

Keeping perception accurate

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Perception should change if an error in perception is detected. Yet how can information that comes through the senses ever indicate that those very senses aren't accurate? Knowledge of objects that arises independently of sensory experience can be used to check the sensory information for errors. For instance, an *a priori* constraint that one object cannot be in two places at the same time would lead to error detection if the sensory systems suggest that one object is in two places. Variants on the classic prism-adaptation phenomenon have revealed new rules about changes in space perception. These variants involve specifying new unusual mappings between visual space and motor (proprioceptive) space, and testing for generalization to novel untrained locations. The research has suggested that there is a preference for changes in space perception that shift space rigidly everywhere, that shrink or expand space uniformly, and that preserve the one-to-one relationship between modalities. Finally, this review discusses the issue that perception must change to remain accurate in the face of childhood growth and adult drift.

A mouse is smaller than a breadbox; dogs have sharp teeth; apples can be red, green, or yellow. These statements illustrate knowledge of the world gained through interaction with objects. World learning typically changes knowledge, thