

The more stable periods show oscillatory activity in lower frequency ranges, specifically in the beta range of EEG (Nikolaev, Gepshtein, Gong, & van Leeuwen, 2010). Gamma and beta activities are generally believed to have complimentary functions (Donner & Siegel, 2011). Intervals of beta synchronization, called *coherence intervals* (van Leeuwen, 2007), last longer when evoked by less ambiguous stimuli than by more ambiguous ones (Nikolaev et al., 2010). The less ambiguous the stimulus, the more information contained in it. Thus, coherence intervals reflect broadcasting

of information across brain areas (van Leeuwen & Raffone, 2001; van Leeuwen et al., 1997). In such a perspective, our brain activity patterns reflect competition between representations, as well as the resolution of the competition, followed by global broadcasting; this qualifies as the mechanism by which our visual system proceeds autonomously from one experience to the next (van Leeuwen, 2007).

Conclusion

A dynamical systems approach can explain how the brain's capacities for self-organization are ideally suited to balance robustness and flexibility. Combining both is essential for perception to be tuned to stimuli impinging from the environment, without being overloaded by them, with just enough variation in perceptual states to lead to proper cognitive interpretations and functional actions. Different sources of change (stochastic and deterministic), different types of noise (microscopic and macroscopic), and different kinds of attractors and dynamics were considered. Moreover, some of these were shown to correlate well with known behavioral effects (e.g., dwell times) and recently discovered specific neural signatures (e.g., coherence intervals and self-organized criticality of synchronization of neural oscillations). Although the review above was aimed at understanding the dynamics of perceptual switching, the theoretical concepts and neural aspects discussed in this context, characterizing the brain as a complex adaptive system, may readily be extended to deal with other aspects of Gestalt formation such as perceptual grouping and object formation (e.g., Hock, Kelso, & Schöner, 1993; Hock & Nichols, 2012; Hock, Schöner, & Giese, 2003).

Hence, there are clearly modern counterparts to Köhler's notion of *Prägnanz* and self-organization that are also empirically fruitful. In addition, as alluded to before, there also modern counterparts to Helmholtz's notion of likelihood and unconscious inference (e.g., the Bayesian approach to perception) and contemporary syntheses of simplicity and likelihood, which also have a strong empirical basis. We discuss these in the next three sections.

Principles of Measurement in a System of Sensors

Introduction

The Berlin school of Gestalt psychology tended to emphasize properties of the system above properties of system elements. They assumed a one-way global-to-local determination, on which properties of elements could be understood only by knowing their places within the system. We now consider a modern view of the determination of systems and their elements in service of visual perception. On the modern view, the determination is two-way: Properties of the system can be traced from properties of elements, and also properties of elements depend on their places in the system.

Elementary versus system processes. Key developments in the sensory physiology of the 20th century had a strong flavor of sensory atomism. Properties of individual sensory neurons came to the fore (Barlow, 1972; Parker & Newsome, 1998), as painstaking studies revealed a great variety and complexity of their receptive fields (Hartline, 1940; Hubel & Wiesel, 1962, 1968; Kuffler, 1953; Maunsell & Newsome, 1987). Indeed, the entire visual system was

conceived from the perspective of single cell as a hierarchy of receptive fields of increasing sophistication, from the relatively simple ones, serving *early vision* (e.g., Adelson & Bergen, 1991), to the more complex, serving *mid-level vision* (e.g., perceptual organization; Nakayama, 1999) and *high-level vision* (e.g., object recognition; Gross & Mishkin, 1977; Ullman, 1996). Yet, as methods of neuronal recording matured and basic facts about neural activity were settled, it became increasingly clear that a theory that rested on single cells alone was incomplete (see also Spillmann, 1999). Antiatomist tendencies started to emerge toward the end of the last century, often appealing to the Gestalt legacy (e.g., Albright, 1994; Albright & Stoner, 2002; Allman, Miezin, & McGuinness, 1985; Gilbert, Ts'o, & Wiesel, 1991; Zhou, Friedman, & von der Heydt, 2000). It is important to note, however, that the resurgent antiatomism of modern neuroscience is synthetic. It rests on the growing understanding of how the function of individual neuronal cells is modulated by these cells' neuronal context, and how the neuronal effects of stimulation are modulated by stimulus context. In other words, the (atom-like) single cells are studied as integral parts of a (holistic) system. The theory developed below is a manifestation of the same synthetic tendency.

Just as with sensory physiology, mainstream behavioral studies of perception were dominated by atomist tendencies for much of the century. Elementary sensory processes, such as detection and discrimination of simple stimuli, were emphasized and often viewed as the sole foundation of sensory science. The increasing rigor of this work was helped by mathematical ideas imported from the theory of linear systems, the theory of communication, and probability theory. At first, these advances appeared foreign to the antiatomist Gestalt ideology. In particular, the linear-system approach to sensory processes is only tenable when stimulus components exert their effects independently of one another, in stark contrast to the Gestalt view of perception. Yet the increasingly rigorous inquiry into elementary sensory processes created a foundation from which new perspectives opened up on how the tension between atomistic and holistic views of perception may be reconciled without suppressing either side. The theoretical outlook presented below rests on a dualistic view of sensory measurement, whose formal manifestation is Gabor's uncertainty principle. As

we show, the dualistic view helps to approach the elementary and system processes within a unified picture.

Intrinsic versus extrinsic processes. The Berlin school of Gestalt psychology focused almost exclusively on processes intrinsic to the perceiving organism. Effects of environmental changes, such as visual aftereffects, were studied to advance understanding of the intrinsic processes (e.g., Köhler & Wallach, 1944). The environment itself did not interest the Berlin Gestaltists beyond the phenomenological analysis of the perceived (behavioral) environment, in contrast to the geographic environment—the source of stimulation (Koffka, 1935). It was the Graz school of Gestalt psychology that addressed the question about structure of geographical environment. Fritz Heider, a philosophically minded offspring of the Graz school, dedicated his early work to the environmental causes of perception (Heider, 1926, 1959). Heider concentrated on the part-whole structure of the chain of physical events that lead to perception, anticipating and influencing the ecological thread in perceptual science advanced by Brunswik (1955) and Gibson (1979). Egon Brunswik, in particular, is credited with the first studies of how perceptual organization depended on regularities of the physical environment (Brunswik & Kamiya, 1953), a theme that flourishes today (see Wagemans et al., 2012, Section 4).

Modern studies of Gestalt phenomena that emphasize statistical regularities of the environment tend to lean on these regularities at the expense of other factors. The environmental bias makes perceptual theory as incomplete as a theory that ignores environmental structure. The framework presented below embraces both the internal and external aspects of perception. This unity is attained by taking an economic perspective. Sensory measurements are ranked by their utility, which depends both on capacities of individual sensors (intrinsic to sensory systems) and on how useful the sensors are in the current environment (extrinsic to the system). To explain this modern synthetic view, we first need to introduce recent results from studies of apparent motion.

Unity of Apparent Motion

An elementary case of apparent motion is illustrated in Figure 4. Two lights (represented in Figure 4A by the unfilled circles) are flashed one after another at different spatial locations s_1 and s_2 , at

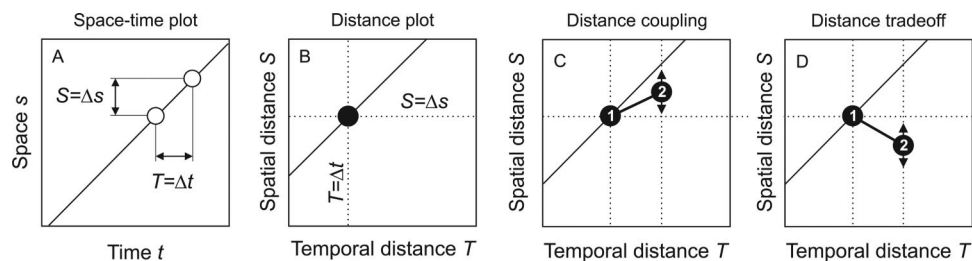


Figure 4. A: Space-time graph (t, s) . Two lights are flashed at distinct locations represented by two circles at coordinates t and s . B: *Distance graph*. The same stimulus is represented by a filled circle in a graph of distances $(T, S) = (\Delta t, \Delta s)$. C–D: Regimes of apparent motion. Two stimuli (represented by filled circles 1 and 2) are shown in each distance graph: one at (T, S) and the other at $(2T, nS)$. In Stimulus 2, the temporal distance is twice longer and the spatial distance is n times longer than in Stimulus 1. What is the magnitude of n ($n > 0$) at which the two stimuli are equally strong? The answer has been inconsistent. According to some studies, the answer is $n > 1$ (distance coupling in Panel C); by others, it is $n < 1$ (distance tradeoff in Panel D). Adapted from “Two Psychologies of Perception and the Prospect of their Synthesis,” by S. Gepshtein, 2010, *Philosophical Psychology*, 23, pp. 244–245. Copyright 2010 by Taylor & Francis. Adapted with permission.

instants t_1 and t_2 , respectively. Motion is seen only for some spatial and temporal distances between the lights. The quality (or strength) of apparent motion depends on the combined effect of spatial and temporal distances between the lights (as shown in the distance graph of Figure 4B). Two regimes of apparent motion can be distinguished. In the regime of space-time coupling (see Figure 4C), the strength of motion is conserved by increasing both spatial and temporal distances between the lights (Koffka, 1935; Korte, 1915). In the regime of space-time tradeoff (see Figure 4D), the strength is conserved by opposite changes of spatial and temporal distances: Increasing one distance must be accompanied by decreasing the other distance (Burt & Sperling, 1981).

Later work showed that the two regimes of apparent motion are special cases of a general pattern. Gepshtein and Kubovy (2007) found that the regime of tradeoff holds at low speeds of apparent motion, and the regime of coupling at high speeds, with one regime changing smoothly into another as a function of speed. The authors derived equivalence contours of apparent motion, which were consistent with the shapes of isosensitivity contours measured at the threshold of visibility (Kelly, 1979; reviewed in Nakayama, 1985). Figure 5 illustrates this idea using a contour plot of spatiotemporal contrast sensitivity. Each contour represents an *isosensitivity set* of stimulus conditions, at which the same amount of luminance contrast makes the stimuli just visible. The conditions marked by warm colors require less contrast to reach the threshold of visibility than the conditions marked by cool colors. If conditions of isosensitivity were similar to conditions of equivalently strong apparent motion, the different regimes of apparent

motion were expected in different parts of distance graph, indicated in Figure 5 by the two pairs of connected circles (as in Figures 4C–4D). The results of Gepshtein and Kubovy were consistent with this prediction. A monotonic relationship held between the isosensitivity contours and the equivalence conditions of apparent motion, indicating that the perception of motion is controlled by similar factors at the threshold of visibility and above the threshold. The fact that regimes of apparent motion occur where they are expected from the threshold measurements indicates that common principles govern perception in both cases.

These results undermine the accepted view of perceptual grouping. They indicate that human vision favors sometimes short and sometimes long spatiotemporal distances, which is inconsistent with the proximity principle (Gepshtein, Tyukin, & Kubovy, 2007), a cornerstone of Wertheimer's (1923) conception of perceptual organization. In other words, the proximity principle does not generalize to dynamic scenes. There is no spatiotemporal proximity principle. Elements of a dynamic display separated by short spatiotemporal distances are not more likely to be perceived as parts of the same object than elements separated by longer spatiotemporal distances. The traditional view needs revision. One direction for such a revision is a theory from principles more general than the empirically observed tendencies. In the following sections, we review such a theory, which explains how the unity of experimental findings about apparent motion, on the one hand, and consistency of these results with results on spatiotemporal sensitivity, on the other, are expected from basic properties of measurement.

Principles of Measurement

Gabor (1946) formalized a fundamental result in the theory of communication that had been increasingly appreciated by engineers early in the 20th century (Hartley, 1928; Gabor, 1952). It is the *uncertainty principle of measurement*. The principle applies to simultaneous measurements of two aspects of any signal: its location and content. At the performance limit of any measuring device, the precision of measuring the location is constrained by the precision of measuring the content, and vice versa. We briefly review this principle in one dimension (see Figure 6) before we turn to its consequences for measurement of motion:

- To measure signal *location* on dimension x is to determine interval Δx that contains the signal. The smaller the interval, the higher the precision (the lower the uncertainty) of measurement.
- To measure signal *content* on x is to determine how the signals varies over x , that is, to measure signal variation. The variation is evaluated by decomposing a signal to its elementary variations: harmonic functions of different frequencies. Because the elementary variations are each characterized by a single frequency, the result of this measurement is called the *frequency content* of the signal (f_x in Figure 6A).
- Measuring signal location and frequency content at the same time presents a challenge. Measurement of location is most precise (least uncertain) when the signal is contained in a very small interval but small intervals cannot capture information sufficient for identifying the (frequency) content of signals precisely. Measurement of signal content is precise on large intervals. In effect, there is a tradeoff in precision of measuring signal location and content.

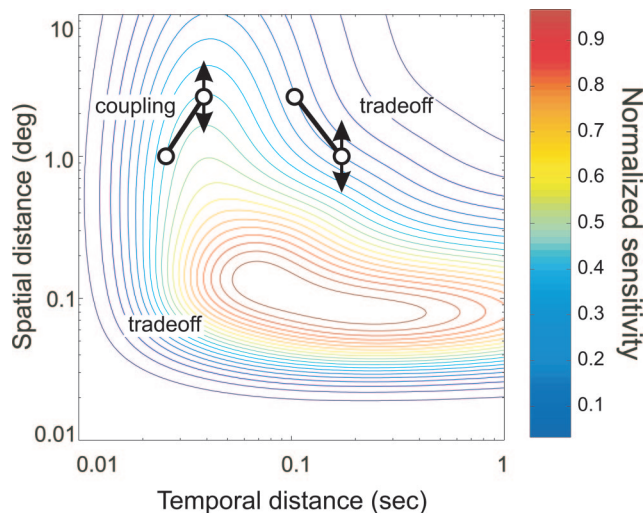


Figure 5. Equivalence contours. The colored curves are the contours of contrast sensitivity reproduced in the distance graph from the spatiotemporal frequency graph of Kelly (1979), using methods explained in Gepshtein and Kubovy (2007). Contour slopes vary across the graph, consistent with the regimes of coupling and tradeoff of apparent motion in different parts of the graph. The two pairs of connected circles are two examples of where different regimes of apparent motion are expected if strength of apparent motion was predicted by contrast sensitivity. Adapted from “The Lawful Perception of Apparent Motion,” by S. Gepshtein and M. Kubovy, 2007, *Journal of Vision*, 7(8), Article 9, p. 6. Copyright 2007 by the Association for Research in Vision and Ophthalmology. Adapted with permission.

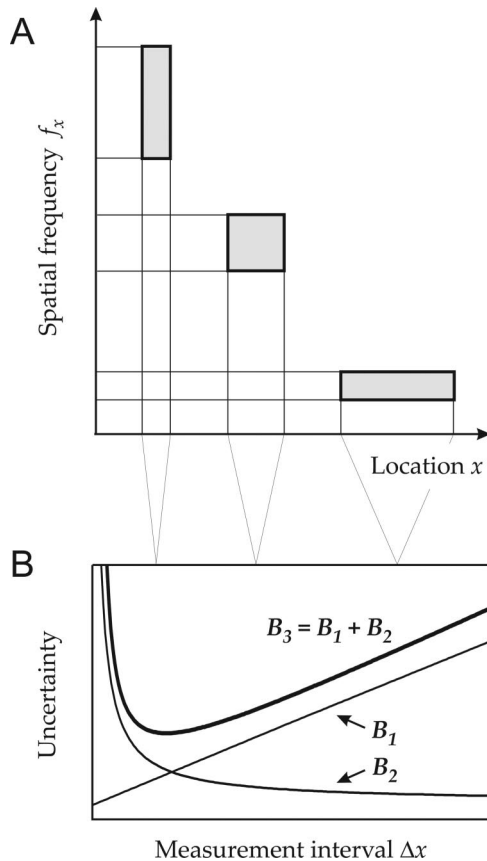


Figure 6. A: Information cells and uncertainty tradeoff. The three rectangles are the information cells. Their projections on dimensions x and f_x represent, respectively, the precision of measuring signal location and content: the larger the projection, the lower the precision (higher uncertainty) of measurement. The cells have the same area (product of intervals on x and f_x) but their shapes vary. B: Uncertainty functions in one dimension. Curves B_1 and B_2 are the uncertainty functions associated with measuring signal location and content, by a sensor of size Δx . The values of B_1 and B_2 are proportional to, respectively, the horizontal and vertical extents of the information cells in Panel A. B_3 is a joint uncertainty function. It represents the uncertainty of simultaneous measurement of stimulus location and content. Low values of B_3 at intermediate magnitudes of Δx indicate that sensors of intermediate size are most suitable for jointly measuring signal location and content. Adapted from “Two Psychologies of Perception and the Prospect of Their Synthesis,” by S. Gepshtein, 2010, *Philosophical Psychology*, 23, p. 250. Copyright 2010 by Taylor & Francis. Adapted with permission.

Gabor gave this tradeoff a formal expression—his uncertainty principle—as follows. At the limit of precision of any measuring device, the uncertainties associated with measuring signal location and frequency content are related. Gabor represented the joined measurements using *information cells* (logons) in (x, f) , shown as rectangles in Figure 6. He proposed that the number of information cells that contain a representation of signal in (x, f) is a measure of the information contained in a signal. Spatial precision of this device can only be increased by decreasing precision of measuring frequency content, and vice versa. To precisely measure both the location and content of a stimulus, visual systems might employ

specialized sensors, tuned to x or f . But biological systems are likely to prefer a compromise to the utter specialization, for two reasons. First, both location *and* content of a signal often need to be measured by the same sensor at the same time, to avoid the problem of matching content to location. Second, biological systems have limited resources. An economical design, in which the same resource (the same sensory neuron or neuronal circuit) performs several functions, has an advantage. According to these considerations, the sensors represented by the information cell in the middle of Figure 6A must be preferred over the specialized sensors. A measuring device that implements this compromise optimally is a *Gabor filter*.

Physiological studies of visual perception have shown that visual cortical neurons are optimized for measuring the location and frequency content of the stimulus in a manner consistent with Gabor’s filter (Daugman, 1985; Glezer, Gauzelman, & Yakovlev, 1986; Kulikowski, Marcelja, & Bishop, 1982; D. M. MacKay, 1981; Marčelja, 1980). The similarity of visual receptive fields and Gabor filters is well established (Jones & Palmer, 1987). Also well established is the interpretation of this similarity, that the particular weighting functions facilitate the joint measurements of the locations and contents of stimuli.

In the following, we review several consequences of the uncertainty principle beyond individual sensors. In particular, we show how the extension of this approach to a system of sensors helps to reveal a unity of results from the statistical and phenomenological traditions in perceptual science.

Systems of Sensors

To understand effects of Gabor’s uncertainty principle for perception of motion, we must study interactions of four uncertainties: two spatial and two temporal, represented by the spatial and temporal logons on the side panels of Figure 7A. Next, we make the same step as in Figure 6B: We combine all uncertainties to a single function in Figure 7B:

- First, recall that increasing the interval of measurement in one dimension has two effects: increasing uncertainty about signal location and decreasing uncertainty about signal content, represented by functions B_1 and B_2 in Figure 7B. The two effects are summarized by joint uncertainty function B_3 (the thick curve).
- Now, we use the same approach, first separately, within the spatial and temporal domains. The spatial and temporal uncertainty functions are represented by the thick curves in Figure 7B.
- Next, we add the spatial and temporal uncertainties for every point in the distance graph. The result is a *spatiotemporal uncertainty function* rendered in Figure 7B as a surface.

The structure of this surface is revealed in a contour plot on the bottom of Figure 7 (a distance graph). The contours are projections of the level curves of the surface, such that each contour is an *iso-uncertainty set* containing (T, S) conditions of the same uncertainty. These conditions are equally suitable for measuring stimulus location and content in space and time. The closer a contour to the point of smallest uncertainty (red disk in Figure 7B), the lower the uncertainty.

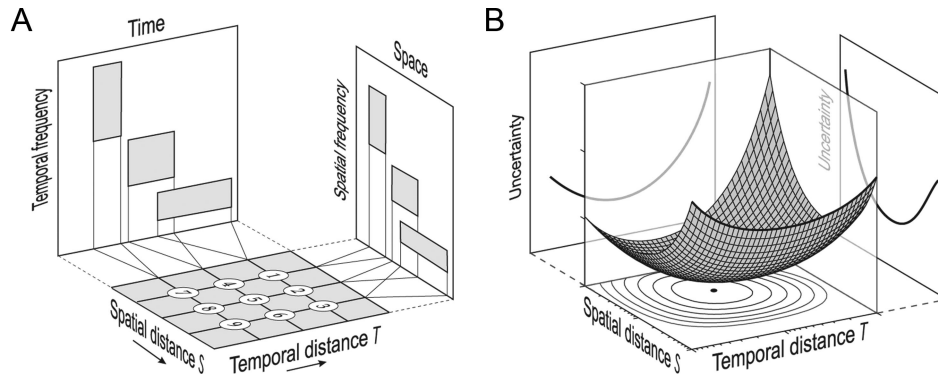


Figure 7. A: Interaction of spatial and temporal uncertainties. The gray panel on the bottom is a distance graph. Each point of it corresponds to two information cells: temporal and spatial. Some of the corresponding logons are shown in the temporal and spatial (x, f) planes in the left and right planes. B: Spatiotemporal uncertainty function. The curves in the side panels represent one-dimensional uncertainty functions: temporal and spatial. The functions describe uncertainties of jointly measuring signal location and signal content (as in Figure 6B), separately in space and time. Summing the spatial and temporal uncertainties for every combination of spatial and temporal distances yields a bivariate uncertainty function, shown as a surface. The circular contours in the distance graph on the bottom are projections of level curves of this surface. Each contour represents a set of equal uncertainty. The central dot in the bottom panel is a projection of the minimum of uncertainty. Panel A is adapted from “Two Psychologies of Perception and the Prospect of Their Synthesis,” by S. Gepshtein, 2010, *Philosophical Psychology*, 23, p. 256. Copyright 2010 by Taylor & Francis. Adapted with permission. Panel B is adapted from “The Economics of Motion Perception and Invariants of Visual Sensitivity,” by S. Gepshtein, I. Tyukin, and M. Kubovy, 2007, *Journal of Vision*, 7(8), Article 8, p. 4. Copyright 2007 by the Association for Research in Vision and Ophthalmology. Adapted with permission.

