THREE Tartini's Devil

PERIPHERAL MECHANISMS THAT UNDERLIE SENSORY ILLUSIONS

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Of the demon myths that surround violinists, the story of Tartini is perhaps the oldest. Renowned for his virtuosity, Tartini is said to have received his inspiration directly from the devil. Unlike that of his successor Paganini, the tale of Tartini's demonic muse was almost certainly bolstered by his ability to produce tones apparently unrelated to the notes he played on his violin. These were not simple overtones, harmonics of a fundamental note, but rather were completely different notes whose temporal progression could differ from that of the notes being played—sometimes rising in pitch when the notes being played were falling, or falling when the notes being played were rising. Tartini had discovered the concept of difference tones, which he called "third sounds" and described in his work *Trattato di musica secondo la vera scienza dell'armonia*.[1] Without recognizing it, he had stumbled onto a fundamental property of sensory systems.

The scientific impact of Tartini's discovery of difference tones has grown over the last twenty years. How we, or more specifically our nervous systems, represent "illusory features" has been debated for decades, but modern studies that explain the perception of Tartini's difference tones might also explain how other sensory systems create illusory perceptions. The fundamental questions come down to: Where in the nervous system are illusory features first encoded, and to what extent do these illusory features affect our perception of the sensory world? Neurophysiological and psychophysical studies have begun to answer these questions, and in the process they argue that at least some illusions are first constructed by sensory receptors, not in the brain.

Colloquially, "sensory illusions" are misinterpretations of the real world—tricks of sensation produced by our sensory systems that mislead us into believing in something that does not exist. It is important to distinguish these illusions from hallucinations or dreams, which are constructed from inner representations without reference to a current stimulus in the world around us. A sensory illusion requires a physical stimulus. The perception of that stimulus, however, is not a faithful representation of what actually exists. We can look at a static black-and-white picture, for instance, and perceive colors or movement. There is a physical stimulus in the surrounding world, but our perception of that stimulus is different from the reality.

In many ways, the perception of illusions is at the heart of neuroaesthetics. If our perceptions were faithful and unbiased readouts of the physical world, there would be no room for interpretation or nuance. Instead, biological systems are constructed in such a way that information is biased to emphasize what is important for survival, reproduction, and—after eons of evolution—neurochemical satiety. Thus the key to understanding sensory perception, and ultimately neuroaesthetics, is not to catalog the different ways in which sensory processing is faithful to the external world, but rather to identify where it imposes its biases and gives rise to illusory perceptions.

Constructing meaningful illusory features from the sensory environment is not a trivial task. Any sort of fault in neural processing can degrade or disrupt a sensory signal, producing the perception of illusory features; however, these would not be meaningful or helpful for survival. The biological processes that produce meaningful illusory features must therefore be precise, despite being distortions of the real world. Because of this precision and the salience of the illusory features we detect, it is generally thought that the neural representation of illusions originates in the cerebral cortex. Indeed, one explanation for why there are so many different areas of cortex subserving a single sensory system is that this allows for multiple stages of "nonlinear" processing, producing increasingly more complex types of illusory features along the way. Emerging evidence tells a more surprising story, however, and the notion that the representation of illusory features may begin within the sensory periphery, like the eyes and ears, is starting to take hold.

In this chapter we review some of the evidence in support of the argument that important illusory features are first encoded in the periphery, specifically in the end-organs of the auditory and visual systems. To many neurobiologists who study the cerebral cortex, the idea that complex sensory processing has already happened before the circuitry of the cortex is engaged seems im-

probable. Nonetheless, evidence from a variety of sources—fruit flies, fish, bullfrogs, and even guinea pigs and cats—suggests that this is precisely the case.

Auditory Illusions and the Bullfrog Ear

Sensory illusions are a part of our everyday experience, although this is hardly ever recognized because of how thoroughly ingrained they are in perception. For instance, it is surprising that an auditory illusion lies at the heart of our ability to tune stringed instruments. One way to tune a string is to compare its tone with a reference tone, but most of us would have very poorly tuned instruments if we simply tried to match two tones according to the similarity of their frequencies. For the average person, the ability to match two frequencies is not very good; a tone can typically be matched to within 10 percent of the reference frequency.[2] Yet despite such poor frequency matching ability, we are able to tune stringed instruments almost perfectly.

What accounts for our ability to tune a string? The answer is in our ability to detect Tartini's third sounds or "beat frequencies." Anyone who has tuned a stringed instrument or a melodic percussion instrument is familiar with a beat frequency: it is a perceived sound whose frequency is equal to the magnitude of the difference between a reference tone and the test tone produced on the instrument being tuned ($F_{beat} = |F_{reference} - F_{test}|$; see figure 3.1). As the frequencies of the reference tone and the tone produced by the instrument being tuned get closer together, the frequency of the beat gets smaller until it finally disappears at the point where the frequencies of the two tones match perfectly. Because we can perceive the beat frequency, our ability to tune an instrument is completely independent of our ability to match two sound frequencies.

Why can we detect a beat frequency? The easy answer would be that it is a sound in the range of frequencies that we can hear, but that would be wrong. In fact, the beat is not a physical sound at all. If it were, air would be compressed and rarefied at the beat frequency, but pressure measurements do not reveal any compression-rarefaction waves at that frequency. Moreover, people lack hearing receptors that are sensitive to sounds below 20 Hz, yet they readily perceive beat frequencies near 0 Hz.[3] The beat is detected

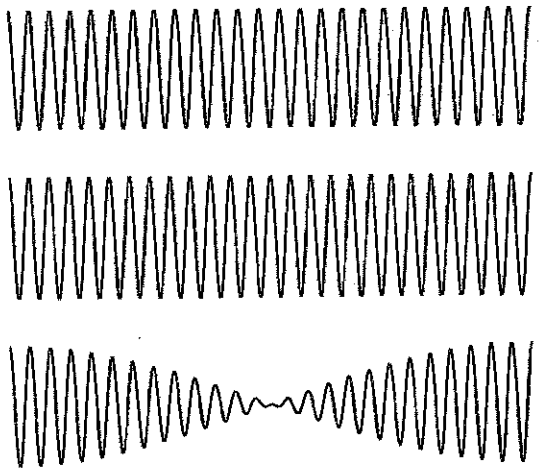


FIGURE 3.1. Auditory beats. The sine wave in the top panel represents the time course of compression and rarefaction of air pressure caused by a single pure tone. The second panel represents the pressure wave form of another pure tone with a slightly different frequency. The bottom panel is the pressure waveform produced by playing both tones together; constructive and destructive interference produces a modulation of the overall intensity at a beat frequency defined by the difference in the two pure tone frequencies.

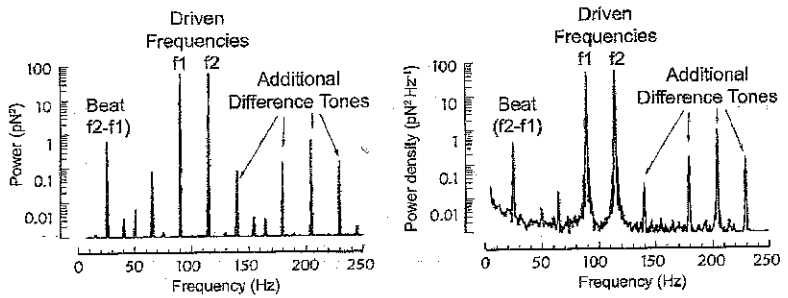


FIGURE 3.2. Hair cell nonlinearity generates difference tones. The left panel shows the power (amplitude) of vibrations at different frequencies, predicted from a model of hair bundle mechanics. In the simulation, the hair bundle was driven by two pure tones, one at frequency f1 and the other at f2. The hair bundle was predicted to vibrate not only at f1 and f2, but also at a series of other frequencies including f2 – f1, 2xf2 – f1, 2xf1 – f2, and so on. The right panel shows measurements of actual hair bundle motion when a physical stimulus composed of two frequencies (f1 and f2) was delivered to an isolated bullfrog hair cell. The actual motion matched that predicted by the model, and recapitulated Tartini's difference tones in a dish. Figure adapted and reprinted by permission from Macmillan Publishers Ltd.: F. Jaramillo, V. S. Markin, and A. J. Hudspeth, "Auditory Illusions and the Single Hair Cell, *Nature* 364, no. 6437 (August 5, 1993): 527–29, ref. 6.

because the sound sensors in the ear are imperfect transducers, introducing distortions into the signal and passing those distortions on to the central nervous system as though they were part of the natural sound.

The mechanism by which auditory beats are first constructed remained unknown until physiologists were able to record the movements of the inner ear in a living animal. If the inner ear responded faithfully to two simultaneously presented pure tones, the resulting vibrations in the inner ear would occur only at those two frequencies. Instead, a variety of frequencies were observed in the vibrations of the inner ear structures,[4] indicating that beat frequencies are introduced by biological tissue at the very first stage of sound processing. If the output of the inner ear were evaluated using the same criteria as those used for a sound-system speaker, it would be rejected because of its poor sound quality.

The source of these extra frequencies was discovered in a collaboration involving an electrophysiologist, a theoretical electrochemist, and a biophysicist.[5] The group knew from previous experiments that the sound-detecting cells of the ear, the hair cells, had mechanical components that did not follow simple rules of oscillatory motion.[6] They had constructed a theoretical model of the motion of the hair cell's hair bundle (the part of the cell that moves in response to sound) and wondered how the model hair bundle would respond if simultaneously driven by two different frequencies. The result of their simulations was surprising: when driven by two pure tones, the hair bundle oscillated not only at those two frequencies (f_1 and f_2), but also at the beat frequency ($|f_1 - f_2|$). Even more surprisingly, there was a large group of additional frequencies in the predicted motion of the bundle, corresponding to a series of difference tones like $2xf_1 - f_2$, $2xf_2 - f_1$, and so on. In a rare example of a closed circle in neuroscience, measurement of the motion of real hair bundles driven by pairs of frequencies recapitulated the model's predictions almost exactly (figure 3.2)—suggesting that Tartini's difference tones, including the beat used to tune stringed instruments, are created by the transduction apparatus of the inner ear.

The key to understanding the significance of this experiment is that it was done in a dish, with individual, isolated hair cells. There was no brain, no neurons, no feedback to modify mechanical movements—just the cells that transduce sound into electrical signals in the ear. Despite the relative simplicity of this biological system, Tartini's difference tones appeared.

Second-Order Processes in Vision

The peripheral origin of difference tones in the auditory system may be a prototype for how other sensory systems introduce illusory features. Visual illusions—in particular, visual beats—can be studied in much the same way as auditory beats. Despite the added dimensions required for vision (auditory stimuli presented to an ear are one-dimensional, varying only in time, while visual stimuli presented to an eye vary in time and two dimensions of space), there is a simple visual analog of auditory beats. Whereas an auditory beat is constructed by simultaneously presenting multiple pure (sinusoidal) tones, visual beats are constructed by simultaneously presenting multiple sinusoidal gratings, the higher-dimensional spatiotemporal analog of pure tones. When visual beats are studied in the laboratory, three-component beats (those generated by adding together three sinusoidal gratings) are typically presented (figure 3.3).

When a stimulus like the one to the right of figure 3.3 is shown, a visual beat (labeled "beat") with a distinct orientation and a lower spatial frequency (more broadly spaced bars) than those of any of its three sinusoidal components is perceived. In the vision sciences literature, three-component beats and other closely related stimuli are often referred to as "second-order" features. Like auditory beats, these features are not part of the physical stimulus; they are illusions. In the visual beat shown in figure 3.3, for example, there are no actual image components that are horizontally oriented or of a low spatial frequency, but a pattern with these properties is perceived nonetheless. We perceive this second-order feature because the visual system, like the auditory system, distorts sensory input in a specific and precise way.

