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Two psychologies of perception and the prospect of their synthesis

Sergei Gepshtein

Two traditions have had a great impact on the theoretical and experimental research of perception. One tradition is statistical, stretching from Fechner's enunciation of psychophysics in 1860 to the modern view of perception as statistical decision making. The other tradition is phenomenological, from Brentano's "empirical standpoint" of 1874 to the Gestalt movement and the modern work on perceptual organization. Each tradition has at its core a distinctive assumption about the indivisible constituents of perception: the just-noticeable differences of sensation in the tradition of Fechner vs. the phenomenological Gestalts in the tradition of Brentano. But some key results from the two traditions can be explained and connected using an approach that is neither statistical nor phenomenological. This approach rests on a basic property of any information exchange: a principle of measurement formulated in 1946 by Gabor as a part of his quantal theory of information. Here the indivisible components are units (quanta) of information that remain invariant under changes of precision of measurement. This approach helped to understand how sensory measurements are implemented by single neural cells. But recent analyses suggest that this approach has the power to explain larger-scale characteristics of sensory systems.

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1. Introduction

> It is often argued academically that no science can be more secure than its foundations, and that, if there is controversy about the foundations, there must be even greater controversy about the higher parts of the science. As a matter of fact, the foundations are the most controversial parts of many, if not all, sciences. Physics and pure mathematics are excellent examples of this phenomenon. (Savage, 1954, p. 1)

Sergei Gepshtein is a Staff Scientist at the Vision Center Laboratory of the Salk Institute for Biological Studies in California, and a Research Scientist at the Theoretical Neuroscience Group of RIKEN Brain Science Institute in Japan.
Correspondence to: Sergei Gepshtein, 10010 N. Torrey Pines Road, La Jolla, CA 92037, USA. Email: sergei@salk.edu

For a long time the foundations of perceptual science were insecure. The trouble began in the early days of modern science, when the study of matter was declared the domain of science and the study of mind the domain of philosophy and religion (Descartes, 1641/1984). This dualism splintered what was to become the science of perception, because perception has two aspects: physical and mental. The physical aspect (publicly observable, third-person) was deemed susceptible to methods of natural science. The mental aspect (private, first-person) was deemed intractable by the scientific method.

The dualism of mind and matter had a lasting impact on perceptual science. Although the expulsion of mental phenomena had arguably helped the sciences to make their spectacular ascendancy, the picture of the world built within the "narrow and efficient scheme of scientific concepts" (Whitehead, 1925/1997, p. 75) was incomplete: it had no room for mental phenomena.

By and large, the physical and mental aspects of perception remained separate disciplines until the second half of the nineteenth century. Then, within a span of one generation, two projects were launched from the two sides of the Cartesian divide, each with the goal of including mental phenomena within a scientific account of perception. In 1860, the physicist Gustav T. Fechner of the University of Leipzig established an influential precedent of theory-driven experimental investigation of perception, in his epochal *Elemente der Psychophysik* (*Elements of Psychophysics*). And in 1874, the Aristotelian philosopher and ordained priest Franz C. Brentano of the University of Vienna advocated an observation-based approach to mental phenomena, in his iconoclastic *Psychologie vom empirischen Standpunkt* (*Psychology from an Empirical Standpoint*) (figure 1).

Fechner approached perception from its physical side, and Brentano approached it from its mental side. The two thinkers originated two traditions that have shaped the modern landscape of perceptual psychology.

Fechner's approach rested on a connection between two publicly observable phenomena: increments of physical stimuli and responses to the increments by human subjects. Since the connection involved a mental process—judgements of stimuli—and since he found a simple mathematical expression for this connection, Fechner believed he established a lawful foundation for a science that included mental phenomena.[1]

Brentano's approach was starkly different from Fechner's. Rather than presume that percepts were sums of minute sensations, Brentano embarked on direct description of salient percepts. He insisted that perception must be studied by direct observation rather than by pursuing a presumed notion, such as Fechner's sensory unit.

The pursuits of Fechner and Brentano had a prodigious effect. Fechner's *Elemente* was received as a breakthrough in research of perception, and indeed as a beginning of scientific psychology. Fechner's combination of statistical modeling and theory-driven experiment created a paradigm that has been followed by generations of psychophysicists, culminating in the signal detection theory and the modern view

Gustav Fechner
(1801-1878)

Franz Brentano
(1838-1917)

Dennis Gabor
(1900-1979)

Figure 1 *The founding fathers.* Fechner launched the tradition of statistical modeling in perceptual science, anticipating the modern view of perception as statistical decision making. Brentano originated the tradition of faithful description of perceptual experience, setting the stage for Gestalt movement and experimental phenomenology. The traditions of Fechner and Brentano emphasize, respectively, the continuous and discrete aspects of perception. Gabor formalized the connection between the continuous and discrete pictures.

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of perception as statistical decision making. And Brentano attracted into his circle many a brilliant mind whose influence was felt far and beyond studies of perception. Brentano and his circle created the momentum that brought about the phenomenological movement, from which sprang the Gestalt movement and the modern work on perceptual organization.

And yet, neither the psychophysical nor the phenomenological tradition has embraced the physical and mental aspects of perception fully. Two psychologies of perception emerged instead. One is the third-person psychology of the psychophysicist. It succeeds in providing publicly observable measures of mental phenomena, but it addresses these phenomena indirectly. The other is the first-person psychology of the experimental phenomenologist. It derives from direct reports of mental phenomena but it is largely removed from the model-driven predictive research that has become commonplace in psychophysics.

In this article I review some key results from psychophysical and phenomenological tradition with an eye on developments that hold promise of a comprehensive perceptual theory that embraces both the physical and mental phenomena. As it has

been the case in the traditions of Fechner and Brentano, much of the following revolves around the notion of *indivisible unit* of perception. To Fechner, finding the unit of sensation was the *raison d'être* of his psychophysics, which is why Fechner's psychophysics is sometimes described as a "quantal" theory of sensation (e.g., von Békésy, 1960). The units were the just noticeable increments of sensations. In Brentano's tradition, the notion of unit was more complicated than in Fechner's. The units were indivisible parts of perceptual *experience*. Brentano attempted a detailed description of the parts of perceptual experience and of their connections. These efforts were greatly enhanced by experimental phenomenology, of which Gestalt Psychology was a prominent and distinct branch.

I present a theoretical perspective that has been suggested by some converging results from the traditions of Fechner and Brentano, but whose foundations (including the notion of indivisible unit) are neither statistical nor phenomenological. The root of this perspective lies outside of psychology. It is a theory of information formulated in 1946 by the engineer and inventor Dennis Gabor. According to Gabor, the information gained in any measurement is limited by an invariant that can be thought of as a unit, or quantum, of information. This view has helped to elucidate how sensory measurements are performed locally: by single sensory neurons at the early stages of visual perception. I demonstrate, using visual perception of motion as an example, how the approach from Gabor has more pervasive consequences for visual perception than the local computations, including the elusive relationship of local and global perceptual processes and a connection between results from the psychophysical and phenomenological traditions.

I argue that the inclusion of physical and mental phenomena within a complete theory of perception requires a broader basis than the psychophysical and phenomenological traditions. The connections between the *empirical laws* of mental and physical phenomena is only a first step toward the complete theory, because empirical results are accidental. They reflect the stimulus choices and other idiosyncracies of research trends and fashions. A complete theory of perception requires that the connections between empirical laws are reforged in terms of general principles that are not confined to the statistical and phenomenological traditions. I use the approach from Gabor's information theory as an illustration of how such complete a theory may look like.

2. The Line of Fechner: Statistical Elements

2.1. Roots

Gustav T. Fechner (1801–1887) planted the seed of what has become the prevailing view of sensation. It is the view that sensations are statistical measurements. Fechner developed his theory and tested it plentifully within a decade preceding the publication of his monumental *Elemente der Psychophysik* (1860). Thanks to this

work, Fechner is remembered as someone who helped to establish psychology as a rigorous experimental science, against the backdrop of philosophical psychologies of his time.

Fechner's contribution was a sophisticated combination of experimental method and mathematical modeling, which I shall parse—for didactic reasons—into three ideas: (a) the notion that psychologically equivalent differences between stimuli are the units for measuring sensations, (b) a statistical model of sensation, and (c) a psychophysical law. Each of these ideas was significant in its own right. But it was their combination that amounted to something greater than their mere sum: the new science of psychophysics. I will briefly retrace these ideas before I turn to their modern incarnations.

2.1.1. Units

Fechner started his career as a physicist "engrossed in the study of atoms."[2] His first publication of 1825 was about the reality of atoms, and he spent much of his career defending the atomic view of matter. It is therefore not surprising that Fechner approached the psychophysical connection from the standpoint of a physicist, and that his approach turned on the premise that sensations should be meaningfully described as combinations of indivisible units:

> In principle our psychic measurement will amount to the same as physical measurement, the summation of so-and-so many multiples of an equal unit. (1860/1966, p. 47)
>
> Measure of sensation will consist of dividing every sensation into equal divisions (that is, equal increments), which serve to build it up from zero. The number of equal divisions we conceive as determined, like inches on a yardstick, by the number of corresponding variable stimulus increments that are capable of bringing about identical sensation increments. We measure a piece of cloth by dividing it into equal parts as determined by the number of yards that serve to cover it. Here the only difference is that instead of covering the sensation magnitude we establish a series of sensation increments. (1860/1966, p. 50)

Fechner found his unit by observing that for every perceptible stimulus there existed a magnitude of stimulus increment that was just noticeable. He assumed that, by virtue of their being equally noticeable, the just-noticeable increments of different stimuli had the *same psychological magnitude*. The just-noticeable increments also made a natural unit of measurement because they could not be divided to smaller sensible parts. In this sense, the sensations of just-noticeable increments of stimulus played the role in theory of sensations the "atom" played in physics.

In making the assumption, that the just noticeable increments of stimulus at different stimulus magnitudes were psychologically equivalent, Fechner anticipated the important notion of psychological equivalence classes, which we will encounter several times: as sets of equal contrast sensitivity, as equivalent conditions of apparent motion, and as equivalence classes of measurement uncertainty.

But what was the nature of the unit? Why could not the increments smaller than the just noticeable be sensed? Fechner did not have a direct answer. But he found a way around this difficulty by connecting the observation of just noticeable stimulus increment with the observation that sensory processes were limited by a random process.

2.1.2. Statistical computations

Fechner observed that "irregular chance fluctuations play a major role" in all the methods of measurement he used:

> The greater the role of chance, the smaller … will be the value that yields the measure of sensitivity, and there is no way of achieving a measure free of these chance effects. (1860/1966, p. 65)

Fechner modeled the fluctuations using the Gaussian Law of Error, which had been known well by his time. The Law had been used in the analysis of errors in astronomical observations as early as 1820s; the errors attributed to imperfections of visual judgement by the observers (Boring, 1929; Stigler; 1986). Fechner made a step beyond the previous efforts: he developed a mathematical argument which today would be called a probabilistic model of sensation.

Figure 2 illustrates Fechner's model using a modern graphical convention.[3] Consider an experiment that consists of multiple presentations of two stimuli *a* and *b*, which do not change across the presentations. The task is to tell, on every presentation, whether *a* or *b* has a larger magnitude. Fechner's model assumes that on different presentations the same stimulus gives rise to different sensations which are distributed according to the Gaussian Law of Error. The two curves in figure 2 represent the two Gaussian distributions *A* and *B*, from the multiple presentations of, respectively, *a* and *b*. The magnitude of *a* is smaller than the magnitude of *b*, reflected in the figure by the maximum of *A* set at a smaller magnitude of sensation than the maximum of *B*. (The figure represents sensed rather than physical magnitudes. Only the sensations, and not the stimuli, are shown.)

As figure 2 makes it clear, the sensations sometimes indicate that *b* is greater than *a* and sometimes that *a* is greater than *b*. Fechner computed the probabilities of these events. Halfway between the most likely sensations Fechner placed a *threshold*, represented in figure 2 by a dashed vertical line. For incorrect responses:

- When stimulus *a* is presented, the probability that the sensation of *a* is larger than the threshold is equal to the area under curve *A* to the right of the threshold (area 2).
- When stimulus *b* is presented, the probability that the sensation of *b* is smaller than the threshold is equal to the area under curve *B*, to the left of threshold (area 3).
- The sum of the two probabilities (i.e., the sum of areas 2 and 3) is the probability of response that *a* is greater than *b*.

The probability of correct response is obtained, similarly, by summing areas 1 and 4.
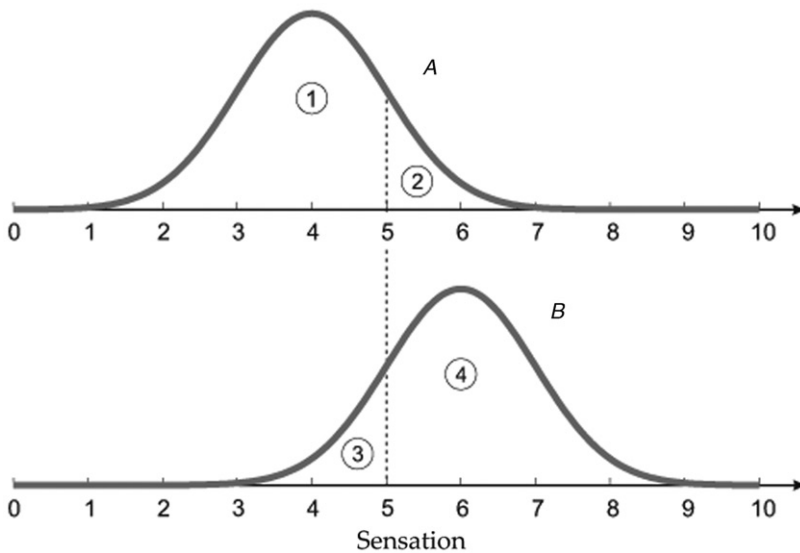
Figure 2 *Fechner's view of sensory measurement*. The two panels represent the frequencies of sensations evoked by two stimuli: *a* (top) and *b* (bottom) on the dimension of *sensation strength*, in arbitrary units. Stimulus *a* has a smaller magnitude than stimulus *b*, and the two magnitudes do not change. But the sensed magnitudes vary across trials. The two curves, *A* and *B*, represent the distributions of sensations of *a* and *b* across the trials. The distributions are assumed to follow the Gaussian Law of Error. The maximal values of *A* and *B* correspond to the "true values" of *a* and *b*. The dotted line is the "threshold," midway between the true values. The circled numbers mark the areas separated by the threshold under curves *A* and *B*.

When the stimulus difference is large, the areas of regions 2 and 3 are small, and the errors are unlikely. As the stimulus difference is decreased, the two areas increase so the errors occur more often, to the point where the stimulus difference is unnoticeable. Accordingly, Fechner defined the threshold as "a point at which . . . a stimulus difference becomes noticeable or disappears" (1860/1966, p. 199).

Fechner's threshold is a boundary of the sensible. But his goal was to measure sensations of any magnitude, not only at the boundary. He therefore asked how the amount of stimulation at the threshold related to the amount of stimulation for salient (suprathreshold) sensations. His answer was the psychophysical law that bears his name today.

2.1.3. Laws
Not only did Fechner equate the sensations evoked by different just noticeable stimuli, but he also equated the increments that were *equally distant* from the just noticeable; the distances measured by counting just noticeable internments. Fechner elevated this proposal to the status of a law. The law consisted of two parts: empirical (Weber's Law) and theoretical (Fechner's Law).

Weber's Law: Ernst H. Weber (1795–1878)—physician, anatomist, and physiologist—was a colleague of Fechner at Leipzig University and a prolific experimentalist. His most important works were on the sense of touch and muscular sensations. In both areas Weber was a founding figure. He extracted the sense of touch (*Tastsinn*) from the vague notion of "common sensitivity" (*Gemeingefühl*), summarized first in *De tactu* (Latin for *Concerning Touch*) of 1834 and then in his influential *Der Tastsinn und das Gemeingefühl* (German for *The Sense of Touch and the Common Sensibility*) of 1846. Weber advanced the hypothesis of "sensation circles"—the areas on the skin in which two-point stimulation could not be distinguished from one-point stimulation—anticipating Sherrington's "receptive fields" by more than half a century (Sherrington, 1906).

In his work on muscular sensitivity Weber discovered a remarkable invariant of human sensitivity, which became a cornerstone of the new science of psychophysics. In his studies on weight discrimination, Weber found that the increment of weight that was least noticeable did not depend on the magnitude of weight, when the increment was expressed as the ratio of the increment to the magnitude of weight.

But Weber did not attempt to present his finding as a general law. It was Fechner who generalized Weber's finding, as follows. First, Fechner wrote the result of Weber as a differential equation:

$$d\gamma = K \frac{d\beta}{\beta} \tag{1}$$

where $d\gamma$ is an increment of sensation γ evoked by increment $d\beta$ of stimulus magnitude β, and K is a positive constant.[4] Fechner called equation (1) the fundamental formula (*Fundamentalformel*). It established a simple relationship between increments of sensation and increments of stimulus: the larger the magnitude of stimulus, the larger the stimulus increment that gives rise to the smallest sensation. By integration, Fechner derived from equation (1) an expression for how the magnitudes (rather than the increments) of sensations related to the magnitudes of stimuli:

$$\gamma = K \ln \beta + C, \tag{2}$$

where C is the constant of integration. Equation (2) is merely Fechner's restatement of equation (1). It is the next step in Fechner's argument that was crucial for his generalization of the Weber's Law.

Fechner's Law: Recall that Fechner made the assumption that just noticeable increments of stimulus always corresponded to the same increment of sensation. As a special case of that assumption, Fechner argued that a just-noticeable increment itself should produce no sensation:

$$\gamma_\beta = 0, \tag{3}$$

where γ_β is the least sensation of stimulus $\beta = b$. On this assumption, equation (2) for just noticeable increment of stimulus becomes:

$$C = -K \ln b. \tag{4}$$

Now, by combining equations (2) and (4) we obtain $\gamma = K \ln \beta - K \ln b$ and thus:

$$\gamma = K \ln \frac{\beta}{b}. \tag{5}$$

This is what Fechner called his measurement formula (*Massformel*) and what others called Fechner's Law or Weber-Fechner Law. Equation (5) says that the magnitude of sensation is a simple function of the magnitude of stimulus, the latter expressed in units of b, the just noticeable increment of stimulus. It is a measurement formula because it expresses the measured quantity (γ) in units of measurement (b).