Economics of Measurement by a System of Sensors

We have reviewed how properties of individual spatiotemporal measurements vary across the stimulus space. This analysis allows us to draw several interesting conclusions about characteristics of motion sensitivity. In particular, it helps to explain why different regimes of apparent motion are observed using different stimuli, and why the proximity principle fails in perception of motion.

The distance graph at the bottom of Figure 7 contains iso-uncertainty contours. If measurement uncertainty was the only force that determined the quality of perceived motion, all stimuli on an iso-uncertainty set would be perceived equally well. Then, the different slopes of these contours in different parts of the graph indicate where different regimes of apparent motion are expected: space-time coupling where the slopes are positive, space-time tradeoff where the slopes are negative. For example, the regime of coupling is expected at high speeds, in the top left region of the graph, and the regime of tradeoff is expected at intermediate speeds, in the top right and bottom left regions.

This way, the empirical inconsistency about combination of spatial and temporal distances in apparent motion is resolved not only empirically but also theoretically. The different regimes of apparent motion occur because the expected quality of sensory measurements varies across the stimulus space. We observe that one of the regimes (coupling) is inconsistent with the proximity principle, but it is consistent with predictions from the uncertainty principle, as it is consistent with empirical observations that space-time coupling holds at some stimulus conditions. This suggests that the uncertainty principle should replace empirical observations as the foundational fact for perceptual theory.

To summarize, the inquiry into basic properties of measurement suggested how an inconsistency in studies of apparent motion can

be resolved. This approach has also helped to understand aspects of perception associated with lower level perceptual processes. Gepshtein et al. (2007) pursued the approach summarized in Figure 7 and also considered the uncertainty associated with relation of the two dimensions of distance graph: speed of motion. They found that the shapes of iso-uncertainty contours that incorporated speed uncertainty were similar to the shapes of isosensitivity contours plotted in Figure 5. That is, they showed that basic considerations of sensory measurement can explain more intricate details of visual sensitivity than the fact that different regimes of apparent motion occur under different conditions of stimulation.

The predictions of equivalent conditions of sensory measurement serve as a prescription for optimal allocation of the limited neural resources. The lower the measurement uncertainty, the more useful these conditions are for the perception of motion. If the visual system allocated its resources according to this expected *utility of measurement*, then better sensory performance (e.g., higher sensitivity) would be expected at conditions where the predicted uncertainty of measurement is low, and equivalent performance would be expected when the uncertainty is the same.

Using this economic framework, it is easy to see how aspects of sensory measurement *intrinsic* to the sensory system relate to its *extrinsic* aspects—that is, those of the sensory environment. Evidently, the utility of sensors that are stimulated infrequently is lower than the utility of sensors stimulated very often. This observation suggests how the intrinsic utility of sensors ought to be modulated in view of the *statistics of stimulation*, and how equivalent conditions of measurement ought to change as the environment changes. The distribution of motion sensitivity across the entire distance graph is expected to change, causing increments or decrements of sensitivity in different parts of the stimulus space.

This argument helps to explain why previous studies of adaptation produced puzzling results. Visual sensitivity was found to sometimes increase and sometimes decrease in response to exposure to adapting stimulus (e.g., Clifford & Wenderoth, 1999; De Valois, 1977). Such results, obtained in different studies that used stimuli at different parts of our distance graph, again become special cases of a larger picture, in which adaptation induced a redistribution of sensitivity across the entire range of stimulation. The question of whether adaptation should increase or decrease visual sensitivity at an individual point in the distance graph can only be answered when we know the distribution of sensitivity in the entire system (Gepshtein, Lesmes, Tyukin, & Albright, 2009).

Conclusion

From this perspective, properties of individual sensors, as well as their contributions to perception, must depend on the place the sensors occupy in the system. This outlook allows one to explain phenomena of motion perception that may appear unrelated to one another, or even contradictory, including the phenomena of apparent motion, spatiotemporal sensitivity, and motion adaptation. The theory of sensory processes that we outlined, although based on experimental findings broader than classic Gestalt phenomena, is very much in line with the Gestalt claim that properties of system elements—the parts—are determined by intrinsic properties of the system—the whole (cf. Wertheimer's fundamental formula of Gestalt theory cited in Section 2). At the same time, however, this synthetic framework allows one to investigate how extrinsic factors (such as the statistics of natural stimulation) affect visual sensitivity, helping to resolve the tension between simplicity and likelihood principles in perceptual science. Two other synthetic frameworks that address this tension are reviewed next.

A Bayesian Approach

Introduction

In traditional Gestalt psychology, the foundation of all different phenomena of perceptual organization lies in the minimum or simplicity principle. A potentially useful alternative synthesis of many aspects of grouping and object formation is provided by Bayesian theory and associated computational mechanisms. The Bayesian approach may be viewed as competing with traditional approaches, but is perhaps better viewed as a comprehensive mathematical framework in which existing principles are unified and placed on a more principled foundation.

In Bayesian approaches to perception (Kersten, Mamassian & Yuille, 2004; Knill & Richards, 1996), all fixation of perceptual belief is assumed to be connected to the calculation of Bayesian posterior probability. Bayesian inference is a provably rational procedure (see Cox, 1961; Jaynes, 1957/1988) that results in an optimal combination of the available evidence with prior beliefs. In perception, generally, this approach entails a rational estimate of the structure of the scene that combines fit to the available image data with the mental set of the perceiver (background knowledge, context, etc.). In this sense, the Bayesian approach exemplifies a principle-based approach to perception (in contrast to a bag of tricks; Ramachandran, 1985), postulating that one coherent rational procedure underlies a wide range of perceptual phenomena,

ranging from visual illusions (Geisler & Kersten, 2002) to motion (Weiss, Simoncelli, & Adelson, 2002) to shape (Feldman & Singh, 2006).

As applied to perceptual grouping in particular, the Bayesian approach entails the selection of an optimal *organization* of the image elements into groups, including contours, surfaces, whole objects, and entire scenes. In this context, the organization to be estimated is an emergent feature or holistic property par excellence. In its reliance on one unifying principle, namely, Bayes' rule, the goal of Bayesian perceptual grouping is to *explain* conventional grouping principles, such as Gestalt rules, as entailments of its central principle, rather than to *assume* them as axioms. In this way, the Bayesian approach aims to reinterpret Gestalt rules as epiphenomena of a more fundamental unifying principle.

The main challenge in formulating Bayesian accounts of perceptual grouping is to develop appropriate likelihood models for objects (and contours, surfaces, etc.), which can be thought of as probabilistic generative models of image structure. Bayesian theory does not directly provide such models, but merely requires that they have the form $p(I|H_i)$ for some set of candidate models $H_1 \dots H_N$, where I is some representation of image data. This expression quantifies the conditional probability of those particular image data under each hypothetical organization. The particular form of such likelihood models then becomes the main focus of inquiry, and may have very different answers in each setting in which it arises. In many cases, the likelihood models adopted implicitly import what amount to familiar Gestalt preferences. An example is when the generative model for contours (see below) presumes approximately collinear paths, which seems to smuggle in the Gestalt conception of good continuation in all but name. Nevertheless, the Bayesian framework allows such biases to be coherently formalized so that (a) their strength can be quantified, (b) predictions about what percepts they engender can be substantiated, and (c) rules of combination can be developed using all the tools of modern statistical theory.

In what follows, (a) we apply the Bayesian approach to grouping principles such as proximity and good continuation, (b) we offer a Bayesian foundation for core concepts from Gestalt theory such as object formation and Prägnanz, and (c) we discuss relationships to other frameworks (simplicity vs. likelihood, minimal model theory, and Bayesian network models).

A Bayesian Approach to Grouping Principles

Proximity. A simple example is the principle of *proximity*, which was among the earliest Gestalt cues to enjoy careful empirical quantification (e.g., Hochberg & Silverstein, 1956; Oyama, 1961). More recent work by Kubovy, Wagemans and coauthors (Claessens & Wagemans, 2005; Kubovy, Holcombe, & Wagemans, 1998; Kubovy & van den Berg, 2008; Kubovy & Wagemans, 1995) has carefully measured the preference for one dot organization over another as a function of interelement distances, generally finding data consistent with a pure distance law in which grouping strength decays exponentially as a function of interelement distance (see Wagemans et al., 2012, Section 3). This approach (a) explicitly establishes a finite set of alternative organizational hypotheses, and then (b) weighs probabilistic evidence in favor of one hypothesis over another. Hence, though not originally formulated in explicitly Bayesian terms, this finding sets the

stage for a Bayesian interpretation mechanism, involving a generative model of dot clusters as foci from which visual elements are generated with probability monotonically decreasing with distance from their centers (Claessens & Wagemans, 2008).

Good continuation. Another example is *collinearity*, which Wertheimer (1923) identified as a Gestalt organizing principle under the admittedly vague phrase *good continuation* (*durchgehende Gerade* or *continuing direction*). In a Bayesian context, the expectation that contours tend to continue approximately straight can be realized as a likelihood model assigning probabilities to specific magnitudes of deviation from perfect collinearity (Feldman, 1996, 1997a; Feldman & Singh, 2005; Singh & Fulvio, 2005, 2007). This likelihood distribution can take several forms, such as a Gaussian (normal) distribution centered at collinear, or a von Mises distribution, which is both more mathematically appropriate (Fisher, 1993) and is supported by neurophysiological data (Swindale, 1998). Whatever the choice, the nature of the likelihood distribution constitutes the system's tacit assumptions about exactly how smooth contours are likely to behave in the environment. The connection between the statistical structure of contours and the empirical statistics of naturally occurring object boundaries has been made more explicit by Elder and Goldberg (2002) and by Geisler, Perry, Super, and Gallogly (2001). In this connection, the Bayesian approach to perceptual organization can be regarded as sharing an essential premise with an older tradition of justifying perceptual biases via arguments from ecological validity (Brunswik & Kamiya, 1953), in that both connect perceptual principles to statistical regularities of the world. More broadly, likelihood models can be developed that are tuned to the characteristics of specific natural object categories (see Wilder, Feldman, & Singh, 2011). But again, placing this argument in a Bayesian framework enormously clarifies the mathematical substance of this connection, showing exactly in what sense, and under what assumptions, perceptual hypotheses are justified by assumptions about the world.