Such a precise distortion system developed during evolution presumably because it conferred a competitive advantage. This evolutionary advantage, whatever it may be, must be substantial because many species even distantly removed from *Homo sapiens* detect second-order features. For instance, shortly after hatching, zebrafish larvae display a reflexive behavior in which

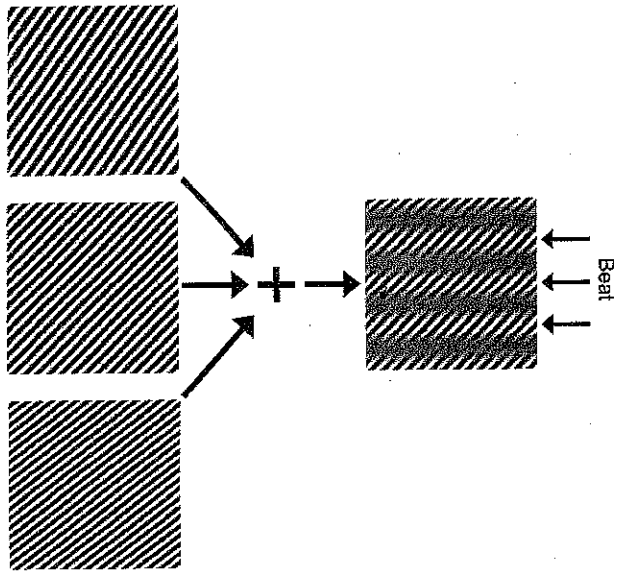


FIGURE 3.3. Constructing a visual beat. A visual analog of the auditory beat seen in figure 3.1 can be constructed by adding together multiple sinusoidal gratings. Three gratings, each with a unique combination of orientation (tilt of the bright and dark bars) and spatial frequency (spacing of the bars), are shown on the left. When the three gratings are added together, constructive and destructive interference produces the visual beat shown on the right.

they follow alongside any low-spatial-frequency object that is moving. They also display this behavior when high spatial frequencies combine to create a low-frequency beat; in other words, they track the beat as if it were actually present in the stimulus.[7] In an analogous study, the sensitivity of fruit flies to second-order visual features was examined. Like zebrafish larvae, fruit flies will follow a drifting bar. If that bar is replaced with a second-order stimulus, the flies track the motion of the second-order pattern.[8] Whether the mechanisms for constructing second-order features are evolutionarily old or have developed independently multiple times, the fact that they are found in a variety of taxa suggests that second-order feature perception is beneficial, perhaps fundamental, to visual perception.

Equally important, these studies indicate that the cerebral cortex is not a necessary processing stage for the detection of second-order features. Neither fruit flies nor zebrafish larvae have a cerebral cortex, so the mechanisms they use do not depend on cortex. The issue is not so clear-cut in mammals in which both a peripheral mechanism (in the eye) and a central mechanism (in the cerebral cortex) have been proposed for the construction of second-order features.[9] Early neurophysiological work in nonhuman mammals suggested that sensitivity to visual beats arises relatively late in visual processing, in secondary visual cortical areas.[10] More recent functional magnetic resonance imaging of brain activity in humans supported this hypothesis.[11]

A parallel set of studies, however, supports a peripheral mechanism for the construction of second-order visual features. A class of retinal ganglion cells and the cells to which they project in the lateral geniculate nucleus (the thalamic nucleus of the visual system that relays information from the retina to the cerebral cortex) have been found to respond to visual beats.[12] The authors of these studies suggest that visual beats are first represented subcortically. More significantly, the responses of these cells, called Y-cells, can account for many properties of cortical responses to the same stimuli, thus calling into question the idea that the cortical representation of beats originates in cortex.[13]

While scientists have a tendency to choose a single mechanism to explain a phenomenon, it is important to note that the existence of peripheral and central mechanisms for constructing second-order features are not mutually exclusive possibilities. Actually, both play a role in the detection of beats. In the auditory system, binaural beats can be perceived when one pure tone is presented to one ear and a different pure tone is presented to the other.[14] Likewise, in the visual system, binocular beats can be perceived when different patterns are presented separately to the two eyes.[15] The representation of binaural and binocular beats necessarily requires central processing at a location that receives input from either both ears or both eyes. This means that beats are not introduced only at a single neural site, but rather at multiple locations, both peripheral and central. That both peripheral and central mechanisms for the construction of beats exist across sensory systems suggests that beat illusions are important components of perception.

