Why a good curve is not hard to find

In studying the history of ideas, it is interesting to see how some concepts fall out of favour, then reappear considerably strengthened with renewed validity from a fresh perspective. The insights of Gestalt psychology into visual perception are following exactly such a trajectory; after years of neglect, these insights are finding hard support in an unlikely place, in the details of the anatomy and physiology of the primary visual cortex (V1).

In the early years of this century, concepts introduced by the school of Gestalt psychologists greatly influenced emerging ideas about our perception of complex entities—of music, of combinations of colours, and, particularly, of complex shapes, line drawings and figures. These concepts hinged around the idea of a "Gestalt", a perceptual "wholeness" of an object, that was somehow integral to its appearing as a single entity. This wholeness could take many different forms (Wertheimer 1938). The visual elements that made up a visual object or pattern could get bound together perceptually due to proximity. In figure 1a, for example, the pairs of neighbouring dots appear to group together and we automatically see the figure as a string of such pairs. Perceptual grouping could arise from similarity: in figure 1b, the dots of similar size automatically group with each other. The grouping could result from what Gestalt theorists termed "good continuation": in figure 1c we automatically see a sinusoid intersecting a square wave. In all these examples, our perception of the particular groupings seems effortless. It takes some effort, in fact to see the elements grouped in some other way—to see figure 1a as a string of dots grouped into more distant pairs, or figure 1c as a series of square corners and wavy arcs, or a string of boxes each with one wavy side.

The problem with Gestalt explanations was that it was hard to formulate Gestaltness in analytical terms. You could tell when an object had good Gestalt but it was hard to think of increasing or decreasing the Gestalt or degree of wholeness in a manner open to experimental testing. This made the concept of Gestalt uncomfortably mystical. Moreover, with the technology of recording the responses of single cortical neurons, starting in the '50's, physiologists began to get a wealth of information at the other end of the scale of size—on how the brain dealt with the smallest elements of a percept. The study of single-cell responses in the visual pathway, from the retina through the cortex, allowed one to see how complex scenes were broken down to their simplest elements, to short line segments, edges, contrasts. The focus of research shifted to understanding how the brain built up a percept hierarchically, starting with these minimal elements (Hubel and Wiesel 1962). For all of these reasons, Gestalt explanations largely fell out of favour.

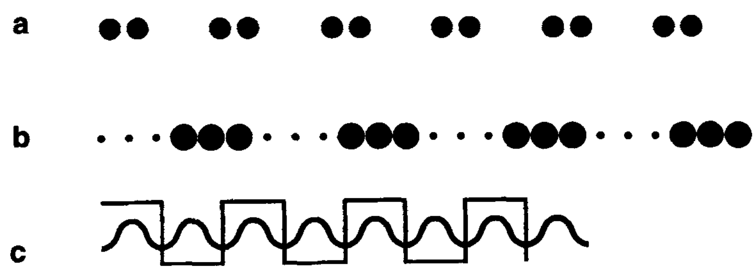

Figure 1. Elements of an image group together by proximity (**a**), similarity (**b**) or through "good continuation" (**c**).

Starting with the late '80's, however, it became clear that the brain did not simply build up percepts in a "bottom-up" manner from the smallest visual elements. In many cases we appeared to first see an entire object in three-dimensional form before fully registering the smaller visual elements that made up the edges or details of the object (Nakayama and Shimojo 1990). One particular Gestalt attribute that got renewed attention and credibility was the concept of good continuation. The difference this time was that tests were designed using psychophysical methods to quantify and analyse the concept of good continuation. In a series of experiments, David Field and his associates used patterns made up of small elongated oblongs to quantify the attributes that made particular elements of visual scenes link up preferentially (Field *et al* 1993). In a typical experiment, they would first show subjects a target object, a "snake" made up of the oblong elements (figure 2a). Then, they would briefly show a visually cluttered image (figure 2b) which sometimes did and at other times did not contain the target snake. Subjects had to say whether or not they saw the snake amidst the clutter. Subjects got worse at picking out the snake from the clutter, in a smooth and measurable manner, as the separation, relative angle, lateral displacement or local curvature between the elements of the snake was increased (figure 2c, d). Field *et al* (1993) proposed that elements of a curve had an "association field" which linked the elements into a complete curve, perceptually, when they were close to each other, with relatively low curvature, no lateral displacement and no relative jitter between the angles made by the line elements (left side of figure 2e). This "association field" got quantifiably weaker as these conditions were progressively violated (right side of figure 2e).