A Bayesian Foundation for Core Concepts From Gestalt Theory

Object formation. Perceptual grouping is sometimes described as the formation of *objects* or units from the initially disparate element of the visual array—that is, groups large enough to be considered whole. Like many aspects of the conventional Gestalt account, this somewhat vague idea can be given a more precise meaning in a Bayesian framework (Feldman, 2007). By its nature, Bayesian theory presumes data-generating stochastic models, here meaning object models whose boundaries and surface properties are generated in a well-defined way that involves a well-defined random component. Such a generative model can (and in complex situations usually does) contain multiple distinct data sources—that is, sources that are generated independently but whose outputs combine to form the ultimate image configuration. A simple example is a *mixture model*, a probability distribution that is formed from the combination of some number of distinct sources each with its own mean and variance (McLachlan & Basford, 1988). Estimation of mixture models is a statistically challenging problem because of the need to estimate the correct separation of the data into component sources—that is, to estimate which component was actually responsible for generating each

datum. The problem of perceptual organization can be thought of as a particularly complex mixture estimation problem, in which the distinct sources have not only distinct means and variances but also distinct geometric properties, surface properties, colors, textures, and so forth. In this view, the objects are the distinct generative sources, but estimating them correctly—solving the perceptual organization problem—is beyond the capacity of contemporary theory.

Prägnanz. Perhaps the most subtle connection between Gestalt and Bayesian approaches to perceptual grouping arises in connection with the term *Prägnanz*, used to encompass a wide range of Gestalt organizational preferences involving harmony, coherence, or simplicity (Kanizsa, 1979; Koffka, 1935; Metzger, 1953). In a Bayesian framework, this admittedly vague and disjunctive term corresponds to a single unifying principle: Bayes' rule. Given appropriate generative models (i.e., assuming that the image configuration was generated stochastically by a model within the assumed model class), the maximum posterior interpretation is, in fact, the optimal interpretation. In particular, it has often been noted that Bayesian models tend to incorporate a preference for simpler interpretations (sometimes referred to as Bayes' Occam), essentially because larger families of hypotheses (involving more parameters, and in this sense inherently more complex) must assign a lower prior probability to each individual hypothesis (Jeffreys, 1961; D. J. C. MacKay, 2003; Tenenbaum & Griffiths, 2001). This observation is part of a larger fabric of connections between simplicity and probability that has been developed in the statistical learning literature, including the principle of minimum description length (Rissanen, 1978), which connects the maximization of the Bayesian posterior to the minimization of the data encoding, and the theory of Kolmogorov complexity (see Li & Vitányi, 1997), which connects the inherent complexity of models to their probability via a universal prior (Solomonoff, 1964a, 1964b). This theme is taken up again below.

Relationships to Other Frameworks

Simplicity versus likelihood. In a Bayesian framework, the central unifying principle of Gestalt theory—*Prägnanz*—may be identified with the central unifying principle of Bayesian theory—maximization of the Bayesian posterior. The question then is where a Bayesian visual system might get its prior and conditional probabilities from, so to speak. According to the likelihood principle, these probabilities relate to frequencies of occurrence in the world, and according to the simplicity principle, they are derived from the simplest stimulus descriptions (i.e., simpler is more likely). Chater (1996) and Feldman (2009) argued that these stances can be reconciled (but see also below). In any case, a Bayesian visual system using simplicity-based probabilities would be in line not only with Bayes' Occam but also with the intuitive workshop metaphor of Adelson and Pentland (1996), who analogized scene interpretation to the construction of a physical model in which total costs (fees to carpenters, painters, and lighting designers) are minimized. Maximizing the posterior minimizes these costs, thus yielding the most economical solution—as long as the costs have been correctly calibrated, that is, as long as the assumptions underlying the generative model are correct.

Minimal model theory. The Bayesian preference for simpler perceptual interpretations over more complex ones defines an

implicit qualitative ordering of interpretations in the model space (Feldman, 2009), which can be made explicit in a lattice or other partial order (Feldman, 1997b, 2003b; Jepson & Mann, 1999; Jepson & Richards, 1992; Richards, Jepson, & Feldman, 1996). This point of view suggests a logical rendition of Bayesian perceptual interpretation, in which Bayes' rule is replaced by a logical operation that selects an extremal interpretation from a structured space of qualitative alternatives. This framework is sometimes termed *minimal model theory* because it entails the selection of a logically minimal model from this partially ordered set. This framework relates closely to Rock's (1983) *avoidance-of-coincidence principle*. This principle holds that interpretations should be preferred in which as few image properties as possible are coincidences, such as accidents of viewpoint or configuration. By this argument, reliable scene representations should be built upon properties that are unlikely to be accidental consequences of viewpoint, sometimes called *nonaccidental properties* (Witkin & Tenenbaum, 1983; see also below for a different model along the same lines). An example is collinearity, which is unlikely to arise accidentally in the image unless it actually occurs in the 3-D scene. Minimal model theory orders interpretations by subset inclusion over the set of accidental configurations. The interpretation that is minimal in this order, among all interpretations consistent with the image, is thus the interpretation that leaves the fewest coincidences unexplained.

Selection of the minimal model discards many of the niceties of a full-blown Bayesian approach, such as a complete quantitative evaluation of the likelihood, in favor of a *qualitative* evaluation of consistency between each interpretation and the image data. But it is broadly consistent with Bayesian inference in that each additional coincidence entails a decrease in the likelihood, so minimizing the coincidences also maximizes the likelihood (see Feldman, 2009). At the same time, this point of view opens the door to the kind of qualitative inference familiar from much of the perceptual organization literature, which often entails selecting among a finite set of distinct alternatives (orderings of surfaces, qualitative classifications of junctions, qualitative classifications of parts, etc.). Moreover, consistent with the discussion above, minimal model theory provides an elegant definition of objects, which are viewed as subtrees of the minimal interpretation bearing a certain type of logical independence from other subtrees (Feldman, 2003a).

Bayesian network models. In its application to perception, Bayesian theory may be regarded as a pure *computational theory* in Marr's (1982) sense, in that it identifies defining attributes of a solution to be selected from the space of possible stimulus interpretations, but does not provide concrete mechanisms for computing it. But a burgeoning literature has taken up this challenge, proposing computationally feasible procedures for approximating the Bayesian posterior. Prominent among these are the many variants of Bayesian belief propagation pioneered by Pearl (1988). In principle, such models may be thought of as models for neural networks because (like real neural networks) they involve strictly local communication between nodes connected by pairwise links. The application of Bayesian network models to perceptual organization is still in its infancy, notwithstanding some promising initial steps in the area of figure-ground organization (Froyen, Feldman, & Singh, 2010; Weiss, 1997). But the broader problem of perceptual grouping constitutes a particularly challenging case

for network architectures because of the need to consider global qualities of the image in order to arrive at the perceived interpretation—that is, the very aspect emphasized in the term *Gestalt*. Most neural network models, by design, consider evidence only across the span of local receptive fields—not the entire image at once—so adapting them to find global optima may require the development of new techniques. Still, this direction may be uniquely promising as a way of combining a neural-like architecture with a well-motivated global objective function.

Conclusion

The Bayesian approach, which has proven to be useful in many areas of perception and cognition, has offered additional insight into classic Gestalt phenomena such as perceptual grouping and object formation, and it has provided a foundation to core concepts from classic Gestalt theory such as *Prägnanz*. It also establishes a bridge between likelihood and simplicity, which is expanded further in the next section.

Structural Information Theory

Introduction

In order to understand simplicity, we need to understand description complexity, and for that, we need a valid notion of information. In the aftermath of Shannon's (1948) breakthrough in communication theory, psychologists started to rethink the concept of information (e.g., Attneave, 1954; Garner, 1962; Hochberg & McAlister, 1953; D. M. MacKay, 1950; Miller & Frick, 1949; Quastler, 1955). This led to the rise of representational coding approaches, which did not quantify the information in a message by the probability of occurrence of the message (as Shannon did) but by the number of parameters needed to specify its content. In other words, applied to perception, they focused on the informational content of Gestalts (for a review, see Hatfield & Epstein, 1985). To this end, they postulated (a) that incoming stimuli are perceptually organized by operations that capture regularity and (b) that Gestalts are reflected by codes that specify the simplest organization (Simon, 1972). Later, in the 1980s and inspired by an increased understanding of the brain's neural network, connectionism began to focus on the flow of information, postulating (a) that this flow is reflected by activation spreading in a network and (b) that Gestalts are reflected by stable patterns of activation (McClelland & Rumelhart, 1981). Still later, in the 1990s, dynamical systems theory (DST) started to focus on the dynamic transitions from any one neural state to the next, postulating (a) that these transitions can be described by nonlinear differential equations and (b) that Gestalts are reflected by attractors in the brain's state space, that is, by relatively stable states towards which the brain can be said to be attracted (Eliasmith, 2001; see also above).

These three approaches (information theory, connectionism, and DST) use different formal tools to model different aspects, which does not mean that they are mutually exclusive. In fact, in the spirit of Marr's (1982) three levels of explanation (computation, algorithm, and implementation), they may provide complementary insights that—together—may explain how percepts are the result of cognitive processes implemented in the brain. In the sections below, this multidisciplinary and typically Gestaltist perspective is

sketched starting from the representational coding approach of structural information theory (SIT).

Central to SIT is the *simplicity* principle, which holds that percepts correspond to the simplest descriptive codes, that is, codes that specify stimulus organizations by capturing a maximum of regularity. The simplicity principle is a descendant of Hochberg and McAlister's (1953) minimum principle, and both are information-theoretic translations of the law of Prägnanz. In the 1960s, Leeuwenberg (1969, 1971) initiated SIT as a representational coding model of visual pattern classification. Nowadays, it also includes a theoretically sound and empirically successful quantification of pattern complexity and empirically successful quantitative models of amodal completion and symmetry perception (e.g., van der Helm, 1994; van der Helm & Leeuwenberg, 1991, 1996; van der Helm, van Lier, & Leeuwenberg, 1992; van Lier, 1999; van Lier, van der Helm, & Leeuwenberg, 1994). To avoid a persistent misunderstanding, it is true that SIT's formal model applies to symbol strings to code patterns and that relatively much attention in the SIT literature is paid to how symbol strings might represent visual stimuli. This does not mean, however, that SIT assumes that the visual system converts visual stimuli into symbol strings. The symbolic representations (which are not discussed here) merely serve to indicate how SIT's information-processing principles might be applied to visual stimuli to attain testable quantitative predictions.

In the sections below, we review how SIT deals with three fundamental questions concerning perceptual organization. First, we address the question of how veridical simple stimulus organizations are; to this end, we specify the relationship between simplicity and likelihood again by means of Bayes' rule but in a different conceptual framework than the one used in the preceding section. Second, we address the question of what should be the nature of the visual regularities to be captured to arrive at simple organizations. Third, we address the question of how simple organizations might be computed; this issue has led to a representational picture of cognitive architecture, which includes connectionist modeling ideas and which honors ideas from neuroscience and DST about neuronal synchronization.

