Chapter 18

Introducing Perception

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So far, we have attended only to the retinal image and the early sensory processing of the incoming visual signals. We have traced the visual signals through several code transformations, all the way to area V1, and provided a simplified sketch of what is known about processing beyond V1. In conjunction with our serial tracing of visual signals, we have explored a variety of system properties that seem most closely tied to early sensory processing. It’s now time to turn to a broader set of system properties – those deriving less closely from studies of sensory processing and more closely from studies of visual perception.

Including perception in the mix occasions a return to the beginning – to the distinctions and relationships between three entities: the perceived world, the physical world, and the neural states that provide the physical basis for the perceived world.

First, we define perception and the perceived world, distinguish it from the physical world, and spell out some of its unique properties. In contrast to our earlier sensory view, the perceptual view centers around the perception of physical objects and their three-dimensional locations.

Second, we define the physical world and contrast it with the perceived world. We introduce the idea that perception doesn’t depend on the incoming sensory information alone – it is both impoverished by sensory processing, and enriched by stored information. We argue, however, that given the confounding of physical variables in the retinal image, the properties of the perceptual world bear a remarkably close correspondence to the properties of the physical world. These correspondences provide an important new set of system properties in search of explanations.
Third, we return to the question of neural codes, and inquire into the relations between high-level neural codes and the perceived world. In particular, we will ask, what are the implications of the new system properties revealed by perceptual phenomena, for deducing or guessing the forms that neural codes might take? And what linking propositions are involved in such deductions and guesses?

And finally, we address the question of neural coding principles. Specifically, a question that has been at the center of theorizing in neuroscience: What makes a good neural code?

In high-level visual processing and its relation to perception, we are leaving the relative safety of sensory processing and embarking on a journey in a land in which much less is known. There are relatively few studies of the neural basis of perceptual effects, and they are in the vanguard of visual neuroscience. How can the lessons of our studies of sensory aspects of vision, guide the journey? How can we use the principles we have learned at the sensory processing level, to generate fruitful hypotheses about what the codes will be like at the cortical level? The goal of this chapter is to capture and make explicit the common assumptions in studies of central visual neurophysiology. We will attempt to bring together themes from philosophy, sensory studies, perception, and neuroscience, and weave them into a coherent story.

18.1 The first entity: The perceived world

18.1.1 Perception is a part of conscious awareness

To discuss and define perception, I begin (as Descartes did) by acknowledging the existence of my own conscious awareness. Given that premise, I define perception as the part of my conscious awareness that is concerned with the status of the world around me, or (in the case of vision) in front of me. The world as represented in my perception can be called the perceived world (or the phenomenal world, or the world as perceived). Moreover, I extend my basic premises to acknowledge that other people – including you, the reader – also have conscious awareness, and perceptions of the world.

Another common way of saying that perception is part of conscious awareness is to say that our perceived worlds are known to each of us from the inside, or from a first person perspective. These phrases are intended to capture the difference between the kind of knowledge we have of our own conscious states, and the kind of knowledge we acquire as scientists, from the outside or from a third person perspective.

In defining perception as a part of conscious awareness, we are choosing a position on one aspect of the mind/body problem. From a perspective innocent of either science or philosophy, I know that I am conscious, and have perceptions that are somehow related to the physical world and the objects around me. I endorse the existence and legitimacy of my own conscious perceptual states, and will not concede an inch to any philosophical position that tries to abolish them, or claim that they are really something else (such as brain states). I can readily agree that perceptual states are intimately related both to the physical world and to brain states, and be intensely curious as to the nature of these relationships – as indeed we are in this chapter. But I insist that perceptual states are neither physical states nor brain states. They are conscious states, known to me from a first person perspective, and can never be legislated or defined away.

At this point, some readers may be thinking that I just became a dualist. Not so. One can distinguish the perceived world from the physical world and still be a materialist or an idealist.
18.1. THE FIRST ENTITY: THE PERCEIVED WORLD

As discussed in the first chapter of the book, the view adapted here is to distinguish between the perceived world and physical world and then concentrate on how they map upon one another. One can have a variety of opinions about causality and still be interested in the mapping between the physical and the perceived. In particular, a materialist can still distinguish the perceived from the physical even though the specifics of the physical world determine the specifics of the perceived world. The two worlds need to be distinguished to study the details of the mapping from one to another.

18.1.2 Properties of the perceived world

What more can we say about the properties of the perceived world? As it happens, the perceived world is in some ways very easy to describe. This is because until we begin to study sensory systems or think about perception, we don’t typically make much of a distinction between the perceived world and the physical world. So to describe the perceived world, we can more or less describe what we have always thought of as the physical world, noting the differences as we go along. What are some of the characteristics of the perceived world?

For some people, one of the most striking yet puzzling properties of the perceived world is its location – out in front of us. That is, some philosophers of perception presume (note the linking proposition) that if perceptual states arise from brain states, they should be located in the same place as brain states; namely, inside the head. But obviously, this is not the case – my perceived world is located outside my head, in the space in front of me. This property of the perceived world, mysterious to those who assumed otherwise, is sometimes called *perceptual projection*.

In any case, my perceived world lies in front of me. It is laid out in a three dimensional space that extends over my whole visual field in two dimensions, and indefinitely far in distance. It is populated with perceived entities called objects. The selection of objects changes as I move about in the world – it can be streets, buildings, people and cars in the morning, books and computer monitors at noon, and trees, rocks and rattlesnakes on Saturday. Importantly, perceived objects have a set of characteristics – perceived shape, size, color, and so on – that usually remain constant, and three-dimensional locations that are typically continuous but more susceptible to change. Other properties of the perceived world include such characteristics as the general light level, the state of the weather, and so on. [Work out a description of your currently perceived world.]

Another interesting property of the perceived world is that there is no strict dividing line between sensory processes, perception and cognition. For example, I may see a dog on the lawn. When the dog moves into my peripheral visual field, the sensory inflow loses spatial detail, but my perception continues. When the dog runs behind a tree, the incoming stimulus information required for perception of the dog is completely removed. But perception is augmented by stored information. Cognition and memory take over smoothly and automatically from perception, and I still sense, or perceive, or “see” that there’s a dog behind the tree.

In contrast to the above example, the perceived world can also be fragile. The perceived world loses many of its characteristics when the light level gets too low, and it goes away entirely when I close my eyes. All of these properties – especially the division of the perceived world into objects with relatively constant characteristics, are system properties in search of explanation.
18.2 The second entity: The physical world

The second of our three entities is the physical world; the world as described by physicists. It consists of matter and energy in wondrously varying configurations. It can be described at several different levels, from subatomic structures through objects as wholes to cosmological descriptions of the universe. At the scale most relevant to the present discussion, the physical world contains physical objects with physical shapes, sizes, and surface properties, at particular physical locations in three-dimensional physical space. It also contains such features as sources of radiant energy (some of which are perceived as light), and physical configurations such as concentrations of tiny water droplets that condense in the atmosphere and fall toward the earth (causing the perception of rain).

But how are we to know about the physical world and its properties? Knowledge of the physical world comes basically from three sources. The first of these is our perceptions. As we said before, from a naive perspective the physical world is pretty much the same thing as the perceived world, and our moment-to-moment knowledge of the physical world is supplied by the perceived world. The second source of information is measurements made with physical instruments – rulers, thermometers, spectrophotometers, telescopes, microscopes, thermocouples, and so on. It is the invention and use of such instruments that allows us to make a firm separation between the perceived and physical worlds (for example, the separation between perceived and physical size, and between color and wavelength composition), even as we note the striking correspondences between them.

The third and most abstract source of information about the physical world is physicists’ models of its properties. Gravitational theory tells us why apples fall from trees, and quantum mechanics tells us about the nature of light. The physicist’s understanding of the physical world is acknowledged to be incomplete, and is open to change as new measuring instruments are invented and new theories are devised.

The physical world differs from the perceived world in that it is continuous, even when the lights go out or we close our eyes. We can find this out with physical instruments, and we know it from physical theory.

18.3 The relationship between perceived and physical worlds

Now that we have carefully distinguished perceived and physical worlds, we can ask again how they relate to each other. A number of points need to be made.

18.3.1 The perceived world is impoverished by sensory limitations

First, the perceived world is impoverished by the limits of sensory processing. Any physical energy that is not transduced by our senses, or any physical stimuli that are below our thresholds, cannot affect the properties of the perceived world. You have seen many examples of information loss in Chapters 1-17. So for example, the electromagnetic spectrum is continuous over many orders of magnitude of wavelength (or energy), whereas the visible spectrum spans only a factor of less than two, between 400 and 700 nm. Lights that deliver too few quanta are undetectable; gratings of spatial frequencies above 60 cy/deg cannot be discriminated from homogeneous fields of light; and so on and so forth. Much of the lesson of the earlier chapters of this book deals with the limitations of our senses with respect to the properties of the physical world.
18.3.2 The perceived world is enriched by qualia

Second, most philosophers and most vision scientists would argue that with respect to the physical world, the perceptual world is also enriched by – how to say it? – the unique properties of perception. We think of the physical property of wavelength composition as colorless, whereas the perceived color of an object has something important added. Philosophers refer to these new properties as perceptual qualities, or qualia. The concept of qualia as perceptual entities is elegantly (if poetically) captured in the following quotation of Whitehead (1925, p. 54) as found in Velmans (2000, p. 112):

"The mind, in apprehending, also experiences sensations which, properly speaking, are qualities of the mind alone. These sensations are projected by the mind so as to clothe appropriate bodies in external nature. Thus the bodies are perceived as with the qualities which in reality do not belong to them, qualities which in fact are purely offsprings of the mind. Thus nature gets credit which should in truth be reserved for ourselves; the rose for its scent; the nightingale for its song; and the sun for its radiance. The poets are entirely mistaken. They should address their lyrics to themselves, and should turn them into odes to self-congratulation on the excellency of the human mind. Nature is a dull affair, soundless, scentless, colorless, merely the hurrying of material, endlessly, meaninglessly.”

A particularly nice metaphor for the relationship between the perceived and physical worlds has been presented recently by the philosopher Max Velmans. A modification of Velmans’ diagram of his view, which he calls a reflexive model of perception, is shown in Figure 18.1. The idea is that the external object, here a cat, sends light to an observer’s eyes. The observer’s visual system captures the light, processes the incoming signal, and creates a series of neural representations of the cat. At some level of neural processing, the neural representation gives rise to a perceived cat. The perceived cat, however, is not perceived to be located within the head of the observer, however, but rather at or near the location of the physical cat.

In summary, to use Whitehead’s phrase, the perceived cat is “projected by the mind so as to clothe” the physical cat in perceptual properties. To unclothe and describe the physical cat, we use physical instruments and physical theory. To study the relation between the clothed and unclothed cats, we call on psychophysics.

18.4 Perceptual constancies

Once sensory processing and qualia are set aside, the striking thing about the perceived and physical worlds is how similar they are. That is, all things considered, perception is remarkably veridical: the properties of perception usually correspond closely to the properties of the physical world. Remarkably, perception carves nature at the joints, and informs us accurately about the physical properties of objects.

Why is this surprising? To capture the difficulty of the problem, perceptual psychologists classically make a distinction between distal and proximal stimuli. Distal stimuli are physical objects: states of the world and the objects in it. Houses, dogs, trees, and other real three dimensional objects are distal stimuli; so are parts or aspects of them, such as their surface properties, distances, and directions and speeds of motion. Proximal stimuli are the representations of stimuli as they occur in the retinal image.

The problem of creating veridical perception stems from the fact that many of the properties
of objects in the physical world are confounded in the retinal image. For example, the retinal image consists of a two-dimensional optical image, with no clear representation of the dimension of distance. The sizes of the images of objects vary with the distance of the physical object. Yet we perceive objects in a three-dimensional space, with sizes that remain constant over variations in distance. The remarkable fact of perception is that we are able to back calculate from the proximal stimulus to create perceptions that correlate closely with the size or other properties of the distal stimulus. In short, somehow, we have size constancy.

These ideas bring us to the important concept of perceptual constancies. A perceptual constancy is the ability to perceive the attributes of objects (distal stimuli) more or less accurately, despite the fact that the physical variables that carry information about these attributes are confounded with other physical variables in the retinal image (the proximal stimuli). If the function of perception is to tell us the characteristics of objects in our immediate environment, and allow us to respond to them wisely, then perceptual constancies are of fundamental importance.

Beyond size constancy, a second and less obvious example is lightness constancy. The lightness of an object is its perceived shade along the perceptual white-grey-black continuum. One of the physical characteristics of the surface of an object is its reflectance – the fraction of the incident light that it reflects. Lightness constancy is the tendency for objects with a constant reflectance to be perceived as a constant shade of white, grey, or black. Perceptual studies show that our lightness constancy is good. Natural objects that are perceived as white all turn out to reflect at most 80% of the incident light (e.g. fresh snow); those perceived as black reflect about 4% (e.g. coal); and those with reflectances in between are perceived as various shades of grey (Wyszecki and Stiles, 1982). That is, the reflectances of natural objects span a range of 20:1.\(^1\) So far, so good. But the problem is that the light incident on our retinas from white, grey and black objects is also influenced by the intensity of the light illuminating them; and the incident light may vary by a

\(^1\)Manmade surfaces can extend the range of reflectances to be from 1% to 99%.
18.5. PERCEPTION AS A GUESSING GAME

<table>
<thead>
<tr>
<th>Kind of Constancy</th>
<th>Object Property (distal stimulus)</th>
<th>Retinal Property (proximal stimulus)</th>
<th>Confounding Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>size</td>
<td>object size</td>
<td>image size</td>
<td>distance</td>
</tr>
<tr>
<td>lightness</td>
<td>reflectance</td>
<td>luminance</td>
<td>illuminance</td>
</tr>
<tr>
<td>color</td>
<td>spectral reflectance</td>
<td>spectral radiance</td>
<td>spectral illuminance</td>
</tr>
<tr>
<td>speed</td>
<td>object speed</td>
<td>image speed</td>
<td>speed of eye movement</td>
</tr>
<tr>
<td>shape</td>
<td>object shape</td>
<td>image shape</td>
<td>viewpoint</td>
</tr>
<tr>
<td>object</td>
<td>all of the above</td>
<td>all of the above</td>
<td>all of the above</td>
</tr>
</tbody>
</table>

Table 18.1: Column 1 denotes the constancy under discussion. Column 2 specifies the object property (distal stimulus) to which the perceptual property corresponds if perception is veridical. Column 3 specifies the relevant sensory input at the retina (proximal stimulus). Column 4 lists the confounding variable that needs to be factored out.

factor of $10^{10}$ or more, totally swamping the relatively small difference caused by the difference in reflectances. How can we back-calculate from the intensity in the retinal image to the reflectances of objects? How can lightness constancy happen?

These and several other perceptual constancies are listed in Table 18.1. In each case, we list the constancy together with the property to which it corresponds in the distal stimulus, and the most relevant proximal stimulus. All of the constancies illuminate the relationship between physical and perceptual worlds – they provide examples of the remarkable correspondence between the properties of the two. Amazingly, when perception clothes physical objects with perceptual properties, the clothing corresponds more closely to the physical properties of the object than it does to the incoming sensory signal. The constancies listed in this table are all considered in the following chapters. This list, however, only illustrates the best known of the many perceptual constancies that one might consider.

The final constancy in Table 18.1 is object constancy. Object constancy is the capacity to perceive an object as retaining its characteristics – size, shape, color, and so on – despite variations in distance, angle of regard, spectrum of illumination, and so on. Object constancy is a combination of all of the other constancies, and is in the ultimate service of veridical perception as a whole. In later chapters, we will return to each of these constancies, and ask how they come about.

18.5 Perception as a guessing game

The physical world is underdetermined in the retinal image. That is, as shown in our discussion of constancies above, many specific combinations of values physical variables are confounded to create equivalence classes in the retinal image, and at least at first glance there would seem to be no source of information that would allow us to sort them out. Retinal image size confounds physical size and physical distance, and many combinations of physical size and physical distance can yield the same retinal image size. Yet perceptually we sort them out, and see both size and distance veridically most of the time. Bumblebees can fly.
18.5.1 The sensory input is augmented by stored information

At this point, we add a major new concept to our treatment of vision science: the incoming sensory signal is not sufficient to specify the identities of the objects in the world in front of us. Rather, our perceptions arise from the combination of the incoming sensory signal with information stored in our brains. This added information has its origins in a combination of our evolutionary history and our developmental experiences. There is more to vision than meets the eye!

For example, who or what is depicted in the cartoon in Figure 18.2? The cartoon consists of only a few curved lines. Surely the incoming stimulus information is insufficient to specify the object. Yet many of us recognize it instantly as the profile of a face, and supply his or her image and identity from memory. This will only be obvious if you are familiar with this particular cartoon (a hint follows at the end of this section). This demonstration by itself should convince you that perception involves the addition of stored information. [Do you see any way around this conclusion?]

When we are operating in the real physical world (not in cartoon land), the incoming sensory signal usually carries much more information about the size, shape, color and location of an approaching object, but the recognition or identification of the object (Hi, Grandma!) and the awareness of many of its hidden properties (Where’s my present?) depend on information retrieved from memory. Similarly, our actions toward physical objects are informed by our knowledge of the properties of the physical world, even when these properties are not included in the incoming sensory signal. We pet the kitten, but avoid the rattlesnake even if we have never been bitten.

Another dramatic case of the use of stored information arises from considering our perception in the peripheral visual field. As we have discussed in earlier chapters, our discrimination on many
sensory dimensions – especially acuity and color – falls off dramatically with retinal eccentricity. If our perception of objects in the periphery were based solely on the incoming sensory information, our peripheral vision would of necessity be blurry and desaturated, and the perceived properties of an object would change as we shift our fixation and move the image of the object from fovea to periphery. But most people report that objects retain their properties across shifts in fixation. [Try it. Do you agree?]

A dramatic example arose while DT was writing the first draft of this chapter. DT and her friend Maureen Powers were writing at opposite ends of MP’s dining room table. MP’s parrot, Phred, was out of his cage, and DT noticed that he was walking around over MP’s head and shoulders with a classic parrot gate. As DT concentrated her attention on the chapter, she was vaguely aware that Phred flew from MP’s head to the screen door in DT’s peripheral vision. Later, she became aware that Phred was walking up and down the screen. Without looking up, she could “see” Phred’s red tail and green body, and the little beady eye that had been eyeing her all week. Wow! Had Phred been miraculously replaced by a dove, DT’s perception would probably not have changed. That is, the perception of peripheral Phred was created out of nearly whole cloth by DT’s perceptual systems! Those processes must contain some rules about the persistence of object properties and the temporal continuity of objects. In DT’s perception, when Phred flew to the screen door he took his colors and identity with him, just as he does in reality. In sum, the details of our peripheral vision are created from memories of our foveal vision, plus some reduced peripheral version of the incoming sensory signals, plus some assumptions about temporal continuity.

Now, had Phred been miraculously replaced by a dove, DT’s perception would probably not have changed. That is, the perception of peripheral Phred was created out of nearly whole cloth by DT’s perceptual systems! Those processes must contain some rules about the persistence of object properties and the temporal continuity of objects. In DT’s perception, when Phred flew to the screen door he took his colors and identity with him, just as he does in reality. In sum, the details of our peripheral vision are created from memories of our foveal vision, plus some reduced peripheral version of the incoming sensory signals, plus some assumptions about temporal continuity.

Here’s a second example: DT and her husband cohabit with a stuffed rabbit named Flopsy (it’s a long story). One day as DT was working on this book, she became too hot, yanked off her grey sweatshirt, and dumped it on a table by her right hand. Soon she began to find thoughts of Flopsy intruding into her mind and distracting her attention. At first she could find no reason for this, but eventually tracked the problem. The grey sweatshirt had fallen into a pose that, in peripheral vision, looked exactly like Flopsy! Now, had DT’s peripheral vision been as good as her foveal vision, she would never have confused Flopsy with the sweatshirt. But her peripheral vision is degraded, and the peripherally processed sweatshirt image was nearly identical to the peripherally processed Flopsy image – a peripheral Flopsy metamer. In fact, it had just the right properties to access memories of Flopsie, and top-down processing filled in her detailed appearance (not to mention her personality). A picture of Flopsy and her metamer are shown in Figure 18.3. By the way, the cartoon in Figure 18.2 is of Alfred Hitchcock an English film director and producer.

To reiterate: the perceptual world contains more information than is supplied by the incoming sensory signals. Perception results from the combination of sensory signals with stored information. Thus there must be additional, non-obvious sources of information available, and used in generating our perceptions. These sources of information may be many, and arise from many origins, both from subtle patterns contained in the retinal image and from information stored within our brains via our evolutionary and developmental histories.

What might these additional sources of information be? This inquiry leads us to a discussion that will introduce some important concepts: cues, heuristics, and the probabilistic nature of perception.
Figure 18.3: Flopsy and her metamer. A. In focus. B. Blurred to simulate peripheral vision.
18.5. PERCEPTION AS A GUESSING GAME

18.5.2 Cues

Some of the extra information required for veridical perception is contained in the incoming sensory signals in the form of cues. Cues are lawful or probabilistic regularities that occur in the mapping between aspects of the physical world and aspects of the incoming sensory signal. As such, they provide potential sources of information about that aspect of the physical world.

To continue with size and distance as examples, distance cues are sources of information regarding the physical distances of objects, and size cues are sources of information concerning the physical sizes of objects. What sources of information about distance and size, other than retinal image size, are available for use as cues?

One potential source of information is accommodation (see Figure 4.9) – the thickness of the lens needed to produce an optimally focussed retinal image. Another is convergence (see Figure 20.2) – the angle between the directions of gaze of the two eyes required to place the two images of a single object on the two foveas. Both of these quantities vary regularly with distance, and thus provide potential distance cues. These and many other distance cues will be discussed more fully in Chapter 23.

Cues are interesting, for several reasons. First, not all cues are obvious. Most potential cues are more or less subtle, like accommodation and convergence, and have to be discovered by intellectual analysis. Moreover, once a potential cue is discovered, one must still ask whether it is actually used by the visual system. One of the interesting aspects of the history of perception concerns the discovery of the many cues that make veridical perception possible, and the research required to find out whether each potential cue is actually used. [Try to figure out some other distance cues.]

Second, although some cues like accommodation and convergence are highly reliable, others are probabilistic and therefore more risky. Importantly, a cue can provide accurate information most but not all of the time, and still be useful. For example, consider the cue of familiar size. Suppose that objects have usual sizes – a house is about 30 feet high – and your perceptual system makes the assumption that most things have their usual sizes most of the time. So if I see a house on the far shore of a lake, and I see it as being the size that houses usually are, I will see it veridically most of the time. However, if it’s a child’s play house, the familiar size cue will mislead me, and if I am using this cue my perception will be wrong.

Third, any given constancy is typically served not by just one cue, but by many. As we have already seen, size constancy is served by at least accommodation, convergence, and familiar size; and there are many more cues to size and distance. The same is true for color constancy, lightness constancy, and so on. In studying cues, then, we will need to discover not only the various potential and actual cues, but also the rules by which they combine their effects.

And finally, many cues involve relatively sophisticated stored information and analyses. The familiar size cue is a good example. In order to use it, my visual system must identify the house as a house, and have access to stored information about the usual sizes of houses. As we will see in Chapter 23, many other distance cues rely on similar complex processing.

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2The size/distance example is chosen here because it is easy to grasp intuitively. However, it suffers from the complication that not all of the sources of information about distance come from the retinal image per se – accommodation and convergence cues come from the ocular musculature. In most of the cases we will encounter later, all of the cues will come from analysis of subtle patterns within the retinal image.


18.5.3 Heuristics: Perceptual guessing rules

When we recognize the existence of cues, the statement that the world is underdetermined in the retinal image can sometimes be seen as unduly pessimistic. For example, it is true that physical size and physical distance are confounded in retinal image size. But the signals that control accommodation and convergence contain information about distance. By using an analysis that combines these signals with retinal image size, it would seem that we actually have the information needed for the veridical perception of size, and the system property of size constancy suddenly seems less mysterious.

In other cases, however, the cues are less straightforward, and the deconfounding less than perfect. For example, the familiar size cue is not perfectly reliable – houses are bigger or smaller than the usual size on, let us say, 1% of occasions. Nonetheless, we would still be well advised to use this cue if we didn’t have others available, and implement the perceptual rule, perceive the house as being the size that houses usually are. Using this rule would allow us to perceive the size of the house veridically on say, 99% of occasions. It’s analogous to intelligent betting in other circumstances: if you know a die contains sixes on five out of six of its faces, you will bet on sixes, even though you won’t be right on every roll.

A heuristic is a stored interpretational rule – a perceptual guessing rule – that the perceiving organism applies to incomplete incoming sensory information. The function of the heuristic is to provide the best possible guess about the situation in the physical world, given imperfect or partial incoming sensory information. The rule, perceive this house as the size houses usually are, is an example of a heuristic. When the term heuristic is used, it is used to emphasize the probabilistic and therefore potentially fallible nature of the enterprise of perception.

The fact that perception is usually veridical, or nearly so, implies that the incoming sensory signal provides a set of cues that, taken together, provide considerable information about the important physical variables. It also implies that our perceptual systems contain a set of heuristics that, in combination with the incoming cues, allow our perceptual guesses to be veridical or nearly veridical most of the time. [Figure out the heuristics used with the cues of accommodation and convergence.]

Where do heuristics come from? The argument is that the cues supplied by the physical world and the perceptual heuristics of organisms that evolved in that world will be tied very closely to each other. Through some combination of genes and experiences, one has developed perceptual heuristics that are complementary to the available cues. We have particular guessing rules because the guessing rules make use of the available cues, and they have evolved to work.

One of the major goals of modern perceptual research is to discover potential cues provided by the physical world through our sensory systems, to see which ones are actually in use; to discover the complementary heuristics; and to find out how the heuristics combine to yield (usually) accurate perceptions. We will develop many other examples in later chapters.

18.5.4 Perception as hypothesis

The set of ideas presented above – the ideas of cues, perceptual heuristics, and fallibility, leads to the idea that all of our perceptions can be more properly viewed as hypotheses than as factual knowledge about the state of the physical world. The term perceptual hypothesis, like the term heuristic, is chosen to emphasize the fallibility of perception.
Once again, why are the concepts of cues, heuristics and perceptual hypotheses so appealing to scientists interested in perception? Up to this point we have probably thought of sensory processing as a deterministic process (ignoring the question of noise). In this context, the terms heuristic and perceptual hypothesis are important and carry novel meanings because both carry explicit or implicit connotations of guesswork and fallibility. The perceived world is a construction that mimics the properties of the physical world as closely as it can; but it is constructed partly on guesswork, and when insufficient information is available, it can be wrong.

Where is the basic source of unreliability? Note that both the sensory system, the heuristic and the perceptual hypothesis can all be deterministic; the basic source of the unreliability is in the incoming sensory signal. Sometimes the information we need just isn’t there. It’s nobody’s fault. Overall, it’s amazing that we do as well as we do, given the apparent confounding of variables in the retinal image.

18.5.5 Perceptual errors and illusions

At other times, of course, our perceptual guesses are wrong. Momentary wrong guesses lead to momentary errors of perception that most of us have experienced. Something that appears to be a nun in a habit turns out to be a black and white signboard; white powder spilled on a coat turns out to be a ray of sunlight, and a deer in a red hat turns out to be a fellow hunter. Perceptual errors doubtless contribute to many traffic accidents – a road that appears to be straight actually curves away to the left, and passing can lead to tragedy.

The view that heuristics can lead us astray also provides a comfortable explanation for the existence of the classical visual illusions (e.g. Figure 18.4). The argument here is that our heuristics evolved to process scenes from the usual three-dimensional physical environment, and can be misapplied to line drawings or two-dimensional photographs. The figure shows the original version of the Ponzo illusion on the left and a photographic version on the right. The road is perceived as being the same size in the world despite its changing size in the image. In contrast, the two horizontal lines are not perceived as the same size despite being the same size in the image. Such illusions and misperceptions can provide clues about which heuristics our perceptual systems are using.

18.6 The third entity: Neural activity

Let’s turn now to the third entity: neural activity and neural codes. In earlier chapters, we have already introduced many of the concepts related to neural coding. Just like retinal neurons, cortical neurons have firing rates, and different stimulus conditions lead to different firing rates – each cortical neuron carries close-coupled information about many features and dimensions of the retinal image at the location of its receptive field. Moreover, different cortical neurons respond to different combinations of features and dimensions, and in general information about any one specific state of the physical world is carried in an ensemble code. Moreover, recodings continue; features that are explicit in the firing rates of individual neurons at one level, can be carried by a population code at the next.
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A.

Figure 18.4: Two versions of the Ponzo illusion. The horizontal lines are the same size on the page but not in the percept. [B. From Rock (1984, p. 152).]

18.6.1 Neural states, perceptual states, and linking propositions

We have argued throughout this book that the system properties defined by psychophysics place important (although usually general) constraints on models of neural activity. We now argue that the properties of perception, such as the constancies defined above, provide a new set of system properties for visual science. What constraints do these new system properties place on our understanding of the neural codings and recodings that might or must exist within the visual cortex? Given the properties of perception, what can we deduce, or assume, or guess, or hypothesize about high-level neural codes? Can perceptual phenomena give us any guidance as to what to look for when we study neural processing in the cortex?

As before, DT will argue that the answer to this question is yes, but that such arguments always involve linking propositions — assumptions about the mapping rules between neural states and perceptual states. If we are reasoning from perceptual states to neural states, we are always using linking propositions. This realization allows us to bring our earlier discussions of linking propositions forward and apply them in the new domain. What linking propositions do we use when we use the properties of perception to glean hints as to the nature of high-level neural codes?

18.6.2 A general linking proposition: Appropriate neural analyses and codes must exist

Some new general, almost tautological, linking propositions can be stated at the outset. At the most basic level, most vision scientists are committed to the belief that perceptual states come about only in conjunction with brain states; that is, that brain states are a necessary condition for the existence of the perceptual world. Moreover, computational algorithms that create the properties of perception — circuits that analyze for particular cues and combine them to create cue invariance; circuits that execute perceptual heuristics; circuits that provide access to memory, and routes for top-down influences on perception — must exist within the visual system. Similarly, high-level neurons and codes that provide the immediate neural basis for conscious perception must
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exist within the visual system. Shades and nuances of all of these linking propositions can be found, implicit or explicit, in the modern literature on cortical processing and perception.

Can we say anything more specific? In particular, do we wish to assume that any more specific forms of isomorphism hold between perceptual states and neural states? Do we wish to assume that the neural representations on which perception is based will bear any specific form of resemblance to the properties or elements of perception?

The modern cortical visual neuroscientist needs to be aware of which variants of linking propositions enter into his assumption structure. Let’s look at some examples.

18.6.3 The “same information content” and many-to-one propositions

Of the three entities – physical states, perceptual states, and neural states – which two have the closest and most necessary resemblance to each other? It can be argued that the relationship between perceptual states and neural states must be particularly close. The perceptual world differs from the physical world – it is impoverished by sensory processing, and enriched by stored information. Neural codes differ from the physical world for the same reasons. But if the perceptual world arises solely from neural activity, the two must be in intimate correspondence. How can we capture the interdependence?

The philosopher Max Velmans (1990) has argued that the physiological representation and the corresponding perceptual representation must have the same information content. Most vision scientists would probably agree with this premise. After all, unless conscious states have an existence independent of brain states, where else would the extra perceptual information come from?

A variant of this idea, however, is that the information content of the two states need not be identical, but that neural states cannot have less information than their corresponding perceptual states. If perceptual states arise solely from neural states, then it follows that all of the information included in a perceptual state must be encoded in the corresponding neural state. That is, any information represented in visual perception must also be represented within the visual system. On the other hand, it seems possible that there could be more states of the visual system than there are states of perception. That is, the mappings from neural states to perceptual states could be one:one or many:one, but not one:many.

If either of the above linking propositions is accepted, other more specific propositions follow. In particular, if stored information is added to the incoming sensory information to create the neural state that underlies a perceptual state, that stored information must be contained in the neural state that underlies the perceptual state. That is, the neural code for perception must include the information added by top-down processing. A similar argument holds for cue invariance and for the operation of heuristics. And on this view, the vividness and detail of peripheral vision implies that there will be a representation of the peripheral visual field in which more detail is expressed than one can find in the incoming sensory signal that originates from the peripheral retina.

18.6.4 Cue analysis and cue combination circuits

Some of the extra information required for veridical perception is contained in the incoming sensory signals in the form of cues. Cues are lawful or probabilistic regularities that occur in the mapping between aspects of the physical world and aspects of the retinal image. As such, they provide potential sources of information about that aspect of the physical world.
We have argued above that veridical perception depends heavily on cues – lawful or probabilistic regularities that occur in the mapping between aspects of the physical world and aspects of the incoming sensory signal. It is the analysis of cues that allows us as perceivers to deconfound certain variables that are confounded in the retinal image, and create veridical perception.

To return to our example of the perception of the distances and sizes of objects: we already know of the cues of accommodation, convergence, and familiar size. But each of these cues is subtle, and each must be analysed in turn, before the information it carries can be made explicit. A common linking proposition in modern visual neuroscience is that cue analysis circuits will be found within the visual system.

18.6.5 The veridicality proposition and neural equivalence classes

Although not as tight as the mapping between perceptual states and neural states, the mapping between the physical world and the perceptual world is also remarkably close. That is, as argued above, the perceptual world bears a closer resemblance to the physical world than it does to the retinal image or the early sensory codes. Therefore, another very appealing linking proposition is that the neural representations on which perception is based will correspond to the properties of the physical world as represented in perception. That is, these neural codes will have a greater resemblance to the properties of the physical world than they do to the properties of the retinal image, or to the early sensory codes. There will be neural algorithms that deconfound the physical dimensions confounded in the retinal image, so that high-level visual codes can bear a close correspondence to the properties of the physical world.

The perceptual phenomenon of cue invariance provides an example. The concept of cue invariance refers to the fact that many different cues can bring about the same perception. For example, the contours of an object – say, a square – can be defined by light/dark boundaries, or chromatic boundaries, or changes in texture, or in a variety of other ways; yet the square is still perceived. Therefore, the veridicality proposition suggests that the neurons that provide the neural representation of the square will also be cue-invariant; they will respond either to light-dark edges, or to chromatic edges, or to texture-defined edges, or to a variety of other edge cues. Similarly, neurons that provide the neural representation of distance should respond to many different distance cues.

The general veridicality of perception provides a similar example. Since we have size constancy and object constancy, we might hypothesize that the neurons that provide the neural basis of size and object perception will provide signals that are invariant over distance and viewing angle. Since we have veridical perception of the speed and direction of motion of an object, despite the confoundings of speed and distance in the retinal image, we might hypothesize that there should be neurons whose signals correspond better to real object motion than to retinal image motion. And so on. All of these hypotheses are instances of the use of the veridicality proposition.

A more specific variant of the veridicality proposition can be stated in terms of the predicted equivalence classes for cortical neurons. If the veridicality proposition is correct, we might expect to find some neurons that respond equally to all distance cues, and other neurons that respond equally to an object regardless of its distance and retinal location. The same object at different locations could be coded by a fixed object signal but a different location signal.

The veridicality proposition underlies many studies in modern visual neurobiology. For example, von der Heydt and Peterhans (1989) have studied the neural basis of form perception by looking for cue-invariant cortical neurons that respond to both real and illusory contours (see Chapter 19).
Will there be neural representations that correspond to the properties of the perceived world? How would we recognize them if we had our electrodes on them? – by their cue invariances and constancy properties.

### 18.6.6 Specific isomorphisms and direct coding

Can we go further? Some theorists have suggested that we can anticipate the kinds of correspondences that will be seen between individual neurons or small populations of neurons, and our perceptions. For example, Horace Barlow (1972) has argued for what he calls *direct coding*: there will be a simple and recognisable isomorphism between the properties of high-level cortical neurons and our perceptions of objects. Specifically, Barlow said that “the active high-level neurons directly and simply cause the elements of our perceptions” (1972, p. 381).

Can we make this proposal more specific? Suppose that we had done a careful, exhaustive set of perceptual experiments, and could make the case that our perception of objects is based on the perception of combinations of a particular limited set of parts. Barlow’s direct coding proposition would then be, the individual neurons in the set of neurons that map to form perception will each be selectively tuned to one of those parts, and the object will be represented by activity in the combination of the neurons that code its parts.

Note that this assumption is not a logical necessity. The neural code that underlies conscious perception could be complex and unrecognizable, and bear no explicit resemblance to the perceptually defined parts of objects. In that case, the mappings from neural states to perceptual states would be complex rather than simple – the neural/perceptual mappings would do a lot of the work of perception. But we neuroscientists would be infinitely gratified – and maybe not even particularly surprised – to find a simple correspondence between the elements of perception and the elements of neural codes.

### 18.6.7 Parallel processing and multiple codes

Up until this point, we have been working under the implicit premise that the visual system has only a single, “final” code to produce – the code that underlies conscious visual perception. However, our exploration of the concept of parallel processing has suggested that the visual system might be called onto produce two or more relatively separate “final” codes, to serve different purposes. The ventral stream may produce one code in the form required to accesses memory, allows object recognition, and provide the neural substrate of conscious visual perception. But the dorsal stream may produce another code, in the form required for motor responses and coordinated action. In short, parallel processing suggests there may be no single “final” code, but rather two or more codes specialized for different purposes.

### 18.6.8 The sufficient-therefore-causal proposition

Finally, there is a very common linking proposition that sneaks into arguments in visual neuroscience, and is worth a cautionary note. The visual system contains examples of neurons that are tuned on particular stimulus dimensions, or to a particular set of stimulus properties – for example, V1 neurons that are tuned for orientation, and respond best to vertical lines. Given these neurons, it is tempting to talk as though this population of neurons codes that stimulus property: that neurons that are tuned to vertical lines are “vertical line detectors”, and signal the presence of vertical
lines. The argument is, neuron X carries the information required to do function F, therefore it “does” function F.

Stated so starkly, it is easy to see the potential fallacies of such arguments. It would be good to be sure that function F is clearly defined. It would be good to find out whether other neurons in other places also have the right properties to “do” function F. It would be good to make a quantitative model to make sure the information needed to “do” function F is actually present, and that there is a feasible neural processing algorithm to go to the next step. And it would be good to decide what it means to say that a particular set of neurons “does” function F in the first place.

18.7 Principles of neural coding

In the previous section we discussed the kinds of neural codes we expect to find at central levels of the visual system, at an abstract and logical level, based on the properties of perception in combination with particular linking propositions. The final question of this chapter is, leaving perception aside for the moment, what do we know about neural codes at the level of single unit recording? What forms do we expect neural codes to take in the cortex, as they recode incoming sensory information, incorporate heuristics, and eventually form the neural basis of our perceptions and actions? Is one kind of coding better than another at a particular processing stage, or for a particular purpose? Questions of this kind are currently coming into prominence in the field of computational neuroscience.

Neural codes can be classified on several different dimensions. A few of them are as follows. Some of them overlap. We begin with a principle that applies to single neurons, proceed through those that apply to populations of neurons, and end with special coding distinctions developed to treat the mapping of neural activity to conscious perception.

18.7.1 All-or-none vs. graded

This distinction applies to the code carried by a single neuron. In some contexts we discuss a single neuron as though it is either firing or not firing; that is, that it has a “trigger feature”, and that either responses or does not. At other times, we think of single neurons as being capable of firing at many different rates, that is, as having a graded response. For a fixed population of neurons, more information can be carried by graded responses than by all-or-none responses.

18.7.2 Redundant vs. independent

A redundant code is one in which the same information is carried by more than a single neuron, so that the firing rates of a set of neurons are correlated and interpredictable. A fully non-redundant code is one in which each neuron’s activity level is independent of the activity level of all of the other neurons. For a set of neurons of a given size, more information can be carried by a non-redundant code than by a redundant one.

Some of the early recodings of the visual system can be thought of as reducing the redundancy of the spatial code. For example, a typical retinal image contains spatial redundancy in the form of large regions of homogeneous illumination. The photoreceptors create a spatially redundant neural code from the spatially redundant retina image. But the center/surround properties of the retinal neurons tend to cancel out the signals from these large regions, and create a less redundant code, in
which the only neurons that are active are those whose receptive fields fall in regions of high local contrast, such as edges. A redundant code in which many elements are active has been recoded into a less redundant code with fewer active neurons, each of which therefore carries more information about the image.

### 18.7.3 Coarse vs. dense

This distinction applies to the number of different kinds of neurons that are in use to code all of the possible values along a stimulus dimension. If relatively few neurons are used, the code is coarse; if many are used, the code is dense. For example, at the level of the photoreceptors, wavelength information is carried by the signals from only three classes of cones – a coarse code. Two-dimensional spatial location, on the other hand, is carried by the activity of a subset of 100 million photoreceptors – a dense code. At the level of V1, orientation is carried by a set of neurons tuned to different orientations, but there is as yet no agreement on the number of different orientations, and thus no agreement on the coarseness vs. denseness of the code.

### 18.7.4 Sparse vs. compact

This distinction and the next apply to high-level neurons that are used to represent a particular object or scene in our perceptions. Suppose that there is a population of N neurons whose activities map to the perceptions objects or scenes. The question is, how many of these neurons, K, or what fraction of them, K/N, are involved in representing any single, particular scene? If only a small proportion of the neurons are active – K/N is small – the code is sparse. In the extreme of sparseness – if K were 1 for each object – we would be back to our old friends the grandmother cell and the yellow volkswagen detector.

On the other hand, if many or most of the neurons are active in representing each object or scene – K/N is large – the code is compact. Moderately compact codes are often referred to as pattern, population, or ensemble codes. In the extreme, the firing rates of all N neurons could participate in the coding of every object or scene. In this case the number of codes available is N times the number of distinct firing levels for each neuron. This extreme is called a factorial code.

### 18.7.5 Direct vs. arbitrary

This distinction applies to the question, discussed above, of whether or not there is a recognisable isomorphism between the neurons that form the neural correlate of perception, and the elements of perception. If the trigger features of the neurons correspond closely to the elements that make up our perception of objects and scenes, the code is direct. If there is no recognisable correspondence, the code is arbitrary. Of course, the sparser the code – the fewer the neurons that participate in it – the more direct it is likely to be. And again, the extreme of a direct code would be a code in which the trigger features of high-level neurons correspond directly to the perception of whole objects – grandmother cells again.

### 18.7.6 Efficient vs. inefficient.

Finally, an efficient code is one that carries a maximum amount of information under the circumstances in which it is used. That is, in an efficient code the responses of each neuron should be
graded, so that there can be many different firing rates for each neuron N in the population; and the individual neurons should be independent, so that each of the possible combinations of firing rates of the N neurons can have a distinctive meaning. Putting these two dimensions together, a factorial code is a maximally efficient code.

In addition, the modern concept of efficiency explicitly includes the idea that the code is matched to the characteristics of the environment in which it is used. That is, different codes will be maximally efficient in different environments. Trivially, if a fish lives in deep water, to which only a narrow band of wavelengths penetrates, it would be inefficient for it to have more than a single kind of photoreceptor. Less trivially, if humans were to live in an environment dominated by low spatial frequencies at vertical orientations, one would expect to find a high fraction of cortical neurons tuned to respond to these features. This notion of efficiency is closely tied to environmental and developmental concepts: the neural code evolves over generations, and develops over a lifespan, to be statistically optimal for the organism in the environment in which it lives.

Modern studies of coding efficiency are concerned with quantifying the statistical properties of natural environments, and with deriving computational models that show that the code the individual is thought to have is optimally efficient given the statistical properties of the environment. For example, some authors have argued for spatial frequency channels with particular bandwidths, on the grounds that these channels will optimize the efficiency of coding for the spatial frequency statistics of natural environments.

In summary, vision scientists are increasingly looking to design principles – principles of neural coding such as these – to predict and/or justify the particular neural codes that are observed within the visual system. In particular, the property of efficiency is receiving much attention. Quantitative computational models increasingly incorporate design principles such as these.

18.8 Barlow’s neural doctrine

In 1972, Horace Barlow wrote a seminal paper entitled: “Single units and sensation: A neuron doctrine for perception”. In this paper (pp. 380-381), Barlow laid out five dogmas which he argued underlay the then-current studies of single neurons, and the theories of neural coding implicit in them. As in the present discussion, the goal was to make these dogmas explicit, in order to examine them. Barlow’s neuron doctrine and its dogmas are still relevant today, and they provide some practice with the concepts of neural coding.

Barlow’s first dogma was: “A description of that activity of a single nerve cell which is transmitted to and influences other nerve cells ... is a complete enough description for functional understanding of the nervous system...” This claim is the neuron doctrine itself – understand individual neurons and their interactions, and you will understand the neural bases for perception and behavior.

Barlow’s second dogma was, “At progressively higher levels in sensory pathways information about the stimulus is carried by progressively fewer active neurons. The sensory system is organized to achieve as complete a representation as possible with the minimum number of active neurons.” Barlow argued that at higher and higher levels of the visual system, the number of available neurons n would get larger and larger, and the fraction k/n that participate in the code for an object would get smaller and smaller. In the extreme, of course, this line of argument leads to grandmother cells, but Barlow did not take the argument to this extreme. He argued instead for population coding at
lower levels, but sparse coding in a large population of neurons at the highest levels of the visual system.

The third dogma was "Trigger features of neurons are matched to the ... features of sensory stimulation in order to achieve greater completeness and economy of representation. This selective responsiveness is determined by the sensory stimulation to which neurons have been exposed, as well as by genetic factors operating during development." In other words, Barlow argued for a minimally redundant and an efficient code – a code matched to the environment in which the organism evolved and developed. This proposal is not restricted to the higher levels of the visual system. Indeed, what is efficient may be different for the sparse code at the highest levels and the compact code in the optic nerve.

The fourth dogma was "... the active high-level neurons directly and simply cause the elements of our perceptions." In other words, Barlow argued for direct coding – a simple and recognizable isomorphism between neural activity and perception.

And finally, the fifth dogma addressed the question, what variable corresponds to impulse frequency in a high-level sensory neuron? Barlow’s answer was: "The frequency of neural impulses codes subjective certainty: a high impulse frequency in a given neuron corresponds to a high degree of confidence that the cause of the percept [i.e. the trigger feature of the neuron] is present in the external world..." Interestingly, Barlow acknowledged the presence of graded responses, but did not want to concede that the many different firing rates of a single neuron could have a wide range of different meanings in a pattern code. By using different firing rates only for the purpose of coding the relative certainty of the same object, he could make graded responses consistent with the fourth dogma – that the active high-level neurons directly and simply cause the elements of our perceptions.

### 18.9 Summary: Bumblebees can fly

In this chapter we have explored the relationships between three entities: the perceptual world, the physical world, and the neural codes that intervene between perceptual and physical worlds.

Everyday experience tells us that our perception is almost always veridical: we can perceive the sizes, shapes, colors, and brightnesses of objects with remarkable accuracy, recognize objects, fill in the details of peripheral perception, and respond appropriately to the physical world on a moment-to-moment basis. By a bumblebees can fly argument, we know that there must be neural computations that allow these remarkable achievements to occur. In fact, we are very good at these perceptual tasks, and they are achieved automatically and effortlessly. For this reason it is sometimes hard to overcome our naive acceptance of these accomplishments, and stop taking them for granted, in order to reach the understanding that such perceptual capacities are remarkable and problematic. Such perceptual problems will be explored in the remainder of this book.

A major principle that enters into an understanding of perception is that the incoming sensory signals are combined with stored information – perceptual heuristics and information from memory – to create veridical perceptions of objects in the world. The physical world is to some degree underdetermined in the retinal image, and physical variables are often confounded. But there are cues (often subtle ones) in the image that, if you know how to interpret them, provide clues as to the characteristics of the physical world. The perceptual system must have stored knowledge of these regularities in the form of perceptual heuristics, and use them in combination with the incoming
cues to create largely veridical perceptions of the physical world. These ideas are deep ones, and they will become more clear through examples in the subsequent chapters.

We also argued that the system properties of perception provide the basis of many of the visual scientist’s hypotheses and speculations concerning the neural codes that underlie perception. Many of these hypotheses and speculations involve linking propositions, and analysis of them allows us to carry forward ideas we have developed in earlier parts of the book. For example, the proposition that perceptual states arise from neural states is probably regarded as certain and even tautological today, whereas Barlow’s proposition that “the active high-level neurons directly and simply cause the elements of our perceptions” – that a sparse code with simple isomorphisms will provide the neural substrate of perception – remains much more speculative.

In any case, it is important to be clear about the assumptions that underlie one’s beliefs about the neural correlates of perception. Why? Because the current assumption structure may work for a while, and assist us in revealing some of the properties of central visual codes. At the same time, it may limit the hypotheses we generate, and lead us to a narrower-than-optimal range of hypotheses and experiments. When the assumption structure is explicit, we can more readily ask what the alternatives are, and think outside the box.

Finally, we examined some of the dimensions – sparseness vs. compactness, directness vs. arbitrariness – on which neural codes can differ, and used Barlow’s neuron doctrine as an exercise in using these new concepts of neural coding.

In the following chapters, we will examine several different aspects of perception – depth and distance, brightness and color, time and motion, and form and object perception – in more detail. In each case, we will address the psychophysical and perceptual properties of the phenomenon, together with whatever is known about the perceptual heuristics and the physiological processing that make the perceptual properties possible.