By this time, physiologists had also identified anatomical structures in primary visual cortex (V1) that seemed well suited to judge good continuation. In their initial work, Hubel and Wiesel (1962) showed that individual neurons in V1 responded specifically to a well-defined receptive field (RF), that is, to a visual stimulus in a tightly defined area of visual space. Moreover, the stimulus had to have specific properties—it had to be a line element, oriented in a particular direction, of a particular colour, etc. These RF properties mapped smoothly over the surface of the cortex. Later, Gilbert and Wiesel (see Gilbert 1992 for a review) showed that neurons in V1 sent out long axons that linked them to other neurons in V1, up to many mm away. These links were very specific: neurons responding to line elements of one particular orientation in one region of space were specifically linked to other neurons responding to line elements of the SAME orientation but in different regions of space. The effect of having such a network was as follows. Each neuron in V1 still responded only when an optimally oriented line element fell within its RF. When different neurons in the large network had line elements in their individual RFs, however, they facilitated or inhibited each other's responses in a well-defined and predictable manner depending on the relative layout of the stimulus elements in space (Kapadia *et al* 1995).

The response properties of such a network fit in very well with the requirements for judging good continuation. Through parallel studies in humans and monkeys Kapadia *et al* (1995) showed that the physiological responses of neurons in monkey V1 to complex stimuli reflected precisely our perceptions of the same stimuli. The experimental question they asked was, how is our ability

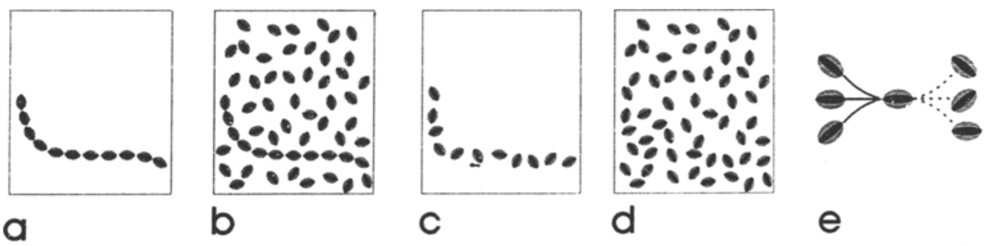

Figure 2. (**a, b**) Easy "snake"; (**c, d**) difficult "snake"; (**e**) pattern of the association field around a visual element, strong on the left and weak on the right.

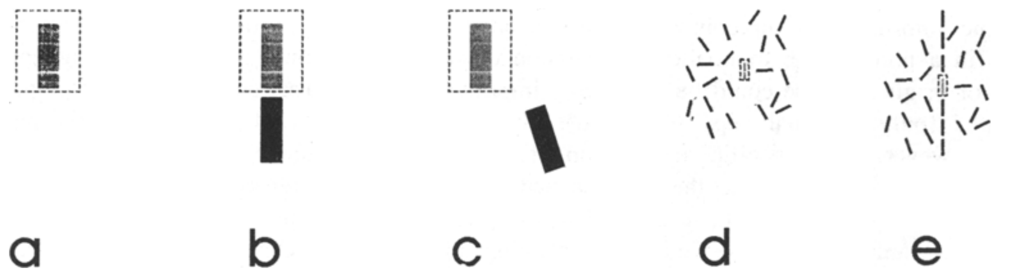

Figure 3. (**a**) Single line element; (**b**) good flank; (**c**) poor flank; (**d**) element in noisy background; (**e**) added collinear flanks.

to detect dim lines affected by putting other patterns in the background? In psychophysical experiments they showed human subjects dim line elements in brief flashes (figure 3a); they varied the brightness of the line elements and measured the brightness value (threshold) at which subjects started just being able to detect the stimulus. When they showed subjects the dim target line along with a bright flanking line (figure 3b), the threshold of detection of the dim target line improved by 40%, i.e., the subjects were able to detect lines that were 40% dimmer than the dimmest single line stimulus. This improvement in the detection threshold varied in a systematic way with the position of the flanking line; a nearby collinear flank gave the strongest improvement in the detection threshold. As the flank was moved further away, or to a different angle, or off to a side, the detection threshold returned, progressively, to the threshold for the single line alone (figure 3c). The experimenters then recorded from single neurons in monkey V1 while the monkeys were shown identical stimuli: either a single line element in the neuron's RF, or the element in the RF along with another flanking element at various relative distances and positions. The response of the neuron to a single line was enhanced up to 5-fold by adding a nearby flanking line (figure 3b). This facilitation was reduced as the flanking line was moved away, to a different angle, or off to a side. The response to a single line was also suppressed by having a noisy background (figure 3d); but the suppression could be overcome by adding collinear flanks (figure 3e). These results make a strong case that facilitation through long-range horizontal connections in V1 plays a significant role in our automatic perception of a "good" contour.

So the apparently mystical and intrinsic Gestalt of good continuation that made particular contours appear more whole could actually have a direct physiological base—in the anatomy and physiology of long-range connections linking neurons in primary visual cortex.

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