The Veridicality of Simplicity

As argued before, the Gestalt school's simplicity principle contrasts with von Helmholtz's (1909/1962) likelihood principle. The latter holds that, for a proximal stimulus, the visual system chooses the interpretation most likely to be true, that is, the one that most likely reflects the actual distal stimulus that caused the proximal stimulus. Hence, by definition, the likelihood principle holds that the visual system is highly veridical with respect to the external world. This would be nice, but to be able to assess this, one needs access to the real probabilities of occurrence of distal stimuli in the external world, while in fact these probabilities are unknown, if not unknowable. The simplicity principle, conversely, holds that the visual system chooses the simplest interpretation, that is, one that can be specified by a minimum number of descriptive parameters. Hence, by definition, the simplicity principle holds that the visual system is highly efficient with respect to internal resources. This would also be nice, but would it yield sufficient veridicality to guide us reliably through the world? In SIT, this question has been

addressed via a line of reasoning that is reviewed next (for more details, see van der Helm, 2000, 2011a).

In the 1950s and 1960s, not only psychologists but also mathematicians began to rethink the concept of information (Kolmogorov, 1965; Solomonoff, 1964a, 1964b). This led to the mathematical domain of algorithmic information theory (AIT), also known as the theory of Kolmogorov complexity or the minimum description length principle (see Li & Vitányi, 1997). Solomonoff (1964a, 1964b), in particular, realized that, in many domains, the probabilities with which events occur are unknown, so that Shannon's approach cannot be applied to make reliable inferences. To circumvent this problem, he turned to descriptive codes and proposed to use artificial probabilities derived from the complexities of these codes (i.e., things with simpler codes get higher probabilities). He was also the first to prove that this can be achieved irrespective of the specific descriptive coding language that is used (see also Simon, 1972). In other words, he showed that simplicity is a fairly stable concept. He also conjectured that those artificial probabilities are universal probabilities in that they allow for fairly reliable inferences in many different situations (or worlds).

In the 1990s, Solomonoff's conjecture proved to be valid in the form of the fundamental inequality (Li & Vitányi, 1997), which holds for an infinite number of imaginable worlds and implies that simplicity-based inference is more reliable as the probability distribution of objects in such a world is simpler. Roughly, the complexity of a probability distribution is given by the number of categories to which it assigns probabilities. Hence, the fundamental inequality implies that simplicity-based inference is more reliable in a world that contains fewer categories to be distinguished (e.g., human-made worlds as opposed to natural worlds). This suggests that the simpler a world is, the more veridical the simplicity principle will be in that world. This does not imply, however, that the simplicity principle is highly veridical in any specific world, but instead, that it might be fairly veridical in many different worlds, possibly including the actual one. (This is where this line of reasoning deviates from the one by Chater, 1996, and Feldman, 2009, outlined above.)

Hence, whereas the likelihood principle is a special-purpose principle in that it is adapted to one specific world with a supposedly known real probability distribution, this line of reasoning suggests that the simplicity principle is a general-purpose principle that promises to be fairly (possibly sufficiently) adaptive to many different worlds without having to know their real probability distributions. The latter is therefore a serious contender not only because it is better quantifiable but also from an evolutionary point of view because the survival value of adaptability to changing environments may be higher when based on a general-purpose principle than a special-purpose one.

Applied to perceptual organization, the discussion above can be sharpened further. To this end, one has to make a distinction between the prior and the conditional of a candidate stimulus interpretation, that is, of a hypothesized distal stimulus H that fits a given proximal stimulus D . In Bayesian terms, the prior is the probability that H occurs independently of D , and the conditional is the probability that D occurs if H were true. Multiplying the prior and the conditional then yields, after normalization, the posterior, which indicates how likely H is given D , under the employed priors and conditionals. Thus, the likelihood principle can be formalized as holding that the visual system chooses the

interpretation with the highest posterior probability, assuming it uses real prior and conditional probabilities. Fair approximations of conditional probabilities can be determined in principle, but a fundamental problem remains that the real prior probabilities are unknown. Alternatively, one might start from the simplicity principle. Then, the prior is the complexity of the simplest code that specifies H independently of D , and the conditional is the complexity of the simplest code that specifies D starting from H . Then, summing the prior and the conditional yields the posterior which indicates how well H fits D . Thus, reflecting Occam's razor, the simplicity principle can be formalized as holding that the visual system chooses the interpretation with the lowest posterior complexity.

Prior and conditional complexities could be converted, as Solomonoff did, into artificial probabilities to model the simplicity principle in Bayesian terms, but this does not automatically yield compliance with the real probabilities as assumed by the Helmholtzian likelihood principle. Indeed, AIT's fundamental inequality implies that the margin between such artificial probabilities and real probabilities is roughly equivalent to the number of categories to be distinguished. In fact, this suggests an interesting difference between priors and conditionals in vision. Priors apply to viewpoint-independent categories of distal stimuli, and most worlds give rise to many different categories of distal stimuli; this suggests that the artificial prior probabilities are not particularly close to the real ones. Conditionals, however, apply to viewpoint-dependent categories of views of distal stimuli, and each distal stimulus gives rise to only a few different categories of views; this suggests that the artificial conditional probabilities might be close to the real ones.

This theoretically inferred difference between priors and conditionals has been supported by van Lier et al.'s (1994)

model of amodal completion. This model treats conditionals differently than the minimal model theory mentioned above, but it also claims to comply with Rock's (1983) avoidance-of-coincidence principle, and it successfully combines prior and conditional complexities to predict whether, and if so how, patterns are amodally completed (see Figure 8). While it is impossible to know if the prior complexities after conversion are close to the real prior probabilities, by all accounts the conditional complexities seem to be close to the real conditional probabilities (van der Helm, 2000, 2011a). This is relevant in everyday situations in which a moving observer gets a growing sample of different views of the same distal scene. It allows the visual system to update its interpretation with each new view in a process that can be modeled by a recursive application of Bayes' rule. During this recursive process, the effect of the first priors fades away as the priors are updated continuously on the basis of the conditionals that then become the decisive entities. Because the simplicity-based artificial conditional probabilities seem to be close to the real conditional probabilities, simplicity seems to provide sufficient veridicality in such everyday situations. Thus, a Gestaltist visual system that focuses on internal efficiency seems to yield external veridicality as a side effect.

The Nature of Visual Regularity

The veridicality finding discussed above is based on the complexity of the simplest codes and holds virtually independently of which specific regularities are chosen to be captured to obtain the simplest codes. However, the primary purpose of such simplest codes in vision is to yield perceptual organizations, and in this respect, it is crucial to capture visually relevant regularities (Simon, 1972). Empirically, it is clear that regularities such as mirror

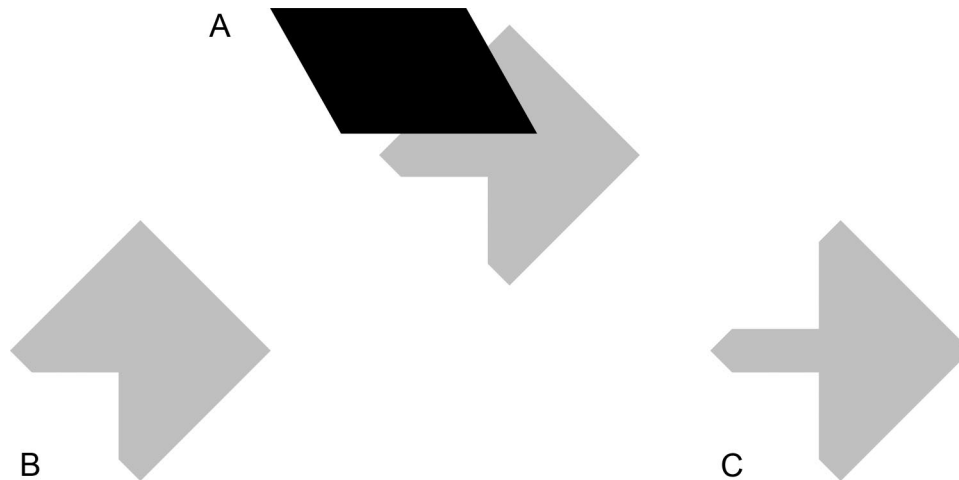


Figure 8. The proximal pattern in Panel A is readily interpreted as a parallelogram partly occluding the shape in Panel B rather than the shape in Panel C. By the likelihood principle, this could be explained by arguing that Panel C would have to take a more coincidental position to yield Panel A; this argument relies on real conditional probabilities and ignores real prior probabilities that are unknown but that, if included, might well undermine this argument. By the simplicity principle, the prior complexities (of the objects as such) and the conditional complexities (of the objects' relative positions in the pattern) converge on a predicted preference for the shape in Panel B. Adapted from "Simplicity Versus Likelihood in Visual Perception: From Surprisals to Precisals," by P. A. van der Helm, 2000, *Psychological Bulletin*, 126, p. 771. Copyright 2000 by the American Psychological Association.

symmetry and repetition are visual regularities (i.e., regularities the visual system is sensitive to), but it is less clear how to distinguish visual from nonvisual regularities. The traditionally considered transformational formalization of regularity (advocated most prominently in perception by Garner, 1974; Palmer, 1983), which proposes a criterion for distinction, seems suited for object recognition but not for object perception. For instance, it cannot account well for human detection of perturbed regularities or for the classical phenomenon that symmetry is generally much better detectable than repetition (e.g., Bruce & Morgan, 1975; Corballis & Roldan, 1974; Julesz, 1971; Wagemans, Van Gool, Swinnen, & Van Horebeek, 1993; for reviews, see Wagemans, 1995, 1997). In SIT, this led to a rethinking of the concept of visual regularity, which resulted in the formalization and implications sketched next (for more details, see van der Helm & Leeuwenberg, 1991, 1996, 1999, 2004; for discussion, see also Olivers, Chater, & Watson, 2004; Wagemans, 1999).

Considering the purpose of regularity detection, visual regularities must meet two general demands. First, they must allow for an easy build-up of internal representations, and second, they must allow for the specification of hierarchical organizations of the input. These two demands are met by the formal properties of holographic regularity and hierarchical transparency, respectively. A holographic regularity is a regularity with substructures that all reflect the same kind of regularity; this implies that its representation can be built up easily from its substructures (see Figure 9). Furthermore, a hierarchically transparent regularity is a regularity such that any other regularity nested in it is a regularity in its own right (i.e., does not depend on this nesting); this ensures that codes specify proper hierarchical organizations. Together, the formal properties of holographic regularity and hierarchical transparency single out three regularities, namely, repetition (or iteration), (mirror and broken) symmetry, and alternation (which covers, among others, the regularity in so-called Glass patterns; see Glass, 1969; Glass & Perez, 1973). Hence, these are the only regularities that meet the general demands mentioned before (van der Helm & Leeuwenberg, 1991), and in SIT, these regularities are therefore proposed to be captured to obtain the simplest codes. In other

words, this formalization provides a theoretical foundation for SIT's coding scheme.