Pointillism: Pixels or Beats?

With the exception of some experimental stimuli used in scientific labs, every visual scene contains second-order image features. Unlike first-order im-

age features (such as boundaries between dark and bright regions) which are defined by variations in light intensity, second-order image features (such as boundaries between differently textured but equally bright pieces of cloth) are defined by variations in contrast.

Despite the omnipresence of these second-order features in natural scenes, it is hard for us as observers to distinguish them from first-order features, in part because the two covary tightly.[16] However, the work of Georges Seurat and other pointillist painters provides an avenue for examining the contributions of first-order and second-order features to the perception of an image. Second-order image features are particularly prominent in pointillist paintings because pointillists used high-spatial-frequency components—small colored dots—to construct large-scale images. With the advent of computer monitors it is easy to claim pixelization as pointillism's greatest insight, yet it more than any other style highlights the perceptual salience of second-order image features. To illustrate this, we consider Seurat's *A Sunday on La Grande Jatte*. In the original painting there are many cues that allow us to segment objects and figures, including differences in hue, brightness, color saturation, and texture. The clearest boundaries are those defined by transitions in light intensity, many of which are apparent in the monochrome version of the painting shown in the top panel of figure 3.4. These transitions from dark to bright are first-order cues, and are arguably the most important features used by the visual system to segment an image.

However, the painstaking use of individual points of color creates more than just light/dark boundaries. Recall that beats are illusory low frequencies arising from interactions between different high-frequency components. In pointillist art, the entire image is constructed from high-frequency components (small dots)—so while there are low frequencies in the image, it is also likely that beats contribute important segmentation cues. To estimate the strength of the second-order features in the pointillist painting *A Sunday on La Grande Jatte*, we have removed the color (top panel, figure 3.4) and processed the monochromatic image using a "filter-rectify-filter" algorithm.[17] This procedure reveals where high-frequency components combine to produce low-frequency beats (bottom panel, figure 3.4).

A great deal of the information defining a visual scene is carried by second-order features, such as changes in texture that cue object boundaries. This point is readily demonstrated in pointillist paintings. In the filter-rectify-filter image in the bottom panel of figure 3.4, the brightest regions indicate where variations in high spatial frequencies give rise to low-spatial-frequency beats. We have marked two regions in the image: one that encloses a patch of sky and is comparatively smooth (square box and another that includes a boundary between the water and the leaves of a tree (rectangular box). In the bottom panel showing the locations of second-order image features, the region of sky is dark because there is little texture variation in

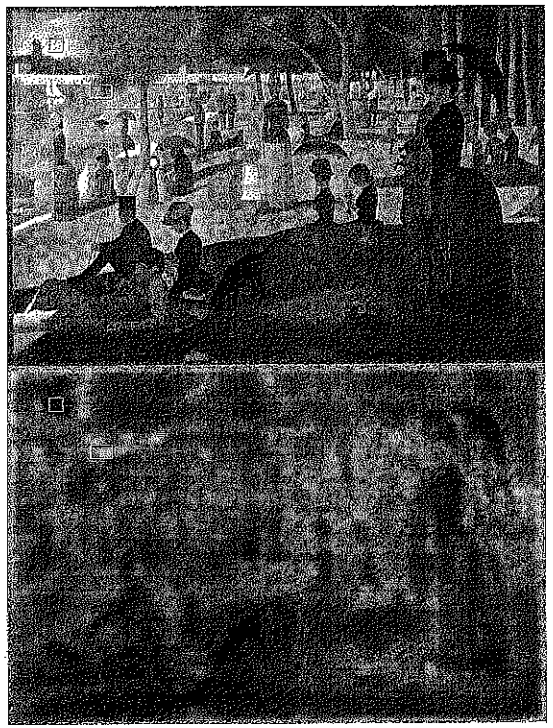


FIGURE 3.4. Second-order information in a pointillist painting. Top: a monochrome image of Georges Seurat's *A Sunday on La Grande Jatte–1884*, 1884–86. Oil on canvas, 81¾ × 121¼ in. (207.5 × 308.1 cm). Helen Birch Bartlett Memorial Collection, 1926.224, Art Institute of Chicago. Photography © Art Institute of Chicago. Reprinted by permission of The Art Institute of Chicago. Bottom: a transformation of the image that shows second-order information. This transformation was accomplished by high-pass spatial filtering, squaring the intensities in the filtered image, and then low-pass spatial filtering. Regions of the painting in which there is little second-order information (square box) and substantial second-order information (rectangular box) are marked in both panels.

that area, while the boundary between the tree and water is bright because there is substantial texture variation between the two regions. Edges are apparent throughout the second-order image precisely because second-order features are a common cue for object boundaries.[18]

Part of the aesthetic interest of pointillism derives from how the paintings change with the distance from which they are viewed. From close by, little overall structure is apparent; just random dots of color are perceived. From far away, the individual dots are no longer visible and the painting appears much like any other painting formed with broad strokes. From intermediate viewing distances, however, the uniqueness of pointillism stands out. Despite clearly being composed of dots scattered about the canvas, pointillist paintings viewed from moderate distances give distinct perceptions of form and structure. Because the perception of second-order features requires both the ability to see high frequencies (which decreases with viewing distance) and the ability to see a large enough area of the image to detect low-frequency variations (which increases with viewing distance), it is at intermediate viewing distances that second-order features contribute most to visual perception. To illustrate this, we present the second-order features of the monochrome version of *A Sunday on La Grande Jatte* as if it were viewed from various distances (figure 3.5). At very long distances only first-order cues of varying light intensity define form. As the viewing distance decreases, beats provide progressively greater information about the structure in the image. Arguably, the unique aesthetic of pointillist paintings at intermediate distances is attributable to the availability of second-order information.

Conclusions

Complexity in sensory perceptions can have many origins—starting with the stimulus itself, ending with emotions overlaid on imagined percepts, and distorted in the middle by the wide variety of encoding and decoding steps of the nervous system. The goal of this chapter has been to identify one class of distortion and to argue that it alters our perception in a specific and meaningful way.

Both the auditory system and the visual system introduce beat frequencies early in the sensory cascade. From a purely mechanistic standpoint this

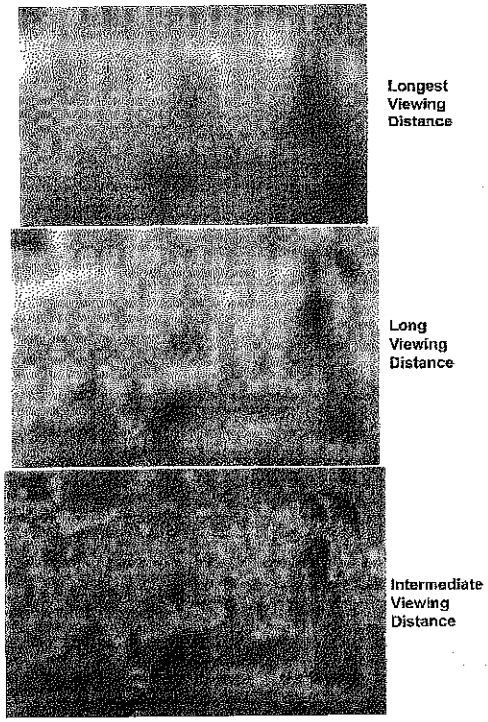


FIGURE 3.5. How second-order information changes with viewing distance. To simulate the effect of viewing distance on second-order information, several versions of the painting shown in the top panel of figure 3.4 were put through the filter-rectify-filter algorithm. To simulate the longest viewing distance, a low-resolution version of the painting in which none of the dots that comprise the painting were visible was analyzed. While first-order information in the form of light intensity remains (not shown), almost no information about the image structure is available from second-order cues. Viewing the image from a closer distance, simulated by analyzing progressively higher-resolution images, increases the amount of image structure defined by second-order cues. The contrast in each panel was stretched to simulate maximal sensitivity to the second-order features detected at each viewing distance; even with maximal sensitivity there is little second-order structure at the longest viewing distances.

does not have to be the case; at least in the visual system there is an alternative pathway that lacks beat distortions (the "X-pathway").[19] It is also known that more central neural stages (in the midbrain or cerebrum) can inject beats, as evidenced by binaural beats (constructed by playing different pure tones separately to each ear)[20] and binocular beats (constructed by showing different patterns separately to each eye).[21]

In a general way, this raises the fundamental question of what exactly the

cerebral cortex contributes to perception. Does it create new features out of simple inputs from the peripheral sensory organs, as is traditionally thought? Or does it receive signals that have already been manipulated to create the important distortions? If the latter is correct, is subsequent processing in the cortex more nuanced, based on an individual's idiosyncratic experience? The most likely answer is a combination of both, but understanding how and to what extent this admixture occurs is a necessary prerequisite to defining the neural underpinnings of perception and aesthetics.

Tartini struggled to understand the physical basis of harmony, producing in the end a flawed theory.[22] Despite this, his discovery of third sounds provided an important clue about the nature of sensory processing. Many important questions remain to be answered regarding the role of beat frequencies in perception. First, it is surprising that we still do not have a compelling explanation for why beat frequencies are so important that they are represented in disparate species and different sensory modalities, and are introduced at multiple stages of sensory processing. A general explanation comes from modern theories of sensory perception which invoke neural processes that evolved over eons to guide interpretation of the world in the absence of context or experience,[23] and it is likely that the mechanisms for detecting beats are among them. But it is still not clear how we would be disadvantaged if sensory processing were limited to first-order cues. Second, because it is challenging to present first-order and second-order features independently, it is difficult to separate their influences on perception. As a result, the extent to which second-order cues influence our appreciation of a piece of music or a particular image is still mostly guesswork. Finally, it is clear that inputs to the cerebral cortex are neither simple nor objective representations of the real world—so how must we change our concepts of high-level processing to accommodate these distorted inputs? Perhaps through the integrated study of neuroscience and aesthetics, we can begin to answer these questions.

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FOUR Sociovisual Perspective

VISION AND THE FORMS OF THE HUMAN PAST

Philip J. Ethington

Cultural studies and many social science fields have been under the spell of an intellectual rift for many decades, united in the belief that the humanities enjoy immunity from dialogue with natural scientists on common areas of inquiry such as "vision" and "visuality." This sense of immunity was institutionalized by the first generation of university-based intellectuals in the late nineteenth century. Wilhelm Dilthey, in the 1890s and the following decade, won a major political fight in Germany for the independence of the human sciences (*Geisteswissenshaften*, including what in English are called the "humanities" and many of the "social sciences").[1] French and Anglophone systems followed suit. The humanities—especially history, art history and criticism, literature studies, philosophy, and classics—were deemed "interpretive" studies concerned with social phenomena, studied not as natural phenomena but as independent of so-called natural laws. Institutions such as language, religious belief, ideologies, political history, marriage customs, and traditions were deemed human inventions that were "real" only in symbolic thought, much as software is considered independent of hardware. To be sure, Marx and many other "founders" like Durkheim tried to establish the study of human institutions on a "scientific" basis, but since Dilthey's leadership in the 1890s, most humanists have insisted that such cultural forms were shaped primarily by other "social facts," rather than being traceable to innate or *natural* facts.[2]

The mind is embodied, however—and since Freud, most humanists have known this while avoiding its implications. Indeed, "embodiment" has become a leading key word among humanists.[3] I argue in this essay that embodiment spells doom for a very old taboo on recognizing that scientific explanations might actually be *valid* and not merely an object of intellectual critique.[4] I will use several exemplars of fine and influential studies of visual culture by