2.2. Modern View

Fechner's *Elemente* is modern psychophysics in embryo. Fechner's approach—by investigating limits of perception, using statistical methods to model the results—became the paradigm of psychophysics. None of the ideas central to Fechner remained dormant, even though some of them had to be rediscovered (Link, 1992).

Fechner's framework had a number of shortcomings. Besides the mathematical indecorum in the derivation of his Law, Fechner's notion of unit of sensation was rooted in observations of sensory fluctuations that had no explanation in his time,[5] and his conception of the threshold was arbitrary.[6] Moreover, Fechner's fundamental conjecture that the magnitude of sensation was a sum of just noticeable sensations had not been confirmed (reviewed in Krueger, 1989).

Key developments in psychophysics sprung from these shortcomings. Mathematical theories of perceptual judgement and scaling were advanced (Falmagne, 1971, 1985; Luce & Galanter, 1963). Sources of randomness in sensory processes became the focus of intensive research (Blakemore, 1990; Geisler, 1989; Hecht, Shlaer, & Pirenne, 1942). The conception of threshold was broadened, a mature expression of which is the exceedingly general Signal Detection Theory (Green & Swets, 1966; Swets, Tanner, & Birdsall, 1961). And new theories about the elementary structure of sensation were advanced, two of which will feature in this section.

But these developments should not obscure the fact that the basic premise of Fechner's psychophysics stayed and became a cornerstone of modern psychophysics: perception can be studied productively by investigating its boundary conditions, using statistical modeling.

I will now present two examples of Fechner's paradigm coming of age. Just as the unit of measurement was pivotal to Fechner's psychophysics, it is pivotal to modern psychophysics. But the meaning of "indivisible unit of sensation" has evolved into other conceptions of the elementary structure of sensations. In my first example, the components are the so-called "cues" from different sensory modalities and submodalities. In my second example, the components are the elementary constituents of spatiotemporal visual stimuli.

2.2.1. Units of uncertainty

Fechner derived his model of sensation from the observation of "irregular chance fluctuations" of sensory judgements. This observation served Fechner's overarching goal of finding a measure of sensation. A different style of thinking came to play as the statistical theory advanced and took stronger hold on perceptual psychology. First, the object of measurement had changed. Second, the unit of measurement had acquired a new meaning.

In Fechner, sensation is the object of measurement by the psychologist who uses the just-noticeable increment of sensation as the unit of measurement. On the modern view, it is the "parameters" of the world that are measured by the sensory system, rather than the sensation is measured by the psychologist.

In Fechner, the just-noticeable increments of sensation are *elementary sensations* that add up to the magnitude of a sensation. On the modern view, the just-noticeable increments are *elementary uncertainties* of sensations. They add up to the uncertainty of a composite sensation. Fechner's notion of a statistical limit of sensation acquired a new meaning, an advance that seems only natural in the hindsight.

This view is part and parcel of the modern theory of sensory "cue integration." A sensory "cue" is, loosely, a source of sensory information. The information is partial because no source of information is infallible: only incomplete information is obtained from sensory measurements. The integration of many measurements helps to reduce the uncertainty.

For instance, the perception of "visual space"—a popular theme in modern vision science—is the perception of object shapes and the distances of objects from one another and the viewer. The perception depends on such cues as binocular disparity, eye vergence, gradient of texture, and motion parallax from vision and also on the cues from other senses (e.g., active touch or haptics). Measurement of each cue is associated with uncertainty, some of which has to do with the ambiguity of projection from the three-dimensional world to the two-dimensional retinal surfaces, and some with the imperfections of biological measurements (e.g., neuronal noise). Some cues are more useful (more "reliable") than others, but their usefulness changes as behavioral tasks or the environment change. In effect, cue integration insures that perception takes advantage of the most useful information at hand (Ernst & Banks, 2002; Gepshtein & Banks, 2003).

Studies of cue integration are concerned with how sensory systems reduce the uncertainty by combining the imperfect estimates of multiple cues in service of active behavior in the three-dimensional environment. This literature has borrowed broadly from mathematical statistics, in particular from statistical decision theory and the theory of estimation. A prevailing theory of cue integration uses the formalism of *maximal likelihood estimation*, to make specific predictions of how results of individual sensory "estimates" should be integrated to reduce the uncertainty (maximize the precision) of the combined "estimate" (Clark & Yuille, 1990; Cochran, 1937; Ernst & Bülthoff, 2004; Landy, Maloney, Johnsten, & Young, 1995), as follows.

As mentioned, different cues carry information of different quality. This fact is represented by cue *reliability*:

$$r_i = \sigma^{-2}, \tag{6}$$

where σ is the standard deviation of errors associated with estimates by cue i. The standard deviation is an equivalent of Fechner's just noticeable difference of sensations.[7] The estimates combined from multiple cues are most reliable when the cues contribute according to their reliabilities. The more reliable a cue the larger its *weight* in the combined estimate. For example, in combination of two cues S_1 and S_2, combined estimate S_c is a weighted sum of the individual estimates:[8]

$$S_c = wS_1 + (1 - w)S_2, \tag{7}$$

where w is weight:

$$w = \frac{r_1}{r_1 + r_2}.$$

The reliability of the combined estimate is simply:

$$r_c = r_1 + r_2. \tag{8}$$

Let us compare Fechner's framework with that of cue integration. Recall that Fechner's measure of sensory uncertainty—the just noticeable stimulus increment—served two functions: the limit of a sensation and also its component. In the framework of cue combination, the two functions are separated. Just noticeable increments are still used to gauge uncertainty of sensory measurements (equation 6), but the role of components in now played by individual estimates S_i (equation 7). Just noticeable increments play a *modulatory* function: they determine how the components are weighted within a sensation.[9]

The theory of cue integration uses measurements of elementary sensations at the threshold to predict magnitudes of supra-threshold sensations (equation 7). The step from threshold to suprathreshold measurements is a fulfillment of Fechner's goal to explain any sensation by measuring limits of sensation.

The theory of cue integration is sometimes called ''weak fusion'' because the cues are assumed to be measured independently of one another. The cues are connected ''weakly'' before they are combined (''fused''). The weak fusion is contrasted with ''strong fusion'' where the measurements are not independent (Clark & Yuille, 1990). I return to this issue in section 4, where I review the notion that even elementary sensory measurements generally combine more than one aspect of sensory information (figure 8).

2.2.2. Spatiotemporal sensitivity

A new theoretical perspective on the nature of visual sensitivity was advanced around the middle of the twentieth century. The advance came to resolve difficulties in the literature on perception of intermittent visual stimulation called *flicker*. Sperling (1964) described a turning point in this development:

> The difficulty in the psychophysics of flicker arises . . . from the staggeringly large number of different possible stimuli. Some of the possible dimensions along which stimuli may vary are spatial dimensions (such as the size or shape of a flickering stimulus, retinal location, the presence of other stimuli), intensity, wavelength composition, prior adaptation of the eye, the shape of the wave form, and the frequency of repetition for periodic stimuli. . . . Some of these dimensions are more troublesome than others—for example waveform—because it is not clear how to extrapolate from one waveform to another; i.e., results obtained with square waves, to those with triangular waves, pulses, sine waves, etc. The spatial variables are similarly difficult because of the difficulty in extrapolating systematically from one spatial pattern of stimulation to another. (p. 4)

Differences in the results of flicker studies were resolved using the formalism of *linear system analysis*, which by the time of this development had become common knowledge in electrical and communication engineering.

A linear system is remarkable in that its behavior can be described fully by its input-output characteristics, using a well-defined, relatively small stimulus set. The response (''output'') of a linear system to any ''input'' is predicted in several steps. The first stage is analytic: the input is separated to elementary components. Then, system response to every elementary component are measured in isolation from the other components. The final stage is synthetic: system responses to the elementary components are combined. In linear systems, the effects of the elementary stimulus components are independent of one another. The whole (system's response to a complex input) is equal to the sum of its parts (the responses to input components).

The components used to derive the input-output characteristics are elementary harmonic functions of different frequencies (figure 3A). Since any stimulus can be approximated by a sum of such components, measuring system responses to the elementary functions allows the researcher to make prediction about system response to any stimulus, as long as the system is linear.

Inspired by Cobb (1934a, 1934b) and Ives (1922), Dutch engineer H. DeLange was first to successfully apply the linear-system approach to flicker sensitivity (De Lange, 1952). Using rotating disks of variable luminance, he measured human sensitivity to temporal modulation of luminance, and showed that the sensitivity to complex waveforms could be predicted from the sensitivity to sinusoidal waveforms.

A similar progress was made in spatial vision. Otto Schade, a Germany-born American television engineer, used cathode ray tubes to measure human sensitivity to waveforms of different spatial, temporal, and spatiotemporal frequencies (Schade, 1956). In particular, he showed that linear-system models described
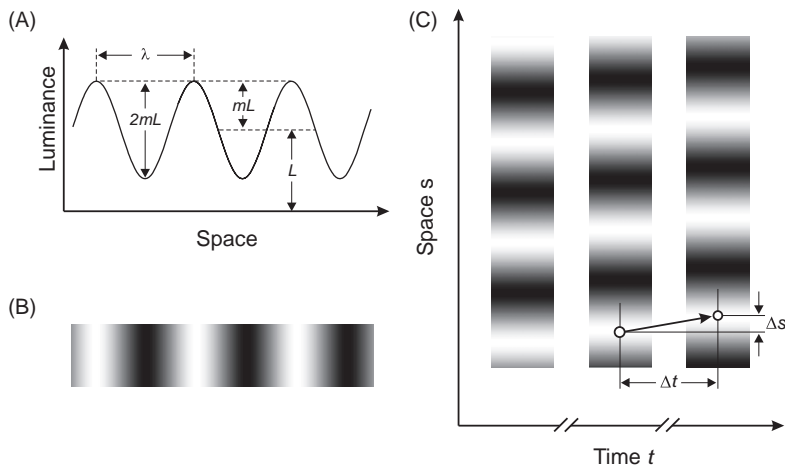
Figure 3 *Luminance gratings.* (A) A sinusoidal waveform: *L* is the average value; λ and *m* are the period and amplitude of modulation. (B) A spatial luminance grating. (C) A spatiotemporal (drifting) grating: rapid sequence of spatial gratings each slightly shifted in the direction of motion. At particular combinations of spatial and temporal parameters (intervals Δ*s* and Δ*t*) the stimulus is perceived as continuous motion with speed $v = \Delta s/\Delta t$.

human sensitivity well when the modulation of luminance was small, close to the threshold of visibility.

Within the next two decades the linear-system approach entered the main-stream of vision science, thanks to influential studies of Campbell and Robson (1968; see also Robson, 1966), Kelly (1969, 1972, 1979), and others (reviewed by Kelly, 1994b).

Because of the potential to predict perception of any stimulus, measures of sensitivity to sinusoidal gratings acquired the flavor of fundamental characteristics of the visual system. A definitive result in this line of research is described next.

Contrast sensitivity: Visual contrast sensitivity to *spatial* stimuli is measured using luminance gratings (figure 3). In such a grating, luminance *l* varies across space or time, *x*, around average luminance *L*:

$$l_x = L[1 + m \sin 2\pi fx], \tag{9}$$

where *f* is the frequency of luminance modulation and *m* is the amplitude of modulation. Figure 3A–B illustrates a spatial luminance grating.

To measure *spatiotemporal* sensitivity, the stimulus must vary in both space and time. This is accomplished using *drifting gratings* (figure 3C). A drifting grating can be thought of as a movie: a sequence of frames, each similar to the spatial grating in figure 3B. But the gratings in subsequent frames are displaced with respect to one another for distance $s = vt$, where *v* is the speed of motion and *t* is the time elapsed
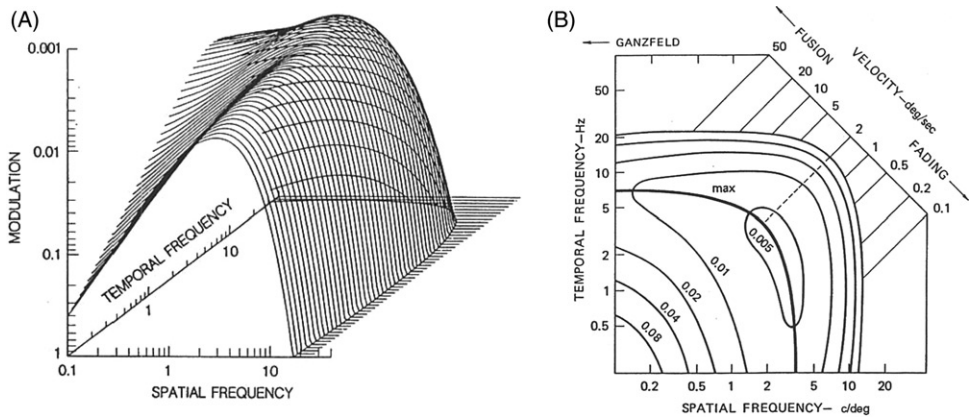
Figure 4 *Spatiotemporal sensitivity*. (A) Spatiotemporal contrast sensitivity surface. (B) Isosensitivity contours. The closed contours are the level lines of the surface in A. They connect stimulus conditions at which the same amount of modulation (*m* in equation 10) is sufficient to render the stimulus just detectable. The lines on the top right are the constant-speed lines; they are parallel to one another in the logarithmic coordinates. The thick curve labeled "max" connects the points of maximal sensitivity across speeds. (Both plots are from Kelly, 1979.)
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from the beginning of the movie. Now the function of luminance across space and time is:

$$l(s, t) = L[1 + m \sin 2\pi f_s(s - vt)], \tag{10}$$

where f_s is the spatial frequency of luminance modulation. The higher the speed, the larger the displacement from frame to frame. Note that besides the two-parameter description (f_s, v), drifting gratings can be described using two parameters (f_s, f_t) where $f_t = vf_s$ is the temporal frequency of luminance modulation.

A definitive characteristic of human visual spatiotemporal sensitivity was obtained by Donald H. Kelly (Kelly, 1979, 1994a). The work of Kelly is a landmark achievement within Fechner's tradition, for two reasons. First, Kelly took an extraordinary care to perform these measurements. Using a custom-made apparatus, perfected over the course of more than a decade, Kelly stabilized stimulus images on the retina and thus separated the effect of stimulus modulation from the effects caused by eye movements (Kelly, 1994a). Second, Kelly's measurements were comprehensive. He estimated detection thresholds over the entire range of visible spatial and temporal luminance modulations.

Figure 4 is a summary of Kelly's results. The plot in figure 4A is a *spatiotemporal sensitivity surface*. The hight of this surface above the frequency plane represents observer sensitivity to drifting gratings (f_s, f_t). Sensitivity is inversely related to the amount of luminance modulation in a *just-detectable* stimulus (*m* in equation 10). The smaller the modulation needed for detection, the higher the sensitivity.

Figure 4B is a different rendering of the same result, helping to reveal essential features of the sensitivity surface:

- *Isosensitivity sets*. The contour lines are the level curves of the surface in panel A. Within a contour the sensitivity is the same to all stimulus conditions. For example, any pair of points from the same contour represents two gratings that are just detectable at the same modulation m.

- *Maximal sensitivity set*. The thick curve labeled ''max'' contains maximal sensitivity stimulus conditions from all speeds. The speeds are marked on the top right axis of figure 4B. The parallel oblique lines projected on the speed axis are the constant-speed lines. On every such line there is a point of highest sensitivity; these points together form the maximal-sensitivity curve (''max'').[10]

The plots of the isosensitivity sets and the maximal-sensitivity set reveal a characteristic ''bent'' shape of the spatiotemporal sensitivity function (to which we return in section 4.2).

The spatiotemporal sensitivity function in figure 4 is a summary of a large corpus of experimental measurements. In this sense, the spatiotemporal sensitivity function has the flavor of an *empirical law*. But it is not recognized a law because it is not simple. An argument is reviewed in section 4 that some properties of the sensitivity function are invariant and this invariance has a simple structure derived from first principles, supporting the view that the sensitivity function is lawful.

2.3. Summary

Fechner was first to create a predictive statistical theory of perception. His approach was upheld and developed by generations of psychophysicists, and then merged with a broader movement toward the statistical view of neural function and cognition (Geisler, 2008; Gigerenzer & Murray, 1987; Maloney, 2002). The work of Fechner and his followers emphasized the publicly observable (''physical'') aspect of the psychophysical connection. But their account of the ''mental'' aspect has been indirect. In particular, the stochastic sensory processes observed by the psychophysicist across experimental trials are not a part of perceptual experience within trials or outside of the laboratory. To detractors, the reduction of perception to statistical processes is suspect. The discrepancy between the assumption of stochasticity of sensations, on the one hand, and the non-stochastic perceptual experience, on the other, is a source of tension between the bottom-up psychophysical view of perception and the top-down phenomenological view, to which I turn next.

3. The Line of Brentano: Phenomenal Elements

3.1. Roots

3.1.1. Brentano's empirical standpoint
Franz C. Brentano (1838–1917) is a pivotal figure in the history of the philosophy of mind and in the movement that separated psychology from philosophy.

An inspiring teacher, rigorous philosopher, non-orthodox interpreter of the classics,[11] Brentano created a dedicated following through his lectures at the Universities of Würzburg (1865–1866) and Vienna (1874–1895), wide-ranging writings, and correspondence. Brentano's disciples formed no cohesive scientific or philosophical school but rather a circle of ideologically kindred individuals: ''a network equal in strength and intensity within German-speaking philosophy to that of the varied schools of Neo-Kantianism'' (Ash, 1998, p. 29). Some Brentanoans (e.g., Husserl and Meinong) went on to create their own philosophical or scientific schools, or facilitated growth of such schools, each developing a different aspect of Brentano's oeuvre.

The empirical standpoint: In his inaugural lecture at Würzburg, the twenty-eight-year-old Brentano announced that ''the true method of philosophy is none other than that of the natural sciences'' (cited in Smith, 1994, p. 28). Captivated by the certainty of natural sciences, Brentano sought to achieve such certainty in his exploration of mental phenomena. The first and most influential expression of this aspiration was his *Psychologie vom empirischen Standpunkt* (*Psychology from an empirical standpoint*) of 1874.

In the *Psychologie* Brentano made a sharp distinction between two kinds of phenomena—mental and physical—and separated the methods required to achieve their certain knowledge (Brentano, 1874/1973):

> What is meant by ''science of mental phenomena'' or ''science of physical phenomena''? The words ''phenomenon'' or ''appearance'' are often used in opposition to ''things which really and truly exist.'' We say, for example, that the objects of our senses, as revealed in sensation, are merely phenomena; colour and sound, warmth and taste do not really and truly exist outside of our sensations, even though they may point to objects which do so exist. John Locke once conducted an experiment in which, after having warmed one of his hands and cooled the other, he immersed both of them simultaneously in the same basin of water. He experienced warmth in one hand and cold in the other, and thus proved that neither warmth nor cold really existed in the water. Likewise, we know that pressure on the eye can arouse the same visual phenomena as would be caused by rays emanating from a so-called colored object. And with regard to determinations of spatial location, those who take appearances for true reality can easily be convinced of their error in a similar way. From the same distance away, things which are in different locations can appear to be in the same location, and from different distances away, things which are in the same location can appear to be in different locations. A related point is that movement may appear as rest and rest as movement. These facts prove beyond doubt that the objects of sensory experience are deceptive. (p. 9)[12]

> We have no right, therefore, to believe that the objects of so-called external perception really exist as they appear to us. Indeed, they demonstrably do not exist outside of us. In contrast to that which really and truly exists, they are mere phenomena. (p. 10)

Brentano further contrasts the deceptive "external perception" with the certainty of "internal perception":

> What has been said about the objects of external perception does not, however, apply in the same way to objects of inner perception. In their case, no one has ever shown that someone who considers these phenomena to be true would thereby become involved in contradictions. On the contrary, of their existence we have that clear knowledge and complete certainty which is provided by immediate insight. (p. 10)

Knowledge of the "things" cannot be certain because of the deceptive nature of external perception. But knowledge of mental phenomena can be certain because it is direct: what we experience in inner perception is the mental phenomena themselves. The goal of Brentano's *Psychology* follows:

> Just as the natural sciences study the properties and laws of physical bodies, psychology is the science which studies the properties and laws of the soul,[13] which we discover within ourselves directly by means of inner perception, and which we infer, by analogy, to exist in others. (1874/1973, p. 5)

Discovering these "laws of the soul" was the focus of what Brentano called *descriptive psychology*, or "psychognosy." The descriptive psychology was contrasted with the *explanatory psychology*, which Brentano also called "genetic psychology." Descriptive psychology—Brentano's main concern—was conceived as a science of the actual laws of mental phenomena rather than of their hypothetical properties. Brentano's descriptive psychology is the fountainhead of the entire phenomenological movement: both its philosophical and experimental incarnations.

Act and content: Fundamental to Brentano's psychology and central to his approach to perception is the concept of *Vorstellung*, which is translated usually as "presentation" and sometimes as "idea" (Simons, 2004, p. 47). *Vorstellung* is one of a "class of mental activities" which Brentano called mental acts:[14]

> We speak of presentation whenever something appears to us. When we see something, a color is presented; when we hear something, a sound; when we imagine something, a fantasy image. (p. 198)

In other words, *Vorstellung* is an act of presenting objects to consciousness, objects being the *content* of the act. We perceive the objects rather than we perceive the presentations of objects, which is why the perceived object is a "physical phenomenon" and the presentation is a "mental phenomenon."

Brentano's "presentation" is part and parcel of his famous conception of intentionality, about the necessary directedness of mental phenomena to their objects.[15] Intentionality is the connection of mental act to its content. In particular, intentionality of perception is the connection between the mental phenomenon of presentation and the physical phenomenon of object. In this sense, intentionality

plays a role in Brentano's psychology similar to the role played by measurement in Fechner's psychophysics.

Elements of consciousness: Brentano's psychology was a creative development of Aristotle's theory of part-whole relations. Brentano wanted his descriptive psychology to "define the elements of human consciousness and the ways by which they are connected" (Brentano, 1995, p. 13). He criticized some earlier views about connections of the "elements"[16] and attempted to develop his own theory of part-whole relationship, presented most fully in his *Descriptive psychology* (1995).

Brentano observed that in spite of its unity "consciousness does not present itself to our inner perception as something *simple*, but it shows itself as something composed of many parts" (1995, p. 15). He observed further that the relations of parts may be of different kinds. For example, parts can be divided to "separable" parts, down to the parts that cannot be further separated. There also exist "distinctional" parts that cannot be separated, but which can be distinguished still, such as halves, sides, etc. Besides the spatial parts, Brentano explored relations between non-spatial properties, such as lightness and color, and how these properties together contributed to identity of perceived objects (reviewed in Smith, 1988).

The influence of Brentano's ideas on scientific psychology was profound, wide-ranging, and indirect: it was mediated by Brentano's disciples, some of whom are featured in sections 3.1.2–3.1.3.

Critique of psychophysics: Brentano's view of Fechner's psychophysics is characteristic of the later relationship between the traditions of Brentano and Fechner. As mentioned, Brentano saw a "clearly defined boundary [between] psychology and natural sciences" (p. 6). He therefore could not approve of the attempt of approaching mental phenomena as if they were physical phenomena in Fechner's psychophysics, which Brentano viewed as an "encroachment of physiology upon psychology and vice versa" (p. 7). Brentano saw the future of psychology lie elsewhere.

Besides Fechner's approach at large, Brentano criticized Fechner's specific idea about the equal elements of sensation. In the psychophysical law of Fechner, Brentano distinguished two aspects: physiological and psychological. The physiological aspect was "to determine which relative differences in the intensity of physical stimuli correspond to the smallest noticeable differences in the intensity of mental phenomena" (pp. 7–8). And the psychological aspect "[consisted] in trying to discover the relations which these smallest noticeable differences bear to one another" (p. 8). Brentano's concern was about the psychological aspect:

> But is not the answer to the latter question immediately and completely evident? Is it not clear that all the smallest noticeable differences must be considered equal to one another? This is the view which has been generally accepted. Wundt himself, in his *Physiological Psychology* ... offers the following argument: "A difference in intensity which is just barely noticeable is ... a psychic value of constant magnitude. In fact, if one just noticeable difference were greater or smaller than another, *then it would be greater or smaller than the just noticeable*, which is a contradiction." Wundt does not realize that this is a circular argument. If someone

doubts that all differences which are just noticeable are equal, then as far as he is concerned, being "just noticeable" is no longer a characteristic property of a constant magnitude. The only thing that is correct and evident *a priori* is that all just noticeable differences are equally noticeable, but not that they are equal. ... On the other hand, the first task mentioned above undoubtedly belongs to the physiologist. Physical observations have more extensive application here. And it is certainly no coincidence that we have to thank a physiologist of the first rank such as E. H. Weber for paving the way for this law, and a philosophically trained physicist such as Fechner for establishing it in a more extended sphere. (1874/1973, p. 8)

That is, either the questions posed by Fechner lied outside of psychology or their extensions into psychology were self-evident and thus did not deserve attention.

Brentano also proposed that Weber's results could have an interpretation different from Fechner's. Brentano's interpretation amounts to what later became the psychophysical "power law."[17]

3.1.2. Brentano's circle

Brentano's ideas were propagated and developed by his students, of whom most notable for perceptual theory were von Ehrenfels, Husserl, Stumpf, and Meinong. Each of these individuals, brilliant and influential in his own way, was stimulated by Brentano's approach to psychology, but each had a different focus.

Christian von Ehrenfels (1859–1932) was a philosophical psychologist, a student of Brentano and Meinong. His place in the Hall of Fame of perceptual theory was secured by a single article of 1890, which made a profound impression on his teacher Meinong, the founder of the Graz school of Gestalt Psychology, and which was lauded by Berlin Gestaltists as an immediate inspiration.[18] In this article von Ehrenfels developed the Aristotelian views of Brentano on the mutual determination of parts and wholes, by introducing the concept of *Gestaltqualitäten* ("Gestalt qualities" or "form-qualities"):

By a Gestalt quality we understand these positive perceptual contents that are linked in awareness with the presence of perceptual complexes consisting of separable elements (that is, each element can be perceived in the absence of the others). We call the perceptual complex, which is essential to the existence of a Gestalt quality, the *foundation* of the quality. (1890, pp. 262–263)

A root of the two important schools of Gestalt Psychology, the article has been scrutinized for a clue of its future significance. What innovation did von Ehrenfels make in this particular article that changed the course of perceptual psychology? Perhaps it was the *enunciation of a new element of consciousness* as von Ehrenfels himself believed? (It would be an element in the sense it was not reducible to its foundation.) But the view of such irreducibility could not have been novel: it had already been amply elucidated in Brentano; in fact it traces back to Aristotle. Or, perhaps the innovation was in von Ehrenfels' idea that some perceptual property can be preserved under changes in its foundation (such as a melody is preserved under

changes in key or instrument)? But this notion, too, had been advanced before von Ehrenfels, by the ever inventive Ernst Mach.[19] Macnamara (1999) offered a credible answer, that von Ehrenfels' significance lies in that he advanced Brentano's approach rather in ideas of von Ehrenfels himself. In particular, von Ehrenfels elucidated how Brentano's views about the mutual determination of parts and wholes plays out *in perception* rather than in cognition. Rather than enunciate a new mental element, or discover a mental conservation principe, von Ehrenfels brought Brentano's insights about the structure of consciousness within the reach of experiment, which precipitated the transition of Brentano's philosophical descriptive psychology into the experimental phenomenology of Graz and Berlin.

Carl Stumpf (1848–1936) was an avid experimenter. Stumpf first studied under Brentano in Würzburg, then under Lotze in Göttingen, and then again under Brentano in Würzburg:

> My student years came at the end of the sixtieth when, after the collapse of the great artificial systems, German philosophy came more to value an empirical orientation. Franz Brentano showed me the way down this path. (translated in Sprung and Sprung, 2000, p. 53)

While at Göttingen, Stumpf met E. H. Weber and Fechner (they came to visit Weber's brother, Wilhelm, a professor of physics at Göttingen) and was a subject in one of Fechner's experiments. This encounter made a deep impression on the young Stumpf, nurturing his taste for experimental research. Stumpf went on to make seminal contributions to the psychology of hearing and to lay foundations of the psychology of music (together with Helmholtz). Among other innovations, Stumpf advanced a conception of psychological "fusion," which he then tested by exploring "primitive" (non-Western) music. Advancing ideas of Brentano, Stumpf upheld the importance of the study of mental phenomena, which he believed was propaedeutic to all other sciences. Influenced by Husserl (a student of both Stumpf and Brentano), Stumpf is credited with the introduction of phenomenology (already a discipline distinct from Brentano's descriptive psychology) into psychology. From 1890 to 1921 Stumpf headed the Psychological Institute at the University of Berlin, helping to establish psychology as a scientific discipline and creating a milieu from which Berlin Gestalt Psychology was born.[20] From 1894 Stumpf was the chair of psychology at the at the University of Berlin, "the most distinguished appointment that Germany could offer" (Boring, 1929, p. 355).

It is not accidental that the three key figures of Berlin Gestalt Psychology—Wertheimer, Koffka, and Köhler—were students of Stumpf, combining sensitivity to foundational questions with experimental vigor. Yet Stumpf did not share with his young proteges their theoretical single-mindedness and proclivity for generalization. He did not approve of

> young scientists of my acquaintance, who have done commendable work in studying [the] laws [of perception of Gestalt, but who] would like to base [on these studies] not only the whole of psychology but even logic itself. (translated in Woodworth, 1931, p. 208)

Edmund Husserl (1859–1938) was trained as a mathematician.[21] Convinced to turn to philosophy by Brentano, Husserl is best known as the founder of phenomenology, a philosophical development of Brentano's descriptive psychology. In his early work—*Philosophy of Arithmetic* (1891)—Husserl wrote about "a certain characteristic quality (*Beschaffenheit*) of the unitary total . . . of the given collection, capable of being grasped in a single glance" (p. 203). Arguably, Husserl went further than von Ehrenfels in clarifying the ontology of the perceived "unitary totals."[22] Husserl held that a specific collection is an instance of a family, the family organized into an hierarchy (a tree) of increasing generality, governed by mathematical (geometric) laws. Properties of the instances are perceived ("apprehended") the way they are because of their similarity to other instances of the same family. In his mature work, Husserl (1900) developed these ideas further, exploring dependencies between parts (constituents) of perceived collections and relationships between perceived collections and objects of perception. Husserl confined his investigations to philosophy.

Alexius Meinong (1853–1920) had a long tenure at the University of Graz (1882–1920), where he founded a school of Gestalt Psychology. Meinong is best known for his ontology of objects, *Gegenstandstheorie* (1904), a development of Brentano ontology, concerned in particular with mental references to objects, whether the objects existed (such as the objects that are *perceived)* or did not exist (imaginary objects or objects that can be named but cannot exist, such as a round square).

Central to Meinong's *Gegenstandstheorie* was the *theory of production*; it is in light of this theory that the entire Graz School should be viewed. Meinong was concerned with objects in general, not only the objects of perception. He distinguished the *inferiora* (or foundations) of complex objects and their *superiora*: the complex (higher-order, relational) objects themselves.[23] Perceiving the inferiora was direct, and perceiving the superiora was an intellectual (cognitive) act: an "act of production." Meinong's position on the indirect perception the complex objects was inconsistent with the view of Berlin Gestaltists, who held that perceiving complexes was direct, while perceiving the components of complexes required an intellectual act.[24]

Graz Gestalt Psychology: Under Meinong's leadership, the Graz school made important experimental and theoretical contributions to psychology of perception, independent of the Berlin Gestalt school. In fact, the Graz school facilitated the rise of Berlin school, by way of experimental contributions (Berliners extensively cited Benussi) and also by the productive polemic on the nature of perceptual *Gestalten* (e.g., Koffka, 1915/1938). Besides Meinong, of particular note in the Graz School are Benussi and Heider.

Vittorio Benussi (1878–1927), Meinong's student and colleague of many years, conducted wide-ranging experimental studies hailed by later students of perception as a Gestalt Psychology before it became an established movement in Berlin. Benussi observed that it was difficult to judge properties of stimulus components because the components interacted in perception and their

judgment depended on properties other than those of the components. Benussi attributed these properties to "prejudgment processing" (*Bearbeitung*),[25] an instance of production. This processing was taken to give rise to "Gestalt presentation" (*Gestaltvorstellung*). That was a step beyond Brentano's view, and it was one of the ideas of the Graz School criticized by the Berlin Gestaltists. After he left Austria, Benussi started a Gestalt movement in Italy, which made important contributions of its own (Kanizsa, 1979; Metelli, 1974; Musatti, 1975), and which persisted after the German Gestalt movement had been decimated (Verstegen, 2000).

Fritz Heider (1896–1988), Meinong's last doctoral student, undertook an ingenious analysis of the causal structure of perception (Heider, 1926, 1959). He asked why some aspects of environment become the objects of perception, while some other aspects become the media and are not perceived themselves. Heider's answer was that different aspects of the environment differ in how strongly their elements are connected. In the objects of perception the elements are connected strongly: the elements constrain each other (they are "coordinated") within the object. In the media of perception the elements are connected weaker: the elements are susceptible to external influences. Here the elements are constrained by ("coordinated" to) external causes, which is why they can mediate. Because of these differences, properties of things propagate through the media and not the other way around. In effect, perceivers "attribute" the causes of stimulation to the objects and not to the media. Heider's thought stimulated theories of Egon Brunswik and James J. Gibson. His ideas will be particularly familiar to students of Gibson's "ecological physics."[26]

The aforementioned polemic of Koffka and Benussi about the foundations of Gestalt theory was a step toward a synthetic view, incorporating the ideas of Graz and Berlin branches of the Gestalt movement. But the polemic was interrupted by World War I.

3.1.3. Gestalt Psychology, Berlin School

The line of Brentano found its most vigorous and influential expression in the Berlin School of Gestalt Psychology, advanced by Max Wertheimer and his associates under the auspices of the Psychological Institute headed by Stumpf, within some two decades from the 1910s to 1930s. The Berlin school crystallized some of the ideas brewing within Brentano's tradition, into what the school founders presented as a self-contained psychological theory, and which was recognized, by both sympathizers and critics, as a new major force in psychology.

As it was a rule in Brentano's tradition, the central concern of Berlin Gestaltists was the faithful description of laws of mental phenomena. To recall, Brentano prescribed the empirical psychology to "define the elements of human consciousness and the ways by which they are connected." On both aspects of Brentano's prescription, Berlin Gestaltists went farther than other followers of the phenomenological traditions had gone, perhaps with the only exception of

Benussi. A key contribution of Berliners (as that of Benussi) was the advance from Brentano's *empirical* approach to a full-fledged *experiential* approach.[27]

Whole-to-part determination: Berlin Gestaltists assumed an extreme theoretical stance toward elements of perception. In their hands, von Ehrenfels' all-around position was dissected: the view that the whole may determine the parts was upheld, and the view that the parts may determine the whole was suppressed. The elements were not given intrinsic identities. Rather than universal building blocks, the elements emerge (and acquire their identities) in accordance to the roles they play within the perceived form (*Gestalt*).

Foundational to Berlin Gestalt School were two papers by Max Wertheimer: on apparent motion (1912) and on principles of perceptual organization (1923). Each of them concentrated on the thesis of whole-to-part determination, and each advanced this thesis with indubitable force.

Where perceived melody was an epitome Gestalt phenomenon to von Ehrenfels, to Wertheimer that role was played by perceived movement. In his first foundational paper Wertheimer talks of a particular kind of apparent motion, which he called "pure" (or "objectless") motion, because no object is perceived to move while motion is still clearly seen.[28]

Apparent motion is perceived when a series of (possibly invisibly dim) lights are presented to observers in rapid succession, at different spatial locations. The series of disjoint presentations gives rise to the experience of smooth motion only under particular spatial and temporal distances between the lights (section 3.2.2). In general, perception depends both on properties of the individual lights and on their relation. Both dependencies were recognized by the Gestaltists (e.g., Koffka, 1935/1963; Korte, 1915). *Relations* of the lights, rather than properties of the lights themselves, were brought to the fore, as evidence of the whole-to-part determination. The "objectless motion" was significant because here the perceptual identity of elementary events is diminished as much as possible.

The argument from apparent motion was based on a contrived laboratory phenomenon. In his second foundational paper, Wertheimer advances his argument from everyday visual experience:

> I stand at the window and see a house, trees, sky. Theoretically I might say there were 327 brightnesses and nuances of colour. Do I have "327"? No. I have sky, house, and trees. . . . The concrete division which I see is not determined by some arbitrary mode of organization lying solely within my own pleasure; instead I see the arrangement and division which is given there before me. . . . When we are presented with a number of stimuli we do not as a rule experience "a number" of individual things, this one and that and that. Instead larger wholes separated from and related to one another are given in experience; their arrangement and division are concrete and definite. (Wertheimer, 1923, translated in Ellis, 1938, p. 71)

From here Wertheimer launches his canon-making study of the "organization in perceptual forms." The study was a series of illustrations designed to convince the

reader that visual perceptual organization was governed by simple rules, and that a proper method for studying perception was "from above downward" (*von oben nach unten*):

> For an approach "from above downward," i.e., whole-properties downward towards subsidiary wholes and parts, individual parts ("elements") are not primary, not pieces to be combined in and-summations, but are parts of wholes. (Wertheimer, 1923, translated in Ellis, 1938, p. 88)

The visual demonstrations pregnant with theoretical significance established a new paradigm in research of perceptual phenomena. The stimulus dimensions studied by Wertheimer were then submitted to experimental manipulations. It was the shift from a largely philosophical discussion to a rich program of experimental investigations that helped Gestalt movement to establish itself as an important branch of scientific psychology.

The work of Wertheimer set in motion a wave of further confirmations of whole-to-part determination: a wide-ranging program of experimental studies into the rules of this determination. Vision was not the only target of these investigations, but it was the favored medium. Perception of visual motion remained an important theme, but much research was also dedicated to perception of static stimuli, in planar and subjectively three-dimensional patterns. Gestaltists and their allies also studied more complex processes: in perception of color and lightness, and in complex spatiotemporal interactions called "events." "In brief, the research areas addressed by the first generations of Gestalt psychologists spanned much of what is now vision science" (Gepshtein, Elder, & Maloney, 2008, p. 1).

But the impressive body of experimental work had several defects, two of which were particularly damaging: exclusiveness and lack of rigor. Exclusive was the focus on whole-to-part determination; it prevented integration of Gestalt Psychology with other approaches to perception. The lack of rigor opened Gestalt movement to stringent attacks from other quarters of experimental psychology.

To Gestalt psychologists, the exclusiveness was not accidental because they were unwilling to leave any room in their theory for the entities that had no phenomenological reality,[29] as it was a rule in Brentano's tradition. Yet, the lack of a well-articulated connection with phenomena inconsistent with the view of whole-to-part determination created a gap which was soon filled by incomprehension. Here is an example:

> The Gestaltist sometimes tries to have his cake and also eat it too as he maintains that there are components which enter into structures and also that there are no components. The issue seems to stand about as it stood twenty years ago. (Murphy, 1949, p. 295)

This is an example of the constructive misunderstanding that Gestalt theory often met. It is a misunderstanding because it fails to correctly represent a basic tenet of Gestalt theory, that elements do not have intrinsic identities; their identities are born from the perceived stimulus structure. It is constructive because the

misunderstanding is not fortuitous. It is not animated by the lack of insight, but rather it betrays high expectations and the refusal to accept incomplete theory, promissory of a new science, but delivering only vague formulations.

To the critics, the abundant experimental phenomenology alone was unsatisfactory. A theory-driven approach was wanted, able to compete with other approaches, perhaps as rigorous and connected to sensory physiology as psychophysics aspired to be. Attempts to supply a broad theoretical framework by Köhler and Koffka (an example of which we will see in a moment) were often applauded by the broader scientific community. And yet, the framework was not rigorous: it was unclear why some, rather than the other, empirical facts were selected as the foundational principles of experimental phenomenology, and the physiological speculations advanced as a part of the framework had ruinous consequences. As the speculations were disproved—or seemed to be disproved—in physiological studies, the disproval tainted the entire Gestalt movement.

Dynamics: It would be unfair to describe Berlin Gestalt Psychology as a movement entirely contained within the line of Brentano. Besides the experimental phenomenology (which was certainly an advancement of Brentano's legacy), Berlin Gestaltists brought in theoretical ideas of their own. One of the ideas has had a lasting impact. It is the idea of "dynamics," in particular "perceptual dynamics," a complex temporal process manifest in perception and neural physiology. The notion of dynamics was borrowed from physics, and used as a guiding metaphor (along with the notions of "field" and "equilibrium") to account for the spontaneity and flexibility of perception.

An empirical foundation for the talk of dynamics was the phenomenon of "perceptual multistability." The stimuli designed to illustrate Gestalt principles could be interpreted several ways. The stimuli were "multistable" in that their perception would not dwell on one interpretation for long. The interpretations would spontaneously replace one another ("switch") in the viewer's mind.

Using multistability, one could experience the dynamics of perception directly, by pitting several factors of perceptual organization against one another. Perceptual "switching" would be observed when the strengths of competing factors were in equilibrium, or near equilibrium, i.e., the strengths were approximately equal. The different interpretations would alternate in the perceiver's mind, the person having only a partial control over perception.

Many of the most striking demonstrations of perceptual multistability were discovered outside of the Gestalt movement (e.g., Jastrow, 1889; Necker, 1832; Rubin, 1915), but it was in the context of Gestalt theory that the demonstrations acquired their theoretical significance. The dynamics was taken to manifest a process intrinsic ("autochthonous") to the brain. Construed as a dynamic physical system, the brain was expected to produce perceptual organizations of the same form as the organizations of physical structures in the world, also a dynamic system. The dynamics of perception was taken to manifest the dynamics of neuronal activity in the brain. The perceptual process and the "brain-process" were said to have the

same form (be ''psychophysically isomorphic''), *Gestalt* being the perceptual aspect of this form (Köhler, 1940).

No broadly accepted theory has emerged from this line of thought, but the focus on dynamics has survived the theoretical infelicity and had a lasting impact on perceptual science because of the ample phenomenological and physiological evidence of complex temporal processes underlying perception.[30]

At the end of the day, it is because of its empirical contributions—the experimental phenomenology, the evidence of whole-to-part (contextual) determination of percepts, and the evidence of perceptual dynamics—that Gestalt Psychology has retained its appeal to generations of researchers, even after the social institute of Gestalt Psychology ceased to exist.

3.2. Modern View

3.2.1. Neogestalt

After several decades of relative obscurity, the ideas and experimental findings of Gestalt psychologists started to enter the mainstream of perceptual research (Albright, 1994; Beck, 1982; Epstein, 1988; Kubovy & Pomerantz, 1981; Palmer, 1999). In the center of attention were the positive contributions of the phenomenological tradition: a plentitude of perceptual phenomena to be studied, explained, and modeled. The ill-fated speculations were acknowledged, the lessons incorporated in new research programs (e.g., Albright & Stoner, 2002; Kimchi & Palmer, 1985; Kubovy & Wagemans, 1995; Palmer & Rock, 1994; Spillmann, 1997).

A buzz term ''neogestalt'' came into existence, which however did not grow institutionalized, perhaps because its meaning has been ambiguous. Sometimes ''neogestalt'' is taken to indicate adherence to the phenomenological tradition: use of direct observations of perceptual structures (''phenomenological reports''). But sometimes ''neogestalt'' merely indicates an interest in the phenomena discovered by the Gestaltists, whether or not the phenomena are studied by phenomenological methods.

The statistical thread: An example of the latter, narrower, version of ''neogestalt'' is a research program that seeks to explain Gestalt phenomena from the statistical structure of perceiver's environment. The antecedents of this line of thought within the line of Brentano were mentioned in section 3.1.2: Heider and Brunswik had concentrated on the causes of perceptual Gestalt in the physical environment. On their view, certain perceptual organizations are more likely than others because they correspond to structures common in the environment. Brunswik submitted this approach to experimental testing (e.g., Brunswik & Kamiya, 1953).

Another antecedent of the statistical approach to Gestalt phenomena is, naturally, the statistical line of Fechner (section 2.1.2). Modern exponents of this statistical approach to perceptual organization rely on the theoretical apparatus developed within line of Fechner. They treat Gestalt phenomena as another instance of statistical perceptual inference: using Bayesian decision-making as the theoretical framework (Knill & Richards, 1996), and using indirect reports (rather than the phenomenal

reports) as the experimental framework (e.g., Burge, Peterson, & Palmer, 2005; Elder & Goldberg, 2002; Geisler, Perry, Super, & Gallogly, 2001).

This work represents a forced marriage of the psychophysical and phenomenological traditions because indirect reports are used to study phenomena whose nature is likely to be distorted by the lack of direct observation (Kubovy & Gepshtein, 2003). It remains to be seen whether the statistical approach can overcome this difficulty and bring the forced marriage to a successful settlement.

The phenomenological thread: In the rest of this section I will review some studies from the phenomenological tradition, which has also offered a prospect of synthesis of the phenomenological and psychophysical traditions, yet by means other than statistical inference. This work concerns a paradigmatic Gestalt phenomenon: visual apparent motion (introduced in section 3.1.3).

The work on apparent motion was possible by a series of innovative studies of grouping by proximity within the phenomenological tradition that used more rigorous experimental methodology (e.g., Kubovy, 1994; Oyama, 1961) than that by the Gestaltists. A key result in this line of work is the "pure distance law" of perceptual grouping proposed by Kubovy, Holcombe, and Wagemans (1998). These studies showed that Wertheimer's principle of grouping by proximity has a simple mathematical form, and that the grouping factor of proximity is independent of other grouping factors. The rigorous understanding of the proximity principle afforded integration of the previously separate principles within an increasingly general framework, where other grouping factors modulate the effect of the basic factor of proximity (Kubovy & van den Berg, 2008; Strother & Kubovy, 2006).

These studies used a stimulus called *dot lattice*, a generalization of the stimulus introduced by Wertheimer (1923). The following study of apparent motion used *motion lattices*: a generalization of dot lattice to space-time, where the dots are separated by both spatial and temporal distances (Gepshtein & Kubovy, 2000, 2007).

3.2.2. Apparent motion

Apparent motion is the experience of motion elicited by rapid sequences of slightly different images. An elementary case of apparent motion is illustrated in figure 5. Here motion is seen when two lights (represented in panel A by unfilled circles) are flashed one after another at different spatial locations. At instant t_1 a flash occurs at location s_1, and at instant t_2 another flush occurs at location s_2. The experience of motion arises for some combinations of spatial and temporal distances between the lights, $S = \Delta s = s_2 - s_1$ and $T = \Delta t = t_2 - t_1$ as we will see in a moment.

The stimulus of figure 5 is represented more compactly in the *distance graph* in figure 5B, the two dimensions of which are the spatial and temporal distances, S and T, of the elementary apparent motion display. Here the stimulus is represented by a single point. The format of distance graph will be used extensively in the rest of this article, to compare results from studies of motion perception that used different stimuli and different experimental paradigms.
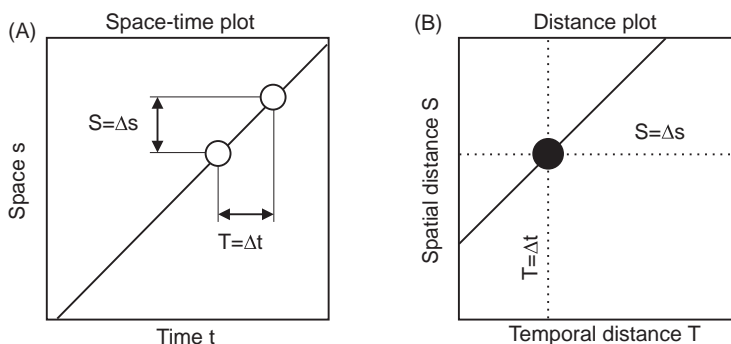
Figure 5 *Two representations of apparent motion.* (A) Space-time graph (t, s). Two points are flashed on the screen at distinct spatiotemporal locations, represented by two circles in the coordinates of time and space: (t, s). (B) Distance graph (T, S). The same stimulus is represented by a point in a graph of distances $(T, S) = (\Delta t, \Delta s)$.

Varying one of the distances between the lights (only the spatial distance or only the temporal distance) affects the perceptual quality—the ''strength''—of apparent motion. Can the perceptual change induced by varying one (say, temporal) distance be compensated by varying its other (spatial) distance?

For example, suppose we have established that a certain combination of spatial and temporal distances of lights gives rise to a vivid experience of apparent motion. Suppose that increasing the temporal distance weakens the experience. Can we restore the original strength of apparent motion varying the spatial distance between the lights? In other words, can different combinations of spatial and temporal distances yield the same strength of perceived motion?

Attempts to answer this question comprehensively produced two apparently inconsistent results, illustrated in figure 6.

Consider figure 6A first. It is a distance plot of two apparent motion. Each stimulus is represented by a dot, as in figure 5B. Stimulus 2 has a longer temporal distance than stimulus 1. Suppose both stimuli give rise to perception of motion. Now fix the spatial and temporal distances of stimulus 1. In stimulus 2, fix the temporal distance and vary the spatial distance. The variation is represented in figure 6 by the double-headed arrows. The goal of this manipulation is to find such a spatial distance in stimulus 2 that the experiences of motion in the two conditions are equally strong.

Different studies implemented these variations of spatial and temporal distances, but found inconsistent results. Two *regimes* of apparent motion were discovered, illustrated in figure 6. In the regime of space-time *coupling* (panel A), the strength of apparent motion is conserved by increasing both spatial and temporal distances between the lights (Korte, 1915). In the regime of space-time tradeoff (in panel B), 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).
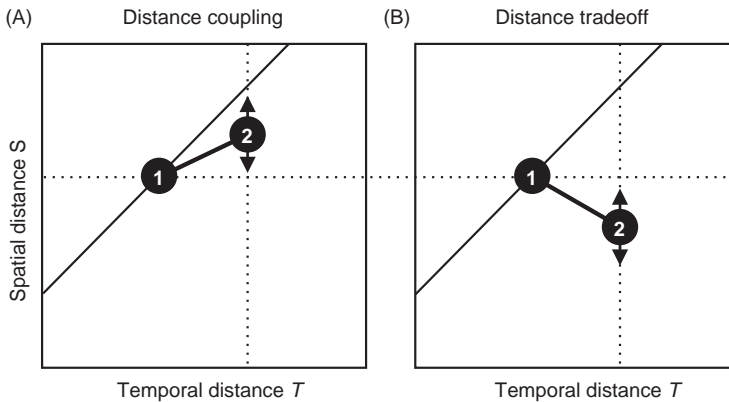
Figure 6 *Regimes of apparent motion*. Stimulus 1 is at (T, S) and stimulus 2 is at $(2T, nS)$. That is, in stimulus 2 the temporal distance is twice longer, and the spatial distance is n times longer, than in stimulus 1. What is the magnitude of n $(n > 0)$ at which the two stimuli are equally strong? The answer has been inconsistent: by some studies, the answer is $n > 1$ (distance coupling, as in A), by others, it is $n < 1$ (distance tradeoff, as in B).

Later work showed, however, that the two regimes are special cases of a general pattern. Gepshtein and Kubovy (2007) found pairs of conditions of apparent motion were perceptually equivalent across a large space of stimulus parameters. It turned out that tradeoff holds at low speeds of apparent motion, and coupling holds at high speeds. One regime changes into another smoothly, as a function of speed. The authors derived equivalence contours of apparent motion, a supra-threshold equivalent of the isosensitivity contours obtained at the threshold of visibility.

Remarkably, the shapes of equivalence contours of apparent motion by Gepshtein and Kubovy (2007) were consistent with the shapes of isosensitivity contours (section 2.2.2). Figure 7 illustrates the consistency of results. The monotonic relationship between the isosensitivity contours and the equivalence conditions of apparent motion indicates that perception of motion is controlled by similar factors at the threshold of visibility and above the threshold. The similarities between different kinds of perceptual motion are investigated in section 4.2, where an attempt is made to understand the forces that shape perception of motion from first principles.

3.2.3. Breach in the empirical foundations

The discovery of a general pattern behind the different regimes of apparent motion has important implications for the accepted view of perceptual organization. As mentioned, the accepted view is an incremental construction on a fundament laid by Wertheimer in 1923. The fundament is a list of empirical principles of grouping (such as grouping by proximity, similarity, and continuity) complemented by statements about other perceptual tendencies (such as the figure-ground organization and the pithiness, or goodness, of perceptual structures). Earlier in this section
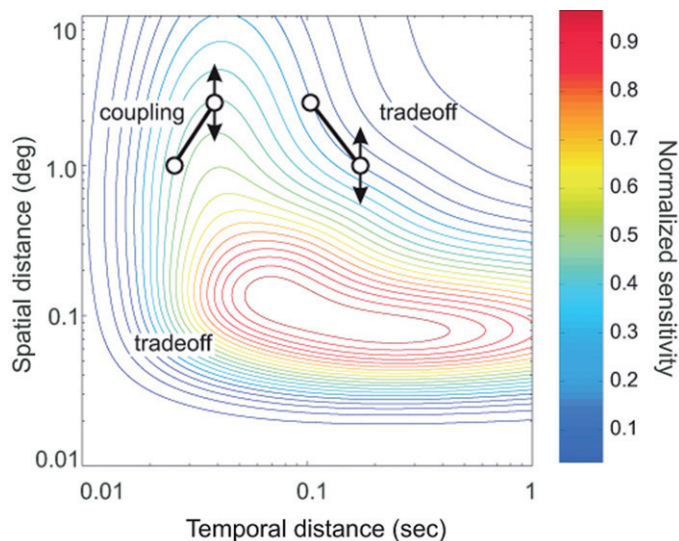
Figure 7 *Isosensitivity contours in the distance graph.* The slopes of contours vary, alternatingly consistent with the regimes of coupling and tradeoff of apparent motion (figure 6). Distance graph is introduced in figure 5. Each point of the graph corresponds to a condition of apparent motion (and can also be thought of as the tuning parameters of a motion-sensitive neuron; Reichardt, 1961). The isosensitivity contours are mapped from figure 4B, as explained in Nakayama (1985) Gepshtein and Kubovy (2007). (The figure is from Gepshtein & Kubovy, 2007.)
Permission: The Association for Research in Vision and Ophthalmology.

I described recent advances within this line of work, using more rigorous definitions and more sophisticated experimental methods than those used by Gestalt psychologists. These advances offer a preview of a possible new incarnation of Wertheimer's approach: a mathematical framework ready for use by machine vision and other artificial perceptual systems.

But the results about the unity of apparent motion undermine the accepted view, as follows. The evidence that human visual system favors sometimes short and sometimes long spatiotemporal distances in the stimulation (Gepshtein, Tyukin, & Kubovy, 2007a) is inconsistent with the proximity principle, a cornerstone of Wertheimer's conception of perceptual organization.[31] 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. These results imply that foundations of the traditional view of perceptual organization need a revision.

A proposal of direction for such a revision is presented in section 4, where the unity of results on apparent motion, and the consistency of these results with results on spatiotemporal sensitivity, are investigated from first principles.

3.3. Summary: Brentano and Gestalt

A clear stance on the separation of physical and mental phenomena by the Aristotelian philosopher Franz Brentano created a social and intellectual momentum toward an explosion of studies in experimental phenomenology. But today researchers of perception are largely unaware of Brentano because the phenomenological approach to perception had become associated with a particular offshoot of Brentano's tradition: Berlin Gestalt Psychology.

The legacy of Berlin Gestalt Psychology is mixed. It contains a tension between a splendid corpus of empirical observations and a crippled theory. On the one hand, Gestalt Psychology is replete with definitive observations of the structure and dynamics of perception: a development of Brentano's ''descriptive psychology.'' On the other hand, Gestaltists dissociated themselves from the clarity of Brentano's analysis, chose a narrow theoretical premise (the primacy of the whole over the part) as the foundation of their entire worldview, and entangled themselves with some ill-fated speculations about physiological mechanisms of perception.

The recent resurgence of interest in discoveries by the Gestalt movement— sometimes lauded as a rebirth of Gestalt Psychology—owes to a large degree to the phenomenological method upheld by the Gestaltists. They carried the phenomenological tradition from Brentano's circle into modern experimental psychology, where their findings are being scrutinized using novel experimental and theoretical tools.

4. The Line of Gabor: Elements of Information

4.1. Roots

Dennis Gabor (1900–1979) was a Hungary-born electrical engineer, physicist, and inventor (figure 1). He is widely known for his work on holography (Gabor, 1949), for which he was awarded The Nobel Prize in Physics in 1971. Holography was one of the many inventions in Gabor's illustrious career, the inventions rested on systematic and wide-ranging theoretical investigations. Gabor's influence on studies of perception is rooted in his efforts to reconcile the *temporal* and *spectral* representations of signals, with the purpose of improving the efficiency of telecommunication (Gabor, 1946, 1952).[32] Gabor developed a representation of signals and a method of measuring their content that had significant implications both for theory of communication and theory of measurement. An outcome of his analysis was a principle (sometimes called ''the uncertainty principle of measurement,'' e.g., Cherry, 1959; Resnikoff, 1989) that compactly summarized the mutual dependency of the temporal and spectral representations.

4.1.1. The uncertainty principle of measurement

Gabor formalized a fundamental result in communication theory that had been increasingly appreciated by communication engineers early in the twentieth century. In 1928, this result was presented as a foundational principle of communication by a

pioneer of information theory, American engineer Ralph V. L. Hartley,[33] in a landmark paper where the concept of "information" was used in its modern, technical sense for the first time. Hartley noted that:

> The total amount of information which may be transmitted over [a system] is proportional to the product of the frequency-range which [the system] transmits by the time during which it is available for the transmission. (1928, p. 554)

Yet it was Gabor's theory where the principle acquired a rigorous mathematical footing. The uncertainty principle applies to simultaneous measurements of two aspects of any signal: its *location* and *content*. At the limit of performances of any measuring device, the precision of measuring the location is constrained by the precision of measuring the content, and vice versa. Let us briefly review the quantities connected by the uncertainty principle.

Signal location: The notion of signal location is intuitively clear. Consider a temporal signal: a process that unfolds in time, t. To measure signal location in time is to determine temporal interval Δt that contains the signal: the smaller the interval the higher the precision (lower the uncertainty) of measurement.

This argument applies to any dimension, but in the following we will be concerned only with the dimensions of space and time. Localizing a signal in space or time amounts to measuring *where* or *when* the signal occurred.

Signal content: The notion of signal content is less intuitive. It has to do with how signals *vary* on the dimension of interest. (For example, the content of a photograph is determined by how the intensity of color varies across the imaging surface.) Signal content is measured by the amount of variations it contains. The measurement is carried out by analysis. The signal is decomposed to *elementary variations*—harmonic functions of different frequencies. The amount of each elementary variation in the signal at hand is a measure of its content.

Because the elementary components of variation are each characterized by a single frequency of variation, the result of this measurement is called the "frequency content" of the signal.

Frequency content of a temporal signal is represented on the dimension of temporal frequency. Just as a point on the dimension of time represents a single temporal instant t, each point on the dimension of temporal frequency represents a single temporal frequency f_t. And just as the precision of measuring temporal location is represented by interval Δt, the precision of measuring temporal-frequency content is represented by interval Δf_t. The smaller the interval the higher the precision of measurement.[34]

The same argument applies to measurement of spatial frequency content. For simplicity, I will use a notational shorthand. When an argument applies equally to spatial and temporal signals, x will stand for s or t. Similarly, f_x (or shorter f) will stand for f_s or f_t.

Measurement "uncertainty" and "precision" are the quantities that represent confidence about outcomes of a measurement. In the following, sizes of

measurement intervals Δx and Δf will be used to evaluate the uncertainty of measurement: the larger the interval the more uncertain the outcome of measurement (and the lower its precision).

Uncertainty tradeoff: Precise measurement of signal location and (frequency) content at the same time presents a challenge. Measuring the location is most precise (least uncertain) when the signal is contained in a very small interval. But very small intervals do not contain sufficient information for precisely measuring the frequency content of signals. Measurement of variation is precise on large intervals. In effect, there is a tradeoff in precision (uncertainty) of measuring signal location and content. Gabor gave this tradeoff a precise expression, which constitutes his uncertainty principle. In its simple form the principle is written as

$$\Delta x \Delta f \geq C, \tag{11}$$

where C is a positive constant. In words, the product of uncertainty about signal location and content is "bounded from below," i.e., cannot be smaller than C. At the limit, where

$$\Delta x \Delta f = C, \tag{12}$$

Δx can be decreased only at the expense of increasing Δf, and Δf can be decreased only at the expense of increasing Δx.

Information cells: Notice that the product of two intervals—Δx and Δf—in equation (12) is the area C of a rectangle in coordinate system (x, f) illustrated in figure 8A. Two sides of this rectangle are intervals Δx and Δf. According to equation (12), the shape of this rectangle can change while its area is conserved: increasing Δx by factor k is accompanied by decreasing Δf by the same factor, and vice versa.

The tradeoff of rectangle sides represents the tradeoff of uncertainties associated with any measurement. Gabor called the rectangles "information cells"—or "logons"—and proposed that the number of information cells that contain a representation of signal in (x, f) is a measure of the information contained in the signal.

Joint measurement of location and content: The diagram in figure 8A makes it clear that a measuring device (a "sensor") operating at the limit of its performance may have

- high precision in measuring location and low precision in measuring content (the cell on the left),
- high precision in measuring content and low precision in measuring location (the cell on the right),

or it may measure both kinds of information with an intermediate precision (the cell in the middle).

A sensory system that seeks to precisely measure both the location and content of stimulation may use specialized sensors, such as the ones represented by information cells on the left and right of figure 8A. But biological sensory systems are likely to
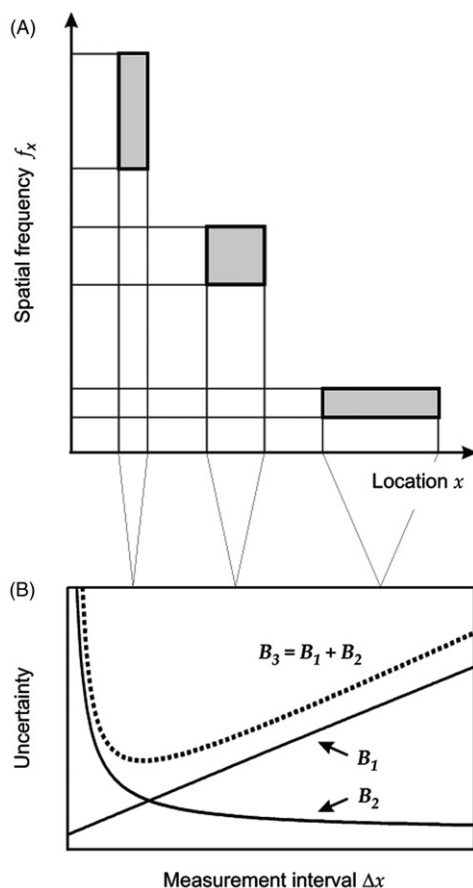
Figure 8 *Information cells and uncertainty tradeoff.* (A) The three rectangles are the information cells: they have the same area (C in equation 12) but their shapes vary. Cell projections on dimensions x and f_x represent, respectively, the precision of measuring signal location (Δx) and signal frequency content (Δf_x). The larger the projection, the lower the precision (higher uncertainty) of measurement. (B) Functions B_1 and B_2 represent the uncertainties associated with measuring signal location and frequency 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. Function B_3 (the dotted curve) represents the joint uncertainty of simultaneous measurement of signal location and content. The low values of B_3 at an intermediate magnitudes of Δx idicate that a sensor of the intermediate size is more suitable for jointly measuring signal location and content than the larger or smaller sensors.

prefer a compromise to the utter specialization, for two reasons. First, both kinds of information—location *and* content—are often needed from the same sensor at the same time (section 4.2). Second, biological sensory systems have limited resources. A frugal design, in which the same resource (the same sensor or sensory neuron)
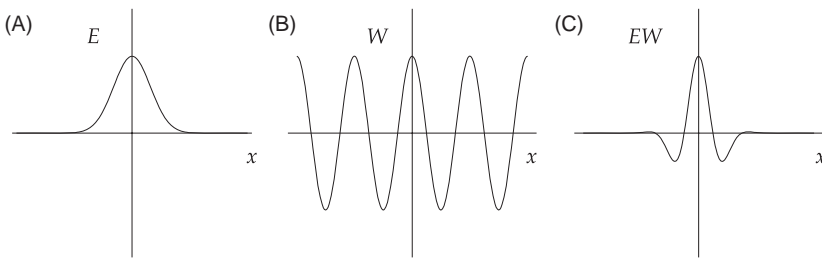
Figure 9 *Gabor filter*. (A) An ''envelope'' function, $E(x)$. (B) A ''carrier'' function, $W(x) = \cos x$. (C) A Gabor function is the product of the envelope and the carrier, $G(x) = E(x)W(x)$. Gabor (1946) showed that the joint localization of signals on x and f_x is most efficient when $E(x)$ is a Gaussian function.

performs several functions, has an advantage. In both respects, the sensors represented by the information cell in the middle of figure 8A must be preferred over the specialized sensors.

The advantage of simultaneously measuring several kinds of information by the same sensor is explained in figure 8B:

- Function B_1 represents the uncertainty of measuring signal location, proportional to *widths* of information cells.
- Function B_2 represents the uncertainty of measuring signal content, proportional to the *heights* of information cells.
- Function B_3 represents the *joint uncertainty* of measuring the location and content: the sum of B_1 and B_2.

The joint uncertainty function has its minimum at an intermediate size of the measurement interval. The medium-size sensors are most suitable for measuring *both* location and content of stimuli. Such sensors will be preferred by a frugal sensory system whose performance depends on having both kinds of information from its sensor.

4.1.2. Gabor filters and visual receptive fields

As mentioned, Gabor (1946) proved that measurements of two fundamental properties of a signal—its location and frequency content—are not independent of one another. At the limit of performance of any measuring device, the precision of measuring one of these properties (say, location) can be improved only at the expense of precision of measuring the other property (content), and vice versa. Therefore, joint measurements of signal location and frequency content can be done well only by way of compromise: by sacrificing some precision of measuring the location and some precision of measuring the content. A measuring device that implements this compromise optimally is called ''Gabor filter,'' illustrated in figure 9.

In a Gabor filter, the strengths of contributions from different points in the filter are ''weighted.'' The weighting has two components: a Gaussian ''envelope'' and a
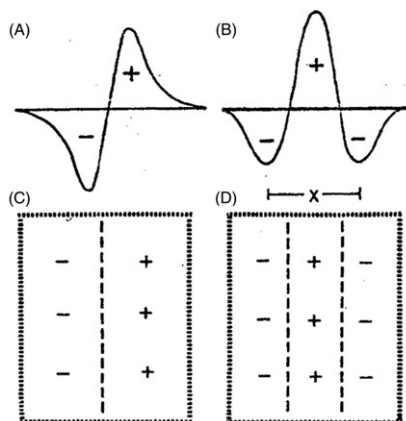
Figure 10 *Receptive fields of cortical neurons in the primary visual cortex of the cat.* (A–B) Spatial "profiles" of the receptive fields: functions of intensity of neuronal response vs. stimulus location in the receptive field. Symbols (+) and (−) idicate the regions of receptive fields whose stimulation respectively increased or decreased neuronal activity: the "on" and "off" regions. (C–D) Spatial maps of the receptive fields. The "on" and "off" regions form parallel strips. Symbol (x) represents the "spread" of one of the receptive fields. (The figure is from MacKay, 1981.)
Permission: Nature Publishing Group.

periodic "carrier" shown in figure 9A–B on a single dimension x. The Gaussian envelope insures that the measurements are localized on x, and the periodic carrier insures that the measurements are also localized on the dimension of frequency f_x (i.e., confined to an interval around the frequency of the periodic function). A sensor with such properties can perform joint localization on x and f_x better than a sensor that is specialized for measurement of location (using a small envelope with no tuning to frequency) or measurement of frequency content (using a large envelope and tuned to frequency).

Physiological studies of visual perception have shown that visual cortical neurons are optimized for measuring the locations and frequency content of visual stimuli in a manner consistent with Gabor's filter (Daugman, 1985; Kulikowski, Marcelja, & Bishop, 1982; MacKay, 1981; Marcelja, 1980). The plots in figure 10A–B represent response intensities of two neurons as a function of stimulus location in their receptive fields. The illustrated neurons responded most vigorously to bright vertical bars against a dark background. The response function in figure 10B has a shape similar to that of Gabor filter in figure 9C. The response function in figure 10A is similar to a Gabor filter in which the periodic weighting function has a different phase (i.e., is shifted over x such that the "carrier" function in figure 9B is a sine function rather than a cosine function).

The similarity of visual receptive fields and Gabor filters is well established (e.g., 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. But perceptual consequences of the uncertainty principle are broader than the measurements by individual sensors. In the following I review some of these consequences. In particular, I show how this approach helps to explain a connection between results from the statistical and phenomenological traditions in perceptual science.

4.2. Modern View

Here I present two examples of how Gabor's uncertainty principle constrains basic visual processes. The first example, about *binocular vision*, is simple in that it concerns a single (spatial) dimension. It illustrates how measuring both the location and content of a stimulus can be crucial for some visual functions. The second example, about *perception of motion*, is more complex: it concerns both the spatial and temporal dimensions of stimulation.

4.2.1. Binocular vision

In animals with forward facing eyes, the same objects are simultaneously viewed from slightly different perspectives. The two images of the visual scene are generally different. The visual system uses these differences—called binocular disparities—as a source of information about the three-dimensional layout of the scene. But to compute the disparities, the visual system must solve a *binocular correspondence problem*: it must find which parts of the left-eye and right-eye images correspond to one another. The ability to solve the binocular correspondence problem is constrained by the uncertainty principle of measurement, as follows.

Binocular matching: The binocular correspondence problem resembles the *I spy* game: it amounts to searching for a small pattern in a larger image. A small pattern from one of the images is used as a ''matching template.'' The template is compared with many patterns in the other image in search for a similar pattern (e.g., Banks, Gepshtein, & Landy, 2004; Kanade & Okutomi, 1994). This procedure, called ''binocular matching,'' is illustrated in figure 11.

Panel A of figure 11 contains two identical random-dot patterns, simulating the left-eye and right-eye images on the retinas of an observer who views a wall decorated with randomly arranged dichromatic tiles.[35] In this illustration, regions of the left-eye image are used as ''matching templates'' (panel B). What regions of the right-eye image contain patterns similar to each template? Three examples are illustrated in the figure, using templates of different sizes:

● *Small templates* localize stimulation precisely, but they capture only little variation of luminance in the image. The content of a small template is not unique, making the matching procedure ambiguous. For example, the smallest template in figure 11 (the smallest square over the left image in A) is as small as one image element so the number of matches is the number of same-colored elements in the right image, illustrated on top right of figure 11B.
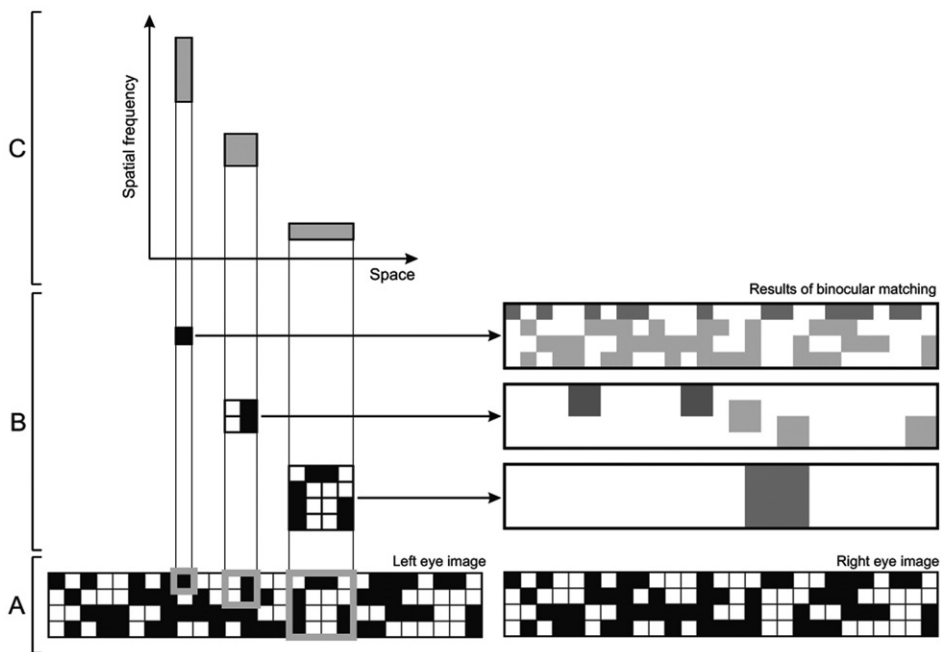
Figure 11 *Binocular matching at different spatial scales.* (A) The left-eye and right-eye images contain identical random-dot patterns. (B) Three regions of the left-eye image at different spatial scales are used as templates for binocular matching. The gray squares in the three panels on the right represent results of matching with the three templates. Each square marks the location of a perfect match. The outcome of matching depends on the size of template: the larger the template the less ambiguous matching, i.e., the fewer matches it produces. (C) Information cells of the matching templates (*cf.* figure 8).

- *Large templates* contain unique variation of luminance. For example, the largest template in figure 11 contains a unique configuration of the elements. Binocular matching produces a unique result, illustrated on bottom right of figure 11B. But the large template has a disadvantage; it receives stimulation from many spatial locations. If the locations correspond to different depths in the stimulus, the template will integrate the contributions from different depths, effectively reducing the resolution of depth discrimination (Banks et al., 2004).
- *Medium-size templates* offer a compromise. They produce fewer false matches than the small templates but they allow better spatial localization of correct matches than the large templates.

Trading uncertainties: We just saw that templates of different sizes have different advantages for binocular matching, depending on the amount of luminance modulation captured by the templates. This fact is a manifestation of the uncertainty principle of measurement, illustrated in figure 11C using an information diagram.

Large templates are useful for solving the binocular correspondence problem because they afford precise measurements of the (frequency) content of luminance within the template. The advantage of large templates for binocular matching is marred by their low spatial resolution, which we have observed above when we noted that the larger the measurement interval (larger the sensor) the less precise are the measurements of signal location. The templates of intermediate size offer a compromise between the low resolution of large templates and the matching difficulties of small templates.[36]

Thus, binocular matching is an illustration of why both signal location and content may need to be measured by the same sensors at the same time. Specialized sensors alone cannot solve the correspondence problem with high spatial resolution.

4.2.2. Perception of motion

Understanding the consequences of Gabor's uncertainty principle in perception of motion is more demanding than in binocular matching because perception of motion involves the dimension of time in addition to the dimension(s) of space.

Figure 12 helps to trace the dependencies between the spatial and temporal aspects of measurement uncertainty. In the distance graph[37] on the bottom of the figure, several stimulus conditions are marked by circled numbers. Some properties of each condition are illustrated with the help of the information diagrams drawn on the side panels: temporal diagram on the left and spatial diagram on the right.[38]

For example, consider condition 1. It represents small spatial and large temporal intervals of measurement. The spatial information cell is stretched along the spatial-frequency axis, i.e., it is formed by a small spatial interval and a large spatial-frequency interval. This means that condition 1 is more suitable for measuring spatial locations (i.e., *where* the stimuli are) than spatial content (*what* the stimuli are). The temporal information cell is stretched along the temporal-distance axis: it is formed by a large temporal interval and a small temporal-frequency interval. This means that condition 1 is more suitable for measuring temporal content than temporal location.

This pattern is reversed at condition 9. The spatial cell of condition 9 is stretched along the spatial-distance axis, indicating a specialization for measuring spatial-frequency content. The temporal cell is stretched along the temporal-frequency axis, indicating a specialization for measuring temporal location.

Evidently, the conditions arranged along the margins of the distance graph (i.e., 1–3, 4, 6, 7–9) are specialized: they are more useful for measuring some aspects of stimulation than its other aspects. A compromise is achieved in the middle of distance graph, e.g., in condition 5. The compromise is represented by ''neutral'' shapes of the information cells: at condition 5 the cells have intermediate sizes in both spatial and temporal domains.

Spatiotemporal uncertainty function: The interactions of four aspects of uncertainty are difficult to picture: each information cell is a tesseract in the four-space
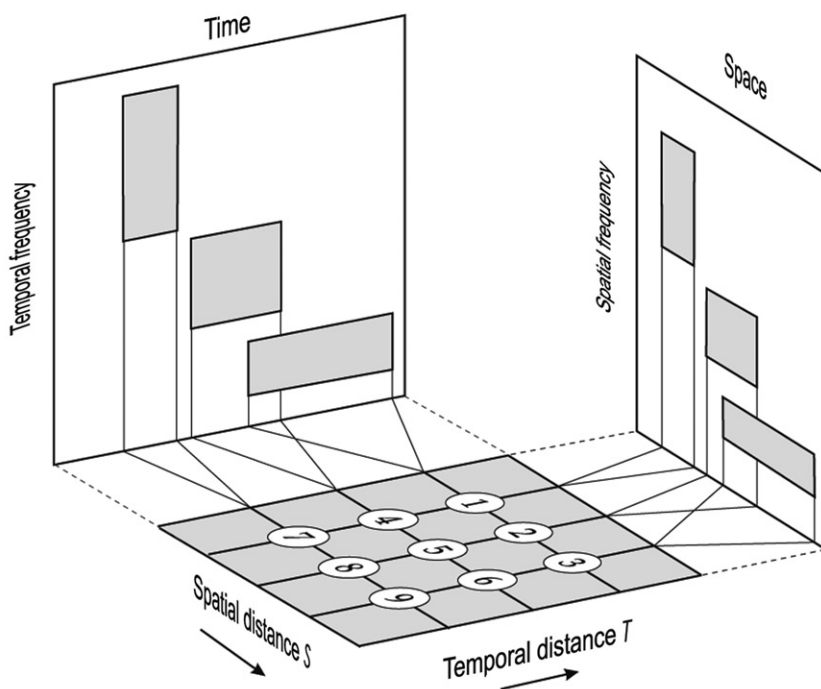
Figure 12 *Interaction of spatial and temporal uncertainties.* The gray plane on the bottom contains a *distance graph*. Each point of it corresponds to two information cells: temporal and spatial. Some of the logons are shown in the spatial and temporal frequency planes (top right and top left). The circled numbers indicate combinations of logons (see text).

of uncertainties. The analysis is simplified by the device of *joint uncertainty function* introduced in figure 8B. The simplification is achieved by collapsing the multiple uncertainties to a single function, as follows.

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 8B. The two effects are summarized by joint uncertainty function $B_3 = B_1 + B_2$: the dotted curve in figure 8B.

Now we use the same approach: first within the spatial and temporal dimensions and then in space-time. The spatial and temporal uncertainty functions are represented by the dotted curves on the side panels of figure 13. Next we add the spatial and temporal uncertainties for every point in the distance graph.[39] The result is a *spatiotemporal uncertainty function* rendered in figure 13 as a surface.

The structure of the two-dimensional uncertainty function is revealed in a contour plot on the bottom of figure 13. The level curves of the surface are projected on the bottom plane. Each contour is an *iso-uncertainty set*: it contains the (T, S) conditions
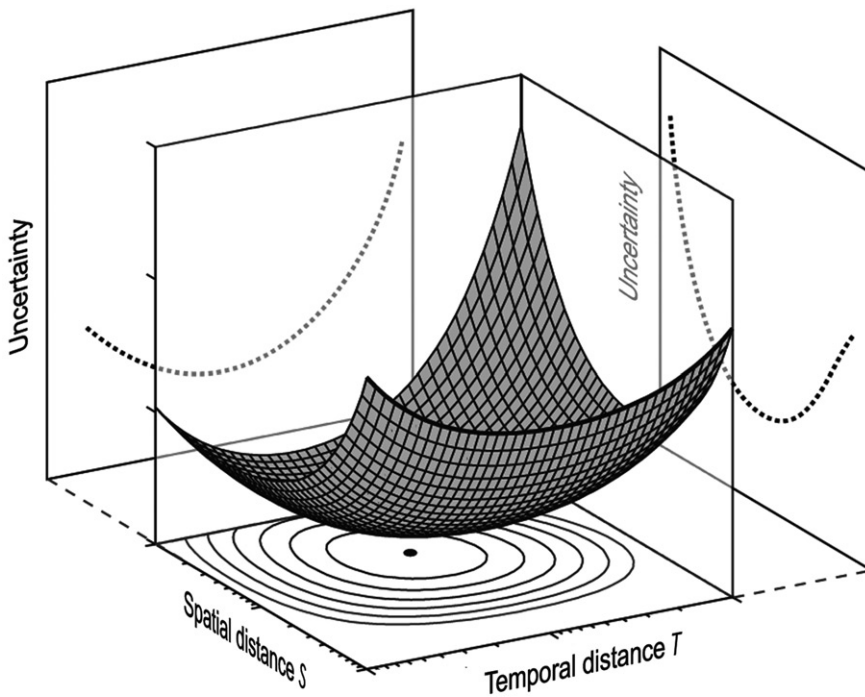
Figure 13 *Spatiotemporal uncertainty function.* The dotted curves on the side panels represent one-dimensional uncertainty functions: spatial on the right and temporal on the left. The functions describe uncertainties of jointly measuring signal location and signal content (as in figure 8B), separately within 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 faceted surface. The circular contours in the distance graph (on the bottom plane) are projections of the bivariate level curves: each contour represents a set of equal uncertainty. The small filled circle marks the projection of the lowest uncertainty.

at which the joint uncertainty is constant. These conditions are equally suitable for measuring stimulus location and content, jointly in space and time. The closer a contour to the point of smallest uncertainty—marked ''Optimum'' in the figure—the lower the uncertainty.

4.2.3. Interim results

We have reviewed some basic properties of the uncertainty involved in measurement of spatiotemporal stimuli. Before we turn to a further analysis of uncertainty, it is useful to note that our results so far can explain why the different regimes of apparent motion are observed using different stimuli, and why the proximity principle fails in perception of motion.
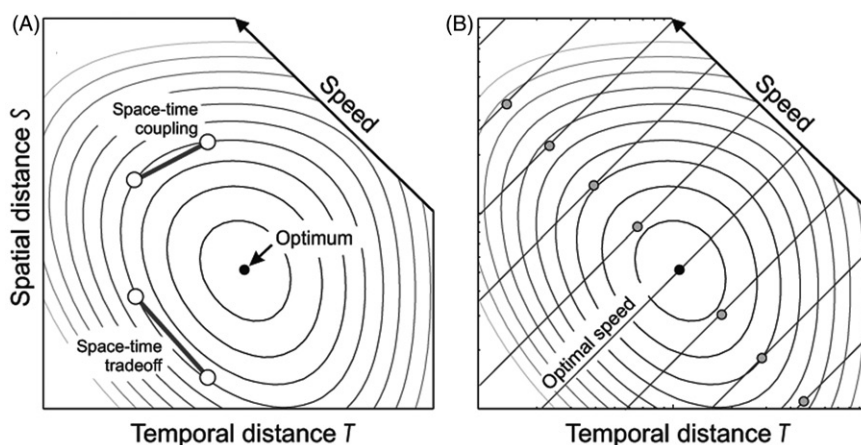
Figure 14 *Properties of measurement uncertainty.* (A) The contours of equal measurement uncertainty from the bottom plane of figure 13. The slopes of contours vary, alternately consistent with the regimes of space-time coupling and tradeoff of apparent motion, indicated by the two pairs of connected circles. The point of lowest measurement uncertainty is marked by the small filled circle (''Optimum''). (B) The points of lowest measurement uncertainty are shown for multiple speeds.

Unity of apparent motion: The distance graph in figure 14 contains the iso-uncertainty contours introduced in figure 13. Suppose that measurement uncertainty was the only force that determined the quality of perceived motion. Then all stimuli on an iso-uncertainty set would be perceived equally well. For example, each pair of connected circles in figure 14 represents stimulus conditions equivalent in that sense. Notice that the connection lines have slopes of opposite sign.

Recall that the different slopes represent different regimes of apparent motion: the positive slopes represent space-time coupling and the negative slopes represent space-time tradeoff (figure 6). It follows that different regimes of apparent motion expected in different parts of the distance graph. For example, the regime of coupling is expected at high speeds, in the top left region of the distance graph, and the regime of tradeoff is expected at intermediate speeds, e.g., the top right and bottom left regions.

This way, the empirical inconsistency about the combination of spatial and temporal distances in apparent motion is resolved not only empirically (section 3.2.2) but also theoretically: the different regimes of apparent motion occur because the expected quality of motion measurement varies across the space of stimulus parameters.

The different regimes of apparent motion are expected from first principles. The expectation would fail if some other factors had intervened, or had a greater effect than the uncertainty principle. Therefore one should test the claim that the different regimes of apparent motion are a consequence of the uncertainty principle rather than some other factor. To do so, predictions should be derived beyond the

known properties of motion perception, and the predictions tested in dedicated experiments (section 5.4).

Failure of the proximity principle: As mentioned in section 3.2.2, the evidence of unity of apparent motion undermines the traditional view of perceptual organization. The traditional view is founded on a taxonomy of perceptual tendencies, codified as principles or laws of perception. The lawful nature of some of these tendencies was confirmed in rigorous studies. And yet, the traditional view lacks a principled foundation. Why these tendencies, rather than some other empirical results, are enshrined as the foundational laws? This concern is aggravated by the evidence that the proximity principle—a staple of the traditional view—does not hold in perception of motion.

Now we have learned, by tracing implications of Gabor's uncertainty principle, that the different regimes of apparent motion in fact expected in different parts of the distance graph, under different conditions of stimulation. One of the regimes (coupling) is inconsistent with the proximity principle in space-time, but it is consistent with predictions from the uncertainty principle. It is therefore natural to consider the basic principle of measurement as a candidate foundational stone of perceptual theory, in place of the empirical statements about perceptual organization. This view is supported by further analysis of uncertainties, reviewed next.

4.2.4. Invariants of motion sensitivity

From the analysis of *measurement uncertainty* we learned that the visual system is expected to combine spatial and temporal distances differently in different stimuli. In the following I review how the expected characteristics of motion perception also depend on the *uncertainty of stimulation*. It turns out that these characteristics are expected to have some invariant properties.

Stimulus uncertainty: It is useful to distinguish between internal and external factors that control sensory measurements. Measurement uncertainty, discussed just above, is an internal factor because it depends on the properties of sensors rather than the sensed signals. The uncertainty associated with sensory stimulation—stimulus uncertainty—is an external factor.

Just as measurement uncertainty, stimulus uncertainty varies across the sensors. For example, the sensors in different parts of the distance graph in figure 14 receive different stimulation. The speed axis on top right of the figure indicates how stimulus speed varies across the sensors. Some of the speeds are more common in the environment than the other speeds. The more common a speed, the more confident (less uncertain) the visual system can be about the expected stimulation. A frugal visual system should not fail to take advantage of this fact. The system should avoid allocating sensors, or it should allocate less sensors, to the speeds that are rare or are not useful for behavior.

The prevalence of stimuli has been extensively used as a measure of stimulus uncertainty in the statistical line of research of perception, where perception is

viewed as statistical inference (section 2.2). In our present framework, too, stimulus uncertainty is expected to have important consequences for perception, but to understand the consequences fully we must study the joint effects of measurement and stimulus uncertainties.

Composite uncertainty: To summarize, we expect that the quality of visual measurements depends on several factors. One factor is the measurement uncertainty, explored using Gabor's uncertainty principle of measurement. The other factor is the uncertainty of stimulation. Here I overview how adding the uncertainty of stimulation to our analysis of uncertainty affects the expected distribution of the quality of measurements.

The argument consists of two steps. First, before I turn to joint effects of measurement and stimulus uncertainty, I review how the different sensors are suitable for measurement of different speeds, a key aspect of stimulation that concerns the perception of motion. I show that this consideration reveals an invariant feature of measurement uncertainty, yet before we take into account the statistics of speed in the stimulation. Second, I turn to the joint effects of measurement and stimulus uncertainty.

The following is an overview of the approach proposed by Gepshtein, Tyukin, and Kubovy (2007b). I will describe its key element in some detail, but the reader is advised to consult Gepshtein et al. (2007b) for a mathematical justification of the steps presented here.

1. Invariant of measurement uncertainty: Figure 14B contains the iso-uncertainty contours along with some lines of constant speed. To recall, each line of constant speed consists of all the (T, S) points where speed $v = S/T$ is constant. On every line of constant speed, there is a point where the uncertainty is the smallest for that speed.[40] Several such points are represented by the small filled circles. (At one of the circles the local minimal uncertainty is also the minimal uncertainty across the entire distance graph.)

Only a few points of minimal uncertainty are shown in figure 14B, for some select speeds. All such points, for all speeds, form a set represented in figure 15 by the black curve. Every points of this set is unique because here the system can measure the speed of motion, and also minimize the spatial and temporal uncertainties of measurement, in the best possible way. In other words, this is a set of optimal conditions for motion measurement. Yet this optimal set is an idealization. Every point of it is determined separately for every speed. In biological vision, measurements are performed by receptive fields, each spanning many speeds. In other words, receptive fields necessarily integrate (average) stimulation over a range of speeds (e.g., Perrone & Thiele, 2001). This fact has important consequences for the perception of motion. In particular, the shape of the optimal set in a system that makes measurements using receptive fields must be different from the shape in the idealized system. When the measurements are made using receptive fields, the optimal set has the shape of a hyperbola in the distance graph (gray curve in figure 15), rather than than an arbitrary shape represented by the black curve.
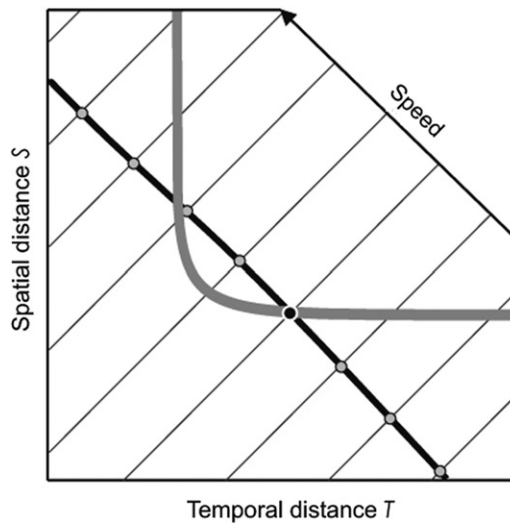
Figure 15 *Optimal sets for motion measurement.* The points of lowest measurement uncertainty for all speeds form a set represented by the black curve. (Figure 14B showed a few such point as small filled circles. Those points are replicated here; they all belong to the black curve.) This curve is an optimal set of motion measurement in an ideal system than can measure each speed in isolation from other speeds. As we take into account the basic fact that motion measurements necessarily average stimulation, the shape of that curve changes to a hyperbola (the gray curve).

The hyperbolic shape is invariant, i.e., does not depend on the parameters of the uncertainty function (Gepshtein et al., 2007b).[41]

A visual system with infinite resources could have measured every speed in isolation from other speeds. Then the optimal set of motion measurement could have any form, including the one represented in figure 15 by the black curve. Just as the choice of sensors for elementary measurements has been guided by the economic force of limited resources (figures 8–9) the prediction of an invariant shape of the optimal set (represented by the hyperbola in figure 15) reflects an economic constraint in real visual systems: the finite number of measuring devices.

2. Equivalence sets of composite uncertainty: Now we are prepared to study the combined effect of stimulus and measurement uncertainty. One way to conduct this study is by the method of coordinates:

● First, the properties of measurement uncertainty and stimulus uncertainty are studied separately. This is done by finding the distribution of each uncertainty across the entire stimulus space: the distance graph. A result of this procedure is two *parametric grids* of uncertainty. One grid parameterizes measurement uncertainty, and the other parameterizes stimulus uncertainty. Each grid spans the entire distance graph, i.e., it tells the amount of uncertainty for every stimulus.

- Second, the effects of two uncertainties are combined. The two grids are superimposed, yielding a coordinate system of uncertainty. Every point on the net has two coordinates: its measurement uncertainty and stimulus uncertainty. This approach allows one to find sets of points characterized by the same amount of composite uncertainty.

The two steps are illustrated in the Appendix. This method allows one to find all the points in the graph for which the distance from the center of coordinates is the same, as if one draws a circle whose center coincides with the center of the coordinate system. These points form an *equivalence set of composite uncertainty* (figure 17 in Appendix). In contrast to the sets of equivalent uncertainty in figure 14, now the equivalence sets take into account both measurement and stimulus uncertainty. The sets in the center of the plot are characterized by smaller composite uncertainty, and are more suitable for motion measurement than the sets in the periphery. Remarkably, the equivalence sets of composite uncertainty have the shapes similar to the shapes of isosensitivity contours we have encountered not once (figures 4, 7). Gepshtein et al. (2007b) proved that the "bent" shape of the theoretical equivalence contours is invariant, i.e., is independent of the specific parameters of the uncertainty function or the distribution of stimuli in the environment. The position of the entire structure in the distance graph may change, for example as the statistics of stimulation change (section 5.4). But the shape of theoretical equivalence contours must be conserved under such transformations.

Allocation of resources: The distribution of composite uncertainty captured by the equivalence contours is a prescription of how a frugal visual system ought to allocate its limited resources, had it been constrained only by measurement uncertainty and stimulus uncertainty. The similarity of these equivalence contours and the sensitivity contours observed in biological vision supports the view the human visual system allocates its resources for perception of motion according to the expected quality of measurements (Jurica, Gepshtein, Tyukin, Prokhorov, & van Leeuwen, 2007).

4.3. Summary

Earlier in this article we saw how an empirical connection was established between some basic results from the psychophysical tradition of Fechner and the phenomenological tradition of Brentano (section 3.2.2). Presently, we have seen how the particular form of this connection is explained from a theoretical perspective that is neither psychophysical nor phenomenological.

The present approach is *normative*. It allowed us to predict characteristics of motion sensitivity in an ideal visual system designed from first principles: the uncertainty principle of measurement and the fact that sensory systems have limited resources. We have already encountered normative approaches in the discussion of modern incarnations of the statistical line of Fechner (section 2.2.1), where the normative theories are used to predict performance of sensory systems constrained by statistics of stimulation. Here the statistical properties of stimulation are also

taken into account. But a key feature of the predicted sensitivity function is independent of stimulus statistics. Thus, the ''bent'' shape of the sensitivity function does not depend on a particular distribution of stimulation; it depends on the uncertainty principle of measurement and the fact that the sensors necessarily average stimulation.

The present study took a *system approach* to perception, by asking how the many parts of a sensory system jointly determine system performance. System approaches are well known in studies of senses (e.g., Regan, Shapley, & Spekreijse, 1985): researchers have long recognized that even simple sensory systems consist of many parts with distinctly different properties. Missing in previous analyzes, however, was the notion that sensory performance depends on the balance (or *equilibrium*) of many factors, an idea anticipated by Gestalt theory (section 3.1.3). Presently, prescriptions of best performance and prescriptions of equivalent performance are derived by studying the conditions of equilibrium between internal and external factors of sensory measurements: the uncertainty principle and the limited resources are the internal factors, and statistics of stimulation is an external factor.

5. Overview and Conclusions

Perceptual science has been bedeviled by several dichotomies, some more general than perception and some specific to it. The overarching dichotomy of *physical* and *mental* aspects of perception set the stage for this article because two important traditions in perceptual science—the psychophysical tradition of Fechner and the phenomenological tradition of Brentano—grew out of the effort to bridge this particular dichotomic gap. I will now summarize how the ideas reviewed above help to reconcile some differences and tensions between the two traditions. I will then turn to the narrower dichotomies, which have their own reasons and histories, but whose divisions run alongside the boundary separating the psychophysical and phenomenological traditions. I will conclude by considering the implications of this analysis for studies of the physical substrate—the *mechanism*—of perception.

5.1. Empirical and Theoretical Unity

I illustrated and contrasted the traditions of Fechner and Brentano by reviewing how they approach the same basic issue in vision science: the perception of motion. The psychophysical approach has been characteristically atomistic, resting on the premise that visual sensitivity to complex stimuli can be predicted from the sensitivities to elementary stimuli. A definitive result in this line of work is the spatiotemporal contrast sensitivity function: a comprehensive description of visual sensitivity to all the perceptible elementary stimuli (figure 4). The sensitivity function is a summary of a large corpus of experimental results. It has helped to discover the unity of results from different methods used to study motion perception within the psychophysical tradition.

In the phenomenological tradition, perception of motion was studied by Gestalt psychologists who viewed it, characteristically, though the lens of whole-to-part determination. Gestalt laws of perceptual grouping is an embodiment of this determination. In the stuides of motion, the laws were established by measuring how the spatial and temporal distances between parts of stimuli determined whether the parts were perceptually linked and thus seen as a single object in motion. Landmarks in this line of work belong to a progression from a law of apparent motion (Korte's law), to a lawful result inconsistent with the Korte's law, to a realization that the seemingly inconsistent results are cases of a more general pattern (section 3.2.2).

The unified result from the phenomenological studies turned out to agree with the unified result from the psychophysical studies. This agreement is a step toward a comprehensive account of perception, incorporating the psychophysical and phenomenological results. But why does the result have its particular shape? Neither the psychophysical nor the phenomenological tradition seems to be prepared to answer this question, because the explanatory efforts have been directed elsewhere. Both traditions sought to establish their basic results—what they deemed to be elementary aspects of perception—in order to explain more complex phenomena. In the psychophysical tradition, "elementary" is sensitivity to frequency components of the stimulus. In the phenomenological tradition, "elementary" is the one-factor interaction between disjoint stimulus parts, such as grouping by proximity in spatial dot lattices. But the basic results themselves remain unexplained, as does their connection to one another.

An effort to fill the gap is presented in section 4, using an approach that is neither statistical nor phenomenological. The approach is rooted in Gabor's theory of information. Using Gabor's notion of unit of information, we investigated the characteristics of motion perception expected from first principles: at the level of individual sensors (the elemental picture) and across the sensors (the systemic picture). It is the interplay of elemental and systemic levels of analysis that lends this approach its explanatory power.

5.2. Elemental and Systemic Pictures

The *elemental* picture is obtained from Gabor's uncertainty principle of measurement. The principle establishes a lawful relationship between two aspects of measurement by any sensor: the location and content of the measured signal. At the limit of sensor's precision, the two aspects of measurement trade off. At one extreme of the tradeoff, the sensors are specialized for measuring signal location; at the other extreme they are specialized for measuring signal content.

The *systemic* picture is obtained by studying how the quality of sensory measurements varies across the full range of sensors, between the extremes of specialization. On this range, there are the sensors that are optimally suitable for measuring motion and the sensors that are less suitable (suboptimal) for this task.

The suboptimal sensors belong to *equivalence classes* of motion measurement: groups of sensors equally suitable for the measurements.

The equivalence classes are theoretical counterparts of the equivalences in measured characteristics of motion perception: isosensitivity in psychophysics and equivalent apparent motion experimental phenomenology. The theoretical equivalence classes have invariant properties, which suspiciously similar to those of biological vision. The finding of similarity between the expected and measured properties of motion sensitivity owes to the systemic view we undertook on both the empirical and theoretical sides of this investigation. Critically, taking the systemic perspective allowed us to understand why the measured characteristics of motion have their particular shapes, and why the characteristics measured using different methods are consistent with one another.

5.3. Dichotomies of Perception

The simple relationship between the elemental and systemic pictures helps to see some old dichotomies of perceptual science in a new light. Consider, for example, the different stimuli preferred in the phenomenological and psychophysical studies. The phenomenological accounts of perception emphasize perceptual *structures*, such as the visual "objects" in which distinct parts are organized in a hierarchical manner. The phenomenal structures were in the focus of Gestalt studies of perception. To manipulate relations between the disjoint parts, Gestalt psychologists and their followers use stimuli that are discontinuous, fragmented, mosaic (e.g., figure 5).

The psychophysicist holds, in contrast, that natural stimulation is generally continuous, and the discrete structures emerge as a result of perception. Rather than put the cart in front of the horse, the psychophysicist prefers stimuli that are not fragmented. The assumption that the continuous stimulation is analyzed to its elementary frequency components (section 2.2.2) makes the psychophysicist prefer stimuli with simple frequency content, such as luminance gratings (figures 3–4), mixtures of gratings, or filtered textures.

The emphasis on naturalistic stimuli and on the physiological underpinnings of perception made the bottom-up and local processes the favored themes for the psychophysicist. The emphasis on perceptual (mental) phenomena made the top-down, global, and contextual processes the favorites of the experimental phenomenologist.

From the perspective of Gabor's information theory, however, some of the dichotomic tensions are dissolved by understanding the relation between properties of the individual information cells (associated with individual sensors) and the distribution of these properties across the entire space of sensor parameters:

- In the elemental picture, the local, bottom-up aspects of perception stand at the foreground: individual sensors are more or less useful for measuring the location or content of a stimulus.

• In the systemic picture, the global, top-down aspects come to the fore: the *system* is equipped with a full range of sensors, some of which are well suitable for the stimulus and task at hand.

A connection between the elemental and systemic perspectives is simple: it emerges naturally as we ask how the expected quality of measurement varies across the sensors (a normative question), and how the system can improve its performance by allocating more of its resources to the conditions that promise greater returns (an economic question).

5.4. Economic Norms and Sensory Systems

As mentioned, the approach from Gabor's information theory is *normative* because it predicts how an ideal sensory system ought to perform at the best of its ability, setting a benchmark of sensory performance. The approach is also *economic* because it is founded on the fact that sensory systems have limited resources such that they must be selective.

We have started off using a simplifying assumption that the resource allocation is system-wide. In other words, we undertook a *system approach* not only in that we explored the entire range of useful stimuli, but also in that we looked into how the entire system can draw from a single pool of resources. In effect, events taking place in different part of the system are not independent of one another. Such dependencies are expected to cause system-wide changes of sensitivity as usefulness of stimuli change, because of changes in the environment or changes in organism goals.

For example, consider the effect of changes in the prevalent features of the environment. Suppose I drive my car on a highway, and then I park in the rest area to enjoy the scenery. The prevalence of speeds in the visual environment changes: from the high speeds prevailing on the highway to low speeds prevailing when I park. From the perspective of optimal resource allocation, a change in prevalence of a stimuli should induce a reallocation of resources. Since the total amount of resources is limited, the reallocation is expected to bring about gains of performance for some stimuli, but also losses for others, the gains and losses forming a predictable pattern.

The changes of visual sensitivity expected in response to changes in the statistics of stimulus speed are illustrated in figure 16. Figure 16A contains sensitivity maps predicted for two visual environments, one dominated by high speeds and the other dominated by low speeds. Figure 16B is a map of sensitivity changes. The expected changes form well-defined foci of increased performance and large areas of decreased performance. These predictions are being tested in motion adaptation studies, using large-scale changes in the statistics of stimulation (Gepshtein, Lesmes, Tyukin, & Albright, 2009).

Figure 16 is an example of how the immediate history of stimulation can guide the reallocation of visual resources. The history indicates which stimuli are expected to be most useful in the prevalent environment. Similarly, the reallocation can be guided by the perceptual task, because different aspects of stimulation are useful for
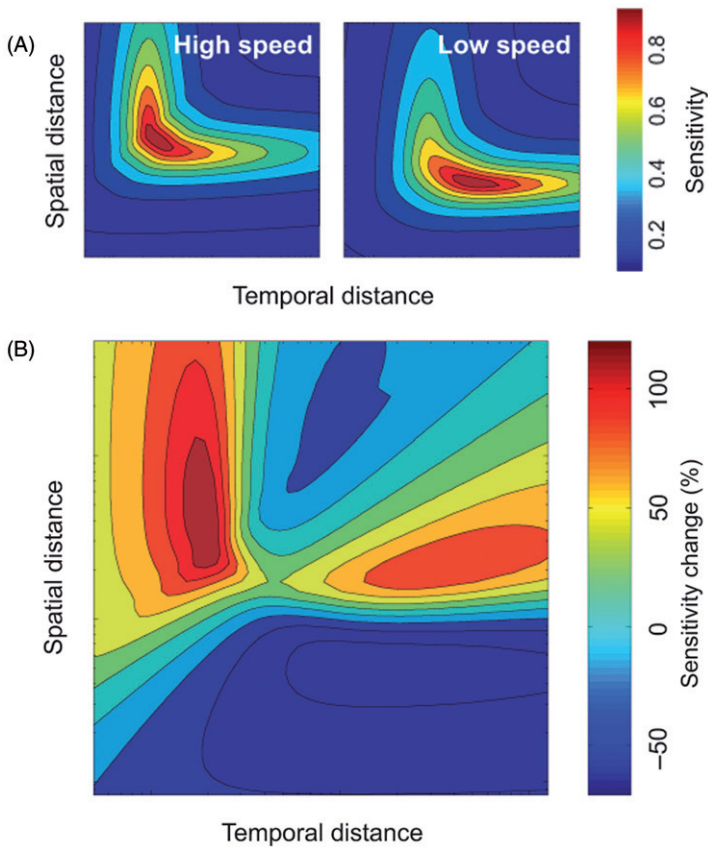
Figure 16 *Reallocation of visual resources.* (A) Sensitivity maps expected in two visual environments, with high and low prevailing speeds of stimulation. The colors represents normalized sensitivity; the warmer the color the higher the sensitivity. (B) A map of expected sensitivity changes. This map is derived from the sensitivities plotted in panel A. The changes are $100 \times H/L$, where H and L are the sensitivities in the high-speed and low-speed contexts of stimulation. Here the colors represents sensitivity changes: increased sensitivity by warm colors and decreased sensitivity by cool colors.

different tasks (e.g., Sperling & Dosher, 1986). The talk about selective allocation of resources is common in research of attention (Desimone & Duncan, 1995). The present framework of selective resource allocation is an explicit implementation of this line of thought: it contains elements of a unified normative theory of sensory adaptation and attention.

5.5. A Broader Outlook

The focus of this article has been on how the *psychology* of perception has contributed to understanding the connection between the physical and mental aspects of perception, and how an integrative theoretical approach, from Gabor's information

theory, helps to reconcile the differences between the psychophysical and phenomenological traditions in psychology. Yet another research tradition, from outside of psychology, has been important to understanding the connection between physical and mental phenomena in perception. It is the tradition that at the time of Fechner and Brentano was emerging as *physiological psychology* (Wundt, 1904) and which is known today as sensory neuroscience.

Many ideas reviewed above—central as they are to the psychophysical and phenomenological lines in perceptual psychology—have also been central to sensory neuroscience. In fact, much of modern sensory neuroscience can be divided to two branches: one kindred to the statistical line of Fechner and the other kindred to the phenomenological line of Brentano.

5.5.1. Mechanism: The statistical line

The statistical line has entered the mainstream of modern sensory neuroscience soon after the modern age began, when Sherrington (1906) introduced the concept of "receptive field." Within a few decades, new exacting methods of recording from single neurons were advanced (Adrian & Matthews, 1927; Hartline, 1940), opening the gate for wide-ranging investigations of neuronal receptive fields in the peripheral and central parts of sensory systems (Barlow, 1953; Hubel & Wiesel, 1962, 1968; Kuffler, 1953; Lettvin, Maturana, McCulloch, & Pitts, 1959). Since the activity of single cells is governed by chance fluctuations, advances in studies of receptive fields were paralleled by advances in understanding the statistics of neuronal activity: from stimulus registration (e.g., Hecht et al., 1942) to the processes that are thought to mediate the phenomenal aspects of perception (e.g., Britten, Shadlen, Newsome, & Movshon, 1992).

This line of research culminated in the idea that single neurons can reliably mediate perception, advanced as a bold hypothesis by Barlow (1972) and supported by later evidence (reviewed in Parker & Newsome, 1998). This development was surprising because one expected that the stochastic fluctuations of neuronal activity would render single cells unreliable computational devices. Yet, the statistical analysis of neuronal activity proved otherwise, using the methods developed within the line of Fechner: initiated in the probabilistic model of sensation by Fechner (figure 2) and matured in the form of the signal detection theory and ideal observer models (section 2.2).

In effect, the statistical line of sensory neuroscience is kindred to sensory psychophysics in two ways: in the emphasis on the statistical aspects of perception and in the elemental focus on individual sensory measurements.

5.5.2. Mechanism: The phenomenological line

The phenomenological line has two branches, each affiliated with an idea advanced by the Gestalt school in the phenomenological tradition of perceptual psychology. One idea is whole-to-part determination (contextual interactions) and the other is perceptual dynamics.

Contextual interactions: This branch emerged as a reaction to the ''neurobiological elementism'' (Albright & Stoner, 2002) of the statistical line in sensory neuroscience, much like the Gestalt movement emerged as a reaction to the elemental tendencies in perceptual psychology. From the elemental perspective, the neurons are described as filters tuned to particular classes of stimuli at particular locations in the visual field. But evidence mounted that neurons are more flexible and adaptable than that. Neuronal responses to stimuli in their ''classical'' receptive fields generally depend on stimuli presented elsewhere (e.g., Albright & Stoner, 2002; Allman, Miezin, & McGuinness, 1985; Gilbert, Ts'o, & Wiesel, 1991; Zhou, Friedman, & von der Heydt, 2000). In effect, the view of receptive field as an invariant characteristic of sensory neuron is being replaced by a more complex view, in which neuronal responses are described using multi-dimensional context-dependent characteristics called ''non-classical'' receptive fields. The many dimensions are the parameters of stimuli outside the ''classical'' receptive fields (Alexander & van Leeuwen, 2009; Swindale, 2004).

Dynamics: This branch has from the beginning dealt with large populations of cells, emphasizing the temporal aspects of their activity. The fact that temporal structure of neuronal activity is complex has been long recognized both in the statistical studies of perceptual mechanisms and in the studies concerned with contextual interactions. But it is in the work on dynamics of large neuronal populations where the temporal structure has been viewed as the key neuronal correlate of perception (e.g., Freeman, 1975, 1991, 1995; van Leeuwen, 2007; van Leeuwen, Steyvers, & Nooter, 1997). Much of this work has concentrated on the question of which aspects of the activity of large ensembles of neurons correspond to perceptual phenomena. The emerging answer is that the association of neuronal activity and perception is mediated through alternating episodes of synchronization and desynchronization of activity in large neuronal networks (e.g., Basar, 1980; Makeig et al., 2002; Nikolaev, Gepshtein, Gong, & van Leeuwen, 2010).

5.5.3. Mechanism: The information line

We saw in section 4 that Gabor's information theory entered perceptual science through the doors of sensory physiology, helping to understand properties of single sensory neurons. We then traced some larger-scale consequences of Gabor's information theory for visual perception, and compared the consequences to behavioral characteristics of the visual ability for perception of motion.

This approach inherited some features from the traditions of Fechner and Brentano:

● From the tradition of Fechner there remains the view that elementary perceptual processes are *measurements*, their properties best understood by the analysis of measurement uncertainties.

● From the line of Brentano, in particular from the Gestalt movement, there remains the emphasis on the holistic view of perception: the view that elemental aspects of perception are determined by properties of perceptual *systems*. For example,

sensitivities (gains) of individual sensors are determined in the whole-to-part fashion, by investigating how the quality of sensory measurements varies across the sensors tuned to the entire range of perceptible stimuli.

Results of this analysis have inspired a series of testable hypothesis about the large-scale properties of visual sensitivity and sensitivity changes (e.g., section 5.4).

Consequences of this approach extend to the enduring question about the relationship between individual neurons and perceptual phenomena. Our analysis is inconsistent with the view that the connection of physical and mental phenomena can be reduced to the correlation between the perceptual sensitivity to a stimulus (a mental process) and the sensitivities of single neurons to this stimulus (a physical process). Consider, for example, the effect of motion adaptation on visual sensitivity illustrated in figure 16. The expected changes of perceptual sensitivity to different stimuli are determined by the overall distribution of sensitivity in the system. That is, whether the perceptual sensitivity to a particular stimulus increases or decreases depends on where the stimulus falls on the global characteristic of sensitivity. In effect, for every single stimulus, one may observe a reliable correlation between the changes of sensitivity in the individual neurons and the changes of behavioral sensitivity. And yet, one cannot *explain* why the sensitivity has increased or decreased for that particular stimulus, as one cannot *predict* for which stimuli the sensitivity would increase or decrease, for as long as the study is confined to the elemental level of the sensory system and the distribution of neuronal sensitivities across the entire sensible range has not been taken into account.

Acknowledgments

Notes

[1]   Fechner called this aspect of his work the ''outer psychophysics,'' to contrast it to the ''inner psychophysics'' whose province was the relation of physiological and mental phenomena.

[2]   The quotation is Fechner's self-description of three years before he published the *Elemente* (Heidelberger, 2004, p. 138).

[3]   Part I of Link (1992) is a review of the evolution of psychophysics from Fechner to the Signal Detection Theory, using this convention. Stigler (1986) presents Fechner's work and the

work inspired by Fechner as a landmark in the history of statistics. Heidelberger (2004) reviews the run-up to Fechner's psychophysics.

[4] The validity of this differentiation, as well as the further steps in Fechner's derivation, received much attention and criticism. Dzhafarov and Colonius (1999) offer a review and a revision.

[5] Recall that Fechner worked before the notion of genuinely nondeterministic physical processes started to be established by Boltzmann and Maxwell in the 1970s.

[6] Fechner's conception of threshold soon provoked a criticism of the eminent Charles S. Peirce (Peirce & Jastrow, 1885). Briefly, the criticism amounted to saying that the concept of threshold was superfluous. Yet this criticism has been recognized as an incremental contribution to Fechner's conception. For example, Link offered: "In spite of Peirce's attack on the definition of the difference threshold, there is little difference between the positions of Peirce and Fechner. In fact, were it not for Fechner's wish to confirm Weber's Law, he too might have used the experimental procedure that we now attribute to Peirce and Jastrow" (1992, chapter 2, p. 23).

[7] Here I assume, for simplicity, that the errors are distributed according to the Gaussian distribution. As mentioned, Fechner assumed the Gaussian distribution of errors. In Fechner's model, the just noticeable differences were associated with a measure of variability called "probable error," introduced by the German mathematician and astronomer Frederick W. Bessel in 1818. The "probable error played the role of the standard deviation in much of the nineteenth-century work on the theory of errors.... [It] was that multiple of the standard deviation that would correspond to the distance from the mean to a quartile if the distribution was in fact normal: Normally distributed errors as likely to be within one probable error of the mean as not" (Stigler, 1986, p. 230).

[8] A simple case of cue integration has errors of the component measurements distributed normally and independently of one another. Oruç, Maloney, and Landy (2003) discuss a more general case, where weighting of cues is similar to (but is slightly more complex than in) equation 7.

[9] But see Domini and Caudek (2009) and MacKenzie, Murray, and Wilcox (2008) for a discussion of how an orthodox Fechnerian theory of cue combination may replace the cue combination formalism of equations (6)–(8).

[10] It is *speed* rather than *velocity* because velocity is a vector quantity defined by direction and speed of motion, whereas the results of Kelly concern the speed of motion rather than its direction. The speed of motion for every point on the frequency plane in figure 4 is the ratio of temporal to spatial frequency of modulation. Also, every point on the frequency plane can be thought of as a stimulus (a drifting grating, also called a "condition of stimulation") to which some motion-sensitive neuron is tuned.

[11] Brentano rediscovered and generalized ("revaluated," McDonnell [2006]) the concept of intentionality: a connection of physical and mental phenomena taken up from Aristotle and the Scholastics (also see endnote 15).

[12] To Brentano, the "objects of sensory experience" are not the objects in the world (which Brentano calls "things"). An "object of sensory experience" is the "content" of mental phenomenon, the content "presented" to the observer.

[13] "In modern terminology the word 'soul' refers to the substantial bearer of presentations and other activities which are based upon presentations and which, like presentations, are only perceivable through inner perception. Thus we usually call soul the substance which has sensations such as fantasy images, acts of memory, acts of hope or fear, desire or aversion" (Brentano, 1874, p. 5). Brentano's "presentation" is explained below (*Act and content*).

[14] Brentano distinguished three classes of mental activities (or acts): presentations, judgements, and emotions. The threefold classification parallels that of Descartes's *Meditations*: ideas (*ideae*), judgements (*judicia*), and emotions (*voluntates sive affectus*) (Brentano, 1902, pp. 13–14).

[15]   It is sometimes said, incorrectly, that Brentano's intentionality is a mental reference to ''things'' in the physical (''outside'') world. In fact, Brentano's intentional reference is more general; it can be directed also to the imaginary (fictitious) and other nonexistent objects. Chapter 2 in Smith (1995) is a lucid discussion of this nuance of Brentano's conception of intentionality and of how it reflects Brentano's non-orthodox reading of the foundations of Western philosophy.

[16]   In particular, Brentano criticized David Hume whose descriptions of the connected elements as ''bundles'' Brentano found inaccurate.

[17]   Stanley S. Stevens (1906–1973), a champion of the ''power law,'' recognized Brentano's priority (Stevens, 1961, p. 3).

[18]   But von Ehrenfels' view on the connections of ''elements of consciousness'' was rejected by Brentano, who viewed it as little different from that of Hume (Boudewijnse, 1999).

[19]   In fact, von Ehrenfels begins his article from a review of Mach's *Analysis of Sensations* (1886; note the ''analysis''). A principled difference between the positions of Mach and von Ehrenfels, significant for understanding of how Gestalt movement rose to prominence, is in the direction of part-whole determination. Whereas for Mach the determination operated exclusively from parts to wholes, for von Ehrenfels the determination operated both ways: from parts to wholes and from wholes to parts.

[20]   In the role of director, Stumpf was succeeded by the Gestaltist Wolfgang Köhler who headed the Institute till 1935.

[21]   In 1883 Husserl earned a PhD in mathematics from the University of Vienna, where his teachers included Leopold Kronecker and Carl Weierstrass, after which he studied philosophy with Brentano (1884–1886) and wrote his habilitation dissertation (On the Concept of Number, 1887) under Carl Stumpf (then at Halle).

[22]   Smith's *Austrian Philosophy* (1995) is an illuminating review of the many threads in the phenomenological tradition from Brentano to modernity. See pp. 251–253 for a discussion of Husserl vis-á-vis von Ehrenfels.

[23]   In this development Meinong was strongly influenced by another student of Brentano, Polish philosopher and logician Kazimir (Kazimierz) Twardowski (1866–1938), also renown for his contributions to Brentano's theory of intentionality.

[24]   The debate between Graz and Berlin anticipated a similar debate about direct perception, more than half a century later, between supporters of the computational (Marr, 1982; Ullman, 1980) and ecological (Gibson, 1979) theories of vision. J. J. Gibson, a champion of the ecological approach, was strongly influenced by both Berlin (through Koffka) and Graz (through Heider) branches of Gestalt movement; his ''ecological physics'' can be read as an exercise in phenomenology of perception (Epstein & Hatfield, 1994).

[25]   Translation by Ash, 1998, p. 93.

[26]   See Heft (2001) for a review of Heider's contribution to the Gestalt movement and ecological psychology. Heider used his approach to perception in studies of inter-personal relations, toward his acclaimed ''attribution theory'' (Heider, 1958).

[27]   Titchener (1921) is a clear discussion of the relationship of the empirical and experimental trends in psychology, and of the role of Brentano in psychology.

[28]   This experience was also called ϕ-phenomenon to contrast it with other experiences of motion labeled by other Greek letters. Steinman, Pizlo, and Pizlo (2000) review this issue with particular attention to the ϕ-phenomenon.

[29]   Indeed, an earnest effort was made to rewrite the entire corpus of psychology from the perspective of whole-to-part determination (Koffka, 1935/1963; Köhler, 1947, 1969).

[30]   The physiological aspect of the dynamics in further discussed in section 5.5.

[31]   In particular, Gepshtein, Tyukin, and Kubovy (2007a) pointed out that ''a generalized (Minkowski) notion of proximity does not apply to the perceptual combination of space

and time the way it applies to the combination of spatial dimensions in perceptual organization of static scenes" (p. 57).

[32]   The temporal representation concerns when a signal occurs and the spectral, or frequency, representation concerns what the signal is: its "content".

[33]   Hartley advanced the view that information can be measured and also proposed a logarithmic measure of information that became the cornerstone of Shannon's influential theory of communication.

[34]   In fact, measuring the frequency content of a signal is equivalent to localizing the signal on the frequency dimension.

[35]   In general the two images are different. Here I use the identical patterns for simplicity.

[36]   Note that measurements of frequency content can be improved by using multiple overlapping templates. For example, a common model of binocular matching is binocular cross-correlation that uses multiple adjacent templates to compute binocular disparity (Banks et al., 2004). The advantage of multiple templates is constrained by the economic fact that visual systems have limited number of sensors, thus alleviating rather than overcoming the limitation of the uncertainty principle.

[37]   Distance graphs are introduced in figure 5. Information diagrams are introduced in figure 8.

[38]   The distance graph representing stimuli (as in figures 5–7) and the distance graph representing sensors (as in figure 12) are generally different. Here I do not elaborate on this distinction, which amounts to the assumption that the correspondence of sensors and stimuli is simple, such as: "the sensors tuned to large spatial distances are selective for the stimuli that contain the correspondingly large spatial distances."

[39]   Imagine the within-dimensional uncertainty functions unfolded over the distance graph: The spatial function would form a trough along the axis of temporal distance, its minimum falling along conditions 2, 5, 8. The temporal function would form a trough along the axis of spatial distance, its minimum falling along conditions 4, 5, 6.

[40]   Imagine a section of the uncertainty function over a constant-speed line. The section will contain a one-dimension function, similar to the functions plotted on the side panels of figure 13. The function will have a unique minimum.

[41]   As the parameters of uncertainty function change, the position of this hyperbolic curve—but not its shape—may change.

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Appendix

Here I review why some spatiotemporal stimuli are expected to be perceived equally well, from the perspective developed in section 4. We have observed, using figure 15, that stimulus averaging by visual receptive fields has an invariant effect on the shape of the the optimal set of motion measurement: the optimal set is "bent" from an arbitrary shape (the black curve in figure 15) to the invariantly hyperbolic shape (the gray curve). The bending of the optimal set is accompanied by the bending of the entire set of uncertainty contours: from a family of roughly circular contour in figure 14 to a family of bent contours similar to the measured contours in figure 7. The mechanism of "bending" is illustrated in figure 17.

Grid of measurement uncertainty: The black curve in panel A represents the optimal condition of speed measurement across all speeds. On this curve, all the components of measurement uncertainty are perfectly balanced. Away from the black curve, measurement uncertainties are imbalanced to some known degree. The gray curves connect the points of the *same imbalance* across all speeds. The farther a gray curve is from the black curve the greater the imbalance, the higher the uncertainty of measurement. Together, the curves form a parametric grid of measurement uncertainty. The black curve is the axis of this grid.
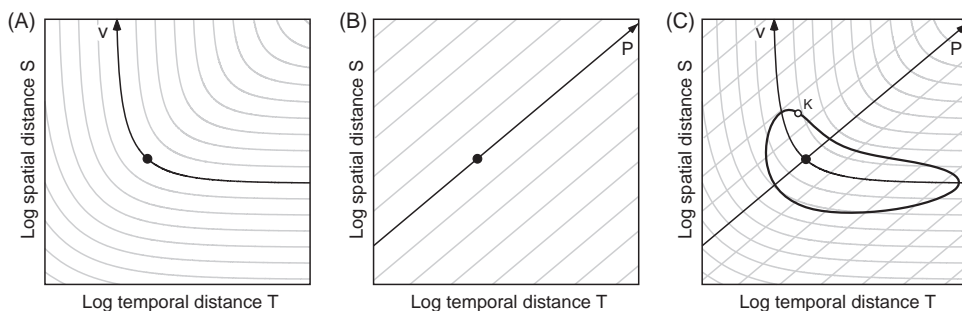

Figure 17 *Coordinates of composite uncertainty.* (A) A parametric grid of measurement uncertainty. (B) A parametric grid of stimulus uncertainty. (C) The two grids from panels A and B are superimposed forming a coordinate system. A circle in the system is represented by the curved contour. It is an equivalence class of motion measurement. Its shape is similar to the shape of isosensitivity contours of human vision (Figure 7).

Grid of stimulus uncertainty: The distance graph is also factorized by the uncertainty of stimulation, illustrated in panel B. Recall that the different speeds are represented by parallel lines in the distance graph: low speeds in the bottom right corner and high speeds in the top left corner. One of the speeds is most common in the stimulation: it is represented by the black line. The father the other speed lines from the black line, the higher the uncertainty that the speeds occur in stimulation. Together, these lines form a parametric grid of speed uncertainty, its axis represented by the black line.

Coordinate system of uncertainty: Superimposing the two grids creates a parametric system of coordinates shown in panel C. The system is curvilinear because the measurement uncertainty grid is curved. A circle in this system of coordinate represents an equivalence class of composite uncertainty: a set of conditions in which both measurement and stimulus uncertainties are imbalanced to the same degree. One such circle is drawn in panel C as a red contour. Many such contours (circles of different radii) form a structure similar to the family of iso-sensitivity contours in figure 7.