Whether this formalization also captures the nature of visual regularity was addressed by testing a regularity-detection model derived directly from this formalization. The formalization suggests that amounts of regularity are to be quantified by the number of nonredundant holographic identity relationships between stimulus parts (E) that give rise to a regularity. Applied to symmetry, E equals the number of symmetrically positioned pairs of identical elements (mirror symmetry is therefore said to have a holographic point structure), and applied to repetition, E equals the number of repeats minus one, independently of the number of elements in each repeat (repetition is therefore said to have a holographic block structure). The model now quantifies the detectability of a regularity in a stimulus by the weight of evidence (W) for this regularity, where $W = E/n$ with n the total number of elements in the stimulus (van der Helm & Leeuwenberg, 1996). A converging body of evidence showed that this holographic model $W = E/n$ provides a fairly comprehensive account of the detectability of single and combined regularities, whether or not perturbed by noise (for reviews, see van der Helm, 2010, 2011b). This suggests that the formalization described above indeed captures the nature of visual regularity. In other words, a Gestaltist visual system that focuses on internal efficiency not only seems to yield external veridicality as a side effect, but if it achieves this efficiency by capturing transparent holographic regularities, then it also complies with human regularity detection, which is believed to be an integral part of the perceptual organization process that is applied to every incoming stimulus.

Cognitive Architecture

The two findings discussed above establish a viable Gestaltist approach to perceptual organization. Notice, however, that both findings apply mainly to the question of what is to be processed rather than how. In fact, any stimulus may give rise to a superexponential number of candidate interpretations, so that evaluating each of them separately to select the simplest one (or one of them,

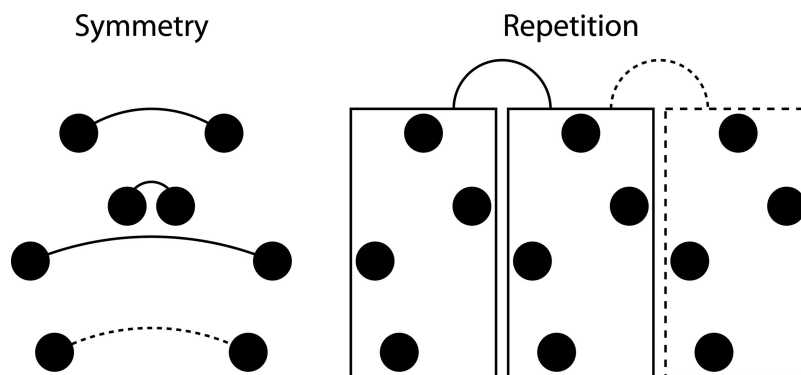


Figure 9. Holographic regularity. A symmetry (at the left) can be expanded by one symmetry pair at a time (dashed arc) preserving its symmetrical nature, and a repetition (at the right) can, independently of the number of elements in each repeat, be expanded by one repeat at a time preserving its repetition nature. Adapted from "Holographic Goodness Is Not That Bad: Reply to Olivers, Chater, and Watson (2004)," by P. A. van der Helm and E. L. J. Leeuwenberg, 2004, *Psychological Review*, 111, p. 262. Copyright 2004 by the American Psychological Association.

in case of several equally simple simplest interpretations) would require more time than is feasible. As we discuss next, this issue has been addressed in SIT by solving the problem of computing the simplest SIT codes of symbol strings, in a way that also suggests how the brain might arrive at the simplest interpretations of visual stimuli (for more details, see van der Helm, 2004, 2012).

In standard connectionist modeling, one fixed neural network is assumed to deal with all possible inputs, and for a specific input, an output is assumed to be selected by activation spreading in this fixed network (see, e.g., McClelland & Rumelhart, 1981). In contrast, although SIT assumes that an output is selected in a computationally comparable way, it also assumes that, preceding this selection, regularity-capturing operations create flexible cognitive networks representing all possible outputs for only the input at hand. For symbol strings, this idea has been implemented in an algorithm whose essence is sketched next.

For an input string, SIT's formal model applies coding rules to extract transparent holographic regularities that have to be recoded in a hierarchically recursive fashion to compute the simplest code. In theory, a string may contain an exponential number of these regularities, and recoding each of these regularities separately would require a superexponential amount of processing time. However, transparent holographic regularities provably group by nature into special distributed representations called *hyperstrings*, each representing an exponential number of similar regularities. Hyperstrings are special in that they allow this exponential number of similar regularities to be recoded in one go, that is, simultaneously, as if only one regularity were concerned (see Figure 10). Thus, there is no need to recode these similar regularities in a serial or parallel fashion, but instead they can be recoded in a *transparallel* fashion. Such a transparallel method has been implemented in

an algorithm (van der Helm, 2004), which is neurally plausible in that it incorporates the three intertwined but functionally distinguishable subprocesses that are believed to occur in the brain's visual hierarchy: feedforward feature encoding (an initial tuning of the visual system to features to which it is sensitive), horizontal feature binding, and recurrent feature selection.

Notice that horizontal feature binding applies to binding of similar features (in the algorithm, these are similar transparent holographic regularities gathered in hyperstrings). It does not apply to integration of different features into percepts, which is taken to result from recurrent feature selection within the visual hierarchy. This is not to be confused with recurrent attentional processing starting from beyond the visual hierarchy, which selects features from already integrated percepts. This functional distinction is somewhat controversial and not that clear-cut, but it seems to explain the primacy or dominance of holistic stimulus features in experimental tasks (see Section 2 above).

Furthermore, the method of transparallel processing by hyperstrings seems to provide a computational explanation of synchronization in the visual hierarchy. Neuronal synchronization is the phenomenon in which neurons temporarily synchronize their activity in transient assemblies. As indicated in the section on the dynamical systems approach, there are various ideas about its cognitive meaning, but both theoretically and empirically, it has been associated with cognitive processing, and 30–70 Hz gamma-band synchronization in particular has been associated with feature binding in perceptual organization. In fact, such temporarily synchronized neural assemblies in the visual hierarchy seem to be horizontal assemblies that also seem involved in binding similar features (Gilbert, 1992). The model discussed above now suggests that hyperstrings can be seen as formal counterparts of these

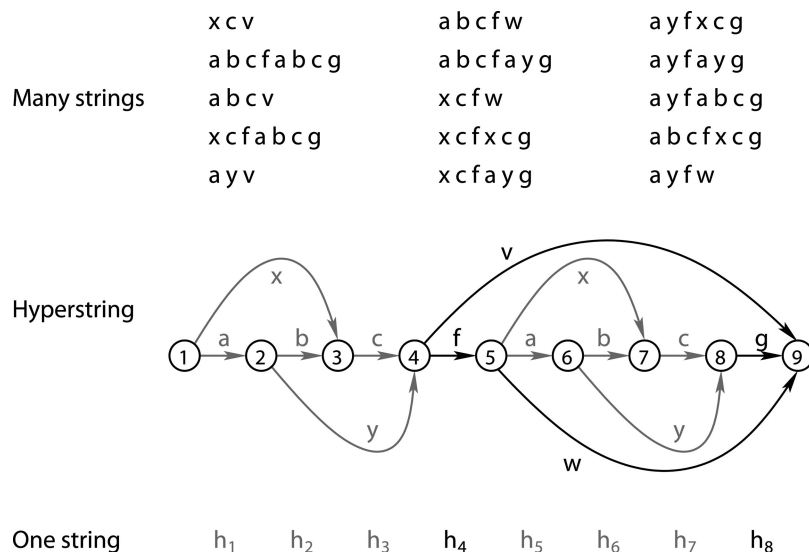


Figure 10. The 15 strings at the top are such that they can be represented each by a path from Vertex 1 to Vertex 9 in a distributed representation. This distributed representation is a hyperstring: Every pair of subgraphs (here, e.g., the gray ones) represents substring sets that are either completely identical or completely disjoint—never something in between. This property implies that the 15 strings can be searched for regularities in a transparallel fashion, that is, in one go, or in other words, simultaneously as if only one string were concerned. Adapted from “Transparallel Processing by Hyperstrings,” by P. A. van der Helm, 2004, *PNAS: Proceedings of the National Academy of Sciences, USA*, 101, p. 10864. Copyright 2004 by the National Academy of Sciences.

transient horizontal assemblies of synchronized neurons. Thereby, it also suggests that synchronization in these assemblies can be seen as a manifestation of transparallel processing of similar features (van der Helm, 2012).

In the model, the intertwined subprocesses of feature encoding and feature binding yield an input-dependent hierarchical network consisting of hyperstrings, and the subprocess of feature selection (which is also intertwined) then backtracks this hierarchical network to obtain the simplest code of the input. Thus, all in all, the model suggests that hyperstring-like neural assemblies are the constituents of flexible cognitive architecture implemented in the relatively rigid neural architecture of the brain. For one thing, this picture of flexible cognitive architecture constituted by hyperstring-like neural assemblies performing transparallel feature processing does justice to both the high combinatorial capacity and the high speed characterizing the perceptual organization process. Furthermore, just as connectionism does, it relies on interactions between pieces of information in distributed representations, and it relates plausibly to neuronal synchronization whose dynamics are a typical topic in DST. In other words, this picture of cognitive architecture opens a pluralist and truly Gestaltist perspective by which complementary insights from representational theory, connectionism, and DST may be combined to obtain a comprehensive account of perceptual organization.

Conclusion

SIT offers another perspective on the relationship between simplicity and likelihood, arguing that a Gestaltist visual system that focuses on internal efficiency yields external veridicality as a side effect. In addition, it specifies the nature of the visual regularities that must be extracted to achieve this efficiency (i.e., transparent holographic regularities) as well as the nature of the cognitive architecture that explains how the simplest organizations are computed (i.e., transparallel processing by hyperstrings).

General Discussion and Conclusion

Gestalt psychology took phenomenal experience as the starting point of its theoretical considerations. We reviewed perceptual grouping and figure-ground organization in the first article (Wagemans et al., 2012) and included a large number of Gestalt phenomena in the present article (configural superiority, global precedence, switching between multistable organizations, apparent motion, object formation, and regularity detection). Such Gestalt phenomena are real and reliable, and they are still the subject of intense investigations to date, independently of the framework in which they arose. In a way, the parts are less than the whole: The theoretical endeavors of the Gestaltists did not similarly stand the test of time. They failed to provide a thorough specification of the concepts of Gestalts as configurations of parts and wholes, and the mechanisms underlying the law of *Prägnanz* as based on a neural isomorphism did not work out. This does not mean that we should reject their intuitions. They protect us from falling back on a naïve mechanistic view, in which perception begins with isolated sensations, thereby denying that phenomenal experience is populated by Gestalten—integrated, coherent structures or forms.

The traditional Gestalt notions have been given fresh blood and a solid backbone by several modern perspectives, reviewed in the

present article. The conceptual and theoretical foundations of Gestalt psychology have been reconsidered in both descriptive and explanatory frameworks.

Descriptive Frameworks

Theories may be discarded but the phenomena do not go away. Many researchers sympathetic to the Gestalt intuitions from a variety of different theoretical convictions have, therefore, made efforts to specify the description by importing theoretical constructs from a variety of external sources. In Section 2, we have shown how the initially vague notion of a holistic Gestalt can be translated into a well-defined concept that allows precise operational definitions and experimentation.

The first operationalization we discussed is grafted onto a notion of representation as a feature space, where features occupy dimensions. In this representation, Gestalts are emergent features of which the characteristics are based on but not expressed by the dimensions. Emergent features are characterized as *integral*, *configural*, or *separable*, based on how strongly the featural components subsist. Whereas *integral* means that the whole is independent of its dimensional components and *separable* means that dimensional components subsist as independent perceptual units, *configural* dimensions occupy a middle ground that is closest to the original Gestalts: differentiated part-whole structures. Note that this notion is more systematic but at the same time more restricted than the original notion of Gestalt because it is tied to the dimensional representation of its components. The notion of dimension can be taken literally or it can be extended into the domain of the metaphorical. Neither way does it offer a connotation of globality that is characteristic of true Gestalts. Any arbitrary emergent property qualifies, in principle, as configural, separable, or integral.

A second idea—even further removed from the original, conceptually speaking—is that of part-wholes being grafted onto the notion of a hierarchical tree, in which a Gestalt is the top-level superstructure, and its substructures are levels of a branching tree. This is the concept underlying the “forests before trees” studies that have helped to establish empirically the primacy of the whole in processing, independently of its size or visibility. Here, the notion of a whole is rigid and well defined conceptually, but the connotation of a whole being a force that binds, shapes, and resists external influences on the configuration of its parts is entirely missing from this account. There is a difference between the whole having priority in processing and the Gestalt observation that the whole determines the appearance of its parts.

In sum, the notion of Gestalt has taken different shapes in these two descriptive frameworks: as configurations in a feature-space versus top-level or superstructures in hierarchical trees. Both descriptions are well defined and capable of suggesting experiments. Each of them captures an aspect of Gestalts but neither of them captures the concept in its entirety. Yet that may have been too much to expect to begin with: Concepts developed closely to experience are not easily expressed in any formalism.

Explanatory Frameworks

We may have answered the need to specify the phenomena to a certain extent, but we are even further removed from answering the

question of how to explain the phenomena. Here again, Gestalt theory has intuitions to offer that are worthy of pursuing with today's instruments: Gestalts emerge spontaneously from self-organizational processes in the brain. Lacking today's advanced nonlinear dynamics and probabilistic and symbolic machinery, the Gestaltists borrowed their explanatory principles from the only source available at the time: the theory of global electrostatic field forces. These are systems residing at equilibria of least energy expenditure, which is at the same time also the simplest possible organization, given the available stimulation (i.e., the law of Prägnanz). With the dismissal of global field theory as a principle for brain organization, the Gestalt concept fragmented, and self-organization, economy, the simplest possible, and "given the available stimulation" each became the starting point for four quite divergent approaches, each of which has been brought in to specify the Gestalt intuition further from a modern perspective.

In Section 3 we saw the aspect of *self-organization* highlighted in a dynamical systems approach to perceptual organization. It claims a solution to the problem of the previous approach: What are the neural mechanisms by which the system achieves optimality? The answer is provided, at least in principle, by the complexity of the neural dynamics that help configure the global architecture of the system, given simple mechanisms of neural growth and adaptation (Gong & van Leeuwen, 2003; Rubinov et al., 2009; van den Berg, Gong, Breakspear, & van Leeuwen, 2012). In addition, this approach does justice to perception as part of an ongoing process instead of a delineated process going from static inputs to static outputs, as in naïve mechanistic approaches. As a counterweight to its potential, however, there are also challenges. For instance, how do we explain the functionality of the system at the level of its behavior? Provided that the system dynamics explain that we perceive Gestalts, which principle governs the selection of those Gestalts that are functional to the system "given the available stimulation" rather than arbitrary others? This could be a matter of selection at an evolutionary level (van Leeuwen, 2007) but how this selection interacts with the proposed mechanisms of neural growth and adaptation remains to be clarified.

The *principle of economy* was given a specification in terms of the optimization of available resources in Section 4. We observed that a system of sensors that work independently at the neural level to minimize its uncertainty is collectively responding optimally to the available patterns of stimulation. It remains an open question whether the proposed mechanism is implemented at the neural level as proposed, and whether it generalizes beyond the realm of motion sensitivity, where it was developed. Clearly, however, these are sophisticated empirical questions, hinting at the great versatility and potential of addressing modern neuroscience from a Gestalt-inspired, holistic perspective. Such questions can now be asked because the general framework has been spelled out, and the necessary tools are now available to be able to test the psychophysical and neural predictions and to model the results, extracting principles, and formulating them quantitatively.

Section 5 specified the conditional "*given the available stimulation*" in terms of likelihood, which motivated a Bayesian approach to perception. In general, the Bayesian approach has been successful in explaining grouping principles such as proximity and good continuation, and it has provided a solid basis for typical Gestalt notions such as objecthood and Prägnanz. Yet, ultimately, all Bayesian theories face the same problem: How to select their

priors? Simply put: We may perceive patterns in accordance with the Gestalt law of symmetry because the more symmetrical arrangement is most likely, but why is symmetry relevant to begin with?

This question is addressed in Section 6, where the aspect of *simplicity* is considered within the context of SIT. This approach has seen substantial development but has retained its roots as an essentially symbolic theory. It states that patterns are preferred according to the greatest simplicity of their symbolic description. The operators used in the symbolic description, such as symmetry, are not arbitrary according to SIT, but based on principled properties of its description language. Over the past decades, SIT has successfully formalized the principles of the language, and solved the problems relating to the computational complexity of their encoding framework. It could be shown that a Gestaltist visual system focusing on internal efficiency yields external veridicality as a side effect, extracting visual regularities in a way that seems to characterize perceptual organization as applied to every incoming stimulus. However, it shares one problem with all symbolic (or even all formal) theories of perception: It must indicate (as van der Helm, 2012, recently began to do) how SIT's encoding algorithms can be mapped onto the way in which the visual system encodes visual information. Real scenes do not consist of discrete, static features, but of continuous and cluttered presentations, in which—over time—various parts are revealed and occluded. What are the units of the visual system's coding language then? In some visual stimuli, we perceive symmetries and other regularities that are not even supported by features in the input (e.g., illusory contours). We cannot understand the Kanizsa triangle as simply a result of binding the features of the visual input, since the features of the triangle are not actually present in the display. This means that the visual system plays an active role in the very constitution of features that it assumes to be given. That insight in turn may help us understand Köhler's (1929/1947) key notion of the *experience error*, wherein we mistakenly attribute our sensory experience to the proximal stimulus activating our receptors.

Conclusion

In sum, the various diverging theoretical approaches that have been motivated by Gestalt problems have all made considerable progress at certain aspects of the conceptual problems, yet none of them has solved the conundrum of Gestalt in its entirety. However, each individual approach, from its own internal consistency, motivates additional detailed research questions that can now be addressed fruitfully. Most importantly, the further specification of the connections between the frameworks, as we have started to do here, will be essential for a synthesis into the conceptually coherent framework that Gestalt theory once was. As the proverbial blind men and the elephant, only together will they make progress in addressing the problem that, a century after its origination, is still in the frontier of scientific exploration: *Why do things look as they do?* Koffka (1935, p. 98) claimed, "Things look as they do because of the field organization to which the proximal stimulus distribution gives rise. This answer is final and can be so only because it contains the whole problem of organization itself." Contemporary vision scientists will not rest until they have addressed all the aspects of this final answer to everyone's satisfaction: the laws of perceptual organization, faithful to perceptual

experience, yet formulated in precise quantitative terms, fully explained in terms of their internal dynamics and ecological validity, spelled out at an algorithmic level and linked to its neural mechanisms, from single neurons to neuronal cell assemblies and whole systems.

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Appendix

Overview of the Article With Section Numbers and Headings, Questions and Issues Raised, Answers Provided, and Some Remaining

Table A1

Section number	Section title	Questions, issues, answers, remaining challenges
1.	General Introduction	We summarize the key ideas of Gestalt theory (Gestalts as wholes being different from the sum of the parts, emergence, self-organization, the law of Prägnanz) and define the challenge of specifying these notions in ways that are satisfactory in light of modern science.
2.	Holism	
2.1.	Holism in Traditional Gestalt Psychology	We briefly review holism as the “fundamental formula” of traditional Gestalt psychology.
2.2.	Modern Approaches to Holism	We clarify core Gestalt notions such as holistic properties, emergent features, configural superiority, and global precedence by providing operational definitions that fit into a more contemporary information-processing framework.
2.2.1.	Garner’s dimensional integrality	We discuss Garner interference and separable versus integral dimensions.
2.2.2.	Emergent features and configural superiority	We discuss emergent features, configural superiority effect, and the theory of basic Gestalts.
2.2.3.	Global precedence	We discuss Navon’s global precedence hypothesis, hierarchical patterns, and the global–local paradigm.
2.2.4.	The primacy of holistic properties	We discuss holistic properties, configural properties, emergent properties, and global properties.
2.3.	Interim Evaluation: New Foundations Needed	—The conceptual clarifications and operational definitions of key Gestalt notions have been useful in making further empirical and theoretical progress (e.g., dissociating attention, perception, decision components), but —We still need stronger theoretical frameworks to provide solid foundations to the Gestalt approach’s major principles.
3.	A Dynamical Systems Approach	
3.1.	Introduction	We discuss how recent developments in nonlinear dynamical systems theory can solve the tension between inert (equilibrium field forces) and active aspects of perception (spontaneous perceptual organization), between stability (attractors) and change (switching).
3.2.	Noise-Driven Models	We discuss the double-well model (two equivalent attractors), internal noise, dwell times, the gamma distribution, sequential dependencies, systems far from equilibrium, cycles of approach and avoidance, and the “visual sniff.”
3.3.	Dynamical Models	—We discuss two switching mechanisms: (1) High-frequency, microscopic noise in sensory channels (in occipital areas). (2) Macroscopic noise in adaptation rates (in parietal areas). —We discuss the dynamics of switching behavior as a phase transition (fast noise with slow dynamics) and neural adaptation.

(Appendix continues)

Table A1 (*continued*)

Section number	Section title	Questions, issues, answers, remaining challenges
3.4.	Dynamic Synchronization and Complex Adaptive Systems	<ul style="list-style-type: none"> —We review long-range dependencies between dwell times and discuss their implications for dynamic synchronization and complex adaptive systems. —We discuss switching governed by fragile attractors in complex adaptive systems consisting of coupled oscillators; self-organized criticality; alternating unstable and stable periods, corresponding to synchronization of high-frequency (gamma range) and low-frequency (beta range) oscillations (coherence intervals).
3.5.	Conclusion	<ul style="list-style-type: none"> —Different sources of change (stochastic and deterministic), different types of noise (microscopic and macroscopic), and different kinds of attractors and dynamics were considered. —Some of these were shown to correlate well with known behavioral effects (e.g., dwell times) and recently discovered specific neural signatures (e.g., coherence intervals and self-organized criticality of synchronization of neural oscillations). —In sum, a dynamical systems approach can explain how the brain's capacities for self-organization are ideally suited to balance robustness and flexibility.
4.	Principles of Measurement in a System of Sensors	
4.1.	Introduction	<ul style="list-style-type: none"> —The original Gestalt notion that perception is mediated by properties of a global neural field was rejected by empirical evidence and was replaced by an atomistic trend in neurophysiology with a focus on single cells. —The original attempt to provide a foundation to the many Gestalt principles in terms of a single general principle (such as the simplicity principle or the law of <i>Prägnanz</i>) failed because of its vagueness. —The focus on simplicity as an autonomous principle intrinsic to the perceiving organism did not allow theorists to capture the important perceptual role of regularities in the natural stimulation. —These limitations are resolved in a new framework, which combines elemental and systemic outlooks on perception, taking into account both intrinsic and extrinsic utility of sensory measurement.
4.1.1.	Elementary versus system processes	The (atom-like) single cells are studied as integral parts of a (holistic) system.
4.1.2.	Intrinsic versus extrinsic processes	From an economic perspective, sensory measurements are ranked by their utility, which depends both on capacities of individual sensors (intrinsic to sensory systems) and on how useful the sensors are in the current environment (extrinsic to the system).
4.2.	Unity of apparent motion	The apparently contradictory findings on apparent motion are unified in a framework derived from basic properties of sensory measurement.
4.3.	Principles of Measurement	We discuss the uncertainty principle of measurement (i.e., tradeoff of uncertainty between measuring signal location and signal frequency content) and Gabor's notion of optimal measurement.
4.4.	Systems of Sensors	We review the consequences of the uncertainty principle beyond individual <i>sensors</i> to the <i>systems</i> level, revealing a unity of results from the statistical and phenomenological traditions in perceptual science.
4.5.	Economics of Measurement by a System of Sensors	<ul style="list-style-type: none"> —We explain that the different regimes of apparent motion (tradeoff vs. coupling) occur because the expected quality of sensory measurements varies across the stimulus space. —We propose how the visual system may allocate its resources according to the expected utility of measurement, determined jointly by the <i>intrinsic</i> utility of sensors and properties of the <i>extrinsic</i> stimulation.
4.6.	Conclusion	The theory based on the distribution of the expected utility of sensory measurements across multiple sensors is a modern incarnation of the Gestalt claim that properties of system elements (the parts) are determined by properties of the system (the whole).
5.	A Bayesian Approach	
5.1.	Introduction	<p>The Bayesian approach is presented as a comprehensive mathematical framework in which existing principles are unified and placed on a more principled foundation; specifically:</p> <ol style="list-style-type: none"> (1) We apply the Bayesian approach to grouping principles such as proximity and good continuation. (2) We offer a Bayesian foundation for core concepts from Gestalt theory such as object formation and <i>Prägnanz</i>. (3) We discuss relationships to other frameworks (simplicity vs. likelihood, minimal model theory, and Bayesian network models).

(*table continues*)(*Appendix continues*)

Table A1 (*continued*)

Section number	Section title	Questions, issues, answers, remaining challenges
5.2.	A Bayesian Approach to Grouping Principles	We discuss proximity and good continuation.
5.3.	A Bayesian Foundation for Core Concepts From Gestalt Theory	We discuss object formation and Prägnanz.
5.4.	Relationships to Other Frameworks	
5.4.1.	Simplicity versus likelihood	In a Bayesian framework, the central unifying principle of Gestalt theory—Prägnanz—may be identified with the central unifying principle of Bayesian theory—maximization of the Bayesian posterior.
5.4.2.	Minimal model theory	The <i>avoidance-of-coincidence principle</i> holds that interpretations should be preferred in which as few image properties as possible are coincidences, such as accidents of viewpoint or configuration.
5.4.3.	Bayesian network models	
5.5.	Conclusion	The Bayesian approach has —Offered additional insight into classic Gestalt phenomena such as perceptual grouping and object formation, —Provided a foundation to core concepts from classic Gestalt theory such as Prägnanz, and —Established a bridge between likelihood and simplicity.
6.	Structural Information Theory	
6.1.	Introduction	—Information theory, connectionism, and dynamical systems theory (DST) use different formal tools to model different aspects but together they may explain how percepts are the result of cognitive processes implemented in the brain. —Starting from the representational coding approach of structural information theory (SIT), such a synthetic, multidisciplinary and typically Gestaltist perspective is sketched. —Specifically, we review how SIT deals with three fundamental questions concerning perceptual organization: (1) How veridical are simple stimulus organizations? (We again specify the relationship between simplicity and likelihood by means of Bayes' rule but in a different conceptual framework than before.) (2) What should be the nature of the visual regularities to be captured to arrive at simple organizations? (3) How are simple organizations computed? This leads to a representational picture of cognitive architecture, which includes connectionist modeling ideas and which honors ideas from neuroscience and DST about neuronal synchronization.
6.2.	The Veridicality of Simplicity	We discuss how the likelihood and simplicity principles deal with the veridicality of perception: A Gestaltist visual system that focuses on internal efficiency yields external veridicality as a side effect.
6.3.	The Nature of Visual Regularity	We argue that —Visual regularities must allow for an easy build-up of internal representations (holographic regularity) and for the specification of hierarchical organizations of the input (hierarchical transparency). —Three regularities satisfy these conditions: repetition, symmetry, and alternation. —A holographic model of regularity detection based on this formalization captures human regularity detection.
6.4.	Cognitive Architecture	—Complementing the two preceding sections addressing <i>what</i> needs to be processed in perceptual organization, we now address <i>how</i> . —Specifically, the way SIT solves the problem of computing the simplest SIT codes of symbol strings also suggests how the brain might arrive at the simplest interpretations of visual stimuli. —Transparallel recoding of hyperstrings of transparent holographic regularities has been implemented in a neutrally plausible algorithm that incorporates three subprocesses in the brain's visual hierarchy: feedforward feature encoding, horizontal feature binding, and recurrent feature selection.
6.5.	Conclusion	—SIT offers another perspective on the relationship between simplicity and likelihood, arguing that a Gestaltist visual system that focuses on internal efficiency yields external veridicality as a side effect. —SIT specifies the nature of the visual regularities that must be extracted to achieve this efficiency (i.e., transparent holographic regularities) as well as the nature of the cognitive architecture that explains how the simplest organizations are computed (i.e., transparallel processing by hyperstrings).

(*Appendix continues*)

Table A1 (*continued*)

Section number	Section title	Questions, issues, answers, remaining challenges
7.	General Discussion and Conclusion	<ul style="list-style-type: none"> —The Gestaltists failed to provide a thorough specification of the concepts of Gestalts as configurations of parts and wholes, and the mechanisms underlying the law of Prägnanz as based on a neural isomorphism did not work out. —However, their intuitions protect us from falling back on a naïve mechanistic view, in which perception begins with isolated sensations, thereby denying that phenomenal experience is populated by Gestalten as integrated, coherent structures or forms. —The conceptual and theoretical foundations of Gestalt psychology have been given fresh blood and a solid backbone in both descriptive and explanatory frameworks.
7.1.	Descriptive Frameworks	<ul style="list-style-type: none"> —The initially vague notion of a holistic Gestalt can be translated into a well-defined concept that allows precise operational definitions and experimentation, in two ways: <ol style="list-style-type: none"> (1) As configurations in a feature space. (2) As superstructures in hierarchical trees. —Both descriptions are well defined and capable of suggesting experiments, but neither of them captures the Gestalt concept in its entirety; hence, there are clearly remaining challenges: <ol style="list-style-type: none"> (1) It does not have the connotation of globality that is characteristic of true Gestalts; any arbitrary emergent property qualifies, in principle, as configural, separable, or integral. (2) It does not have the connotation of a whole being a force that binds, shapes, and resists external influences on the configuration of its parts; there is a difference between the whole having priority in processing and the Gestalt observation that the whole determines the appearance of its parts.
7.2.	Explanatory Frameworks	<ul style="list-style-type: none"> —Gestalt theory's intuition about Gestalts emerging spontaneously from self-organizational processes in the brain was specified by the theory of global electrostatic field forces: systems residing at equilibria of least energy expenditure, which is at the same time also the simplest possible organization, given the available stimulation (i.e., the law of Prägnanz). —With the dismissal of global field theory as a principle for brain organization, the Gestalt concept fragmented: Economy, self-organization, the simplest possible, and "given the available stimulation" each became the starting point for four divergent approaches, each specifying the Gestalt intuition further from a modern perspective: <ol style="list-style-type: none"> (1) Section 3 specified <i>self-organization</i> in a dynamical systems approach to perceptual organization, explaining how the system achieves optimality by the complexity of the neural dynamics that help configure the global architecture of the system, given simple mechanisms of neural growth and adaptation; in addition, this approach does justice to perception as part of an ongoing process instead of a delineated process going from static inputs to static outputs, as in naïve mechanistic approaches. (2) Section 4 specified the <i>principle of economy</i> in terms of the optimization of available resources; we observed that a system of sensors that work independently at the neural level to minimize its uncertainty is collectively responding optimally to the available patterns of stimulation. (3) Section 5 specified the conditional "<i>given the available stimulation</i>" in terms of likelihood, which motivated a Bayesian approach to perception; this allowed a synthetic view on simplicity and likelihood, a coherent explanation of grouping principles such as proximity and good continuation, and a solid basis to typical Gestalt notions such as objecthood and Prägnanz. (4) Section 6 specified <i>simplicity</i> within the context of SIT, stating that patterns are preferred according to the greatest simplicity of their symbolic description, using operators that are based on principled properties of its description language, formalizing the principles of the language, and solving the problems relating to the computational complexity of their encoding framework. —At the same time, each of these explanatory frameworks is also confronted with remaining challenges: <ol style="list-style-type: none"> (1) It remains an open question whether the mechanism is really implemented at the neural level as proposed, and whether it generalizes beyond the realm of motion sensitivity, where it was developed. (2) How do we explain the functionality of the system at the level of its behavior? Which principle governs the selection of those Gestalts that are functional to the system "given the available stimulation" rather than arbitrary others? How does selection at an evolutionary level interact with the proposed mechanisms of neural growth and adaptation?

(*table continues*)(*Appendix continues*)

Table A1 (*continued*)

Section number	Section title	Questions, issues, answers, remaining challenges
7.3.	Conclusion	<p>(3) It remains to be seen how fruitful this Bayesian synthesis of likelihood and simplicity will be in the long run; moreover, all Bayesian theories face the problem of explaining how to select the priors.</p> <p>(4) It remains to be studied further how SIT's encoding algorithms can be mapped onto the way in which the visual system encodes visual information.</p> <p>—The various theoretical approaches that have been motivated by Gestalt problems have all made considerable progress at certain aspects of the conceptual problems, yet none of them has solved the conundrum of Gestalt in its entirety; hence, there are important remaining challenges:</p> <p>—Each individual approach motivates additional detailed research questions which can now be addressed fruitfully.</p> <p>—The further specification of the connections between the frameworks, as we have started to do here, will be essential for a synthesis into the conceptually coherent framework that Gestalt theory once was.</p> <p>—Only together will these frameworks make progress in answering <i>Why do things look as they do?</i> in sufficient detail, regarding all of its aspects: the laws of perceptual organization, faithful to perceptual experience, yet formulated in precise quantitative terms, fully explained in terms of their internal dynamics and ecological validity, spelled out at an algorithmic level and linked to its neural mechanisms, from single neurons to neuronal cell assemblies and whole systems.</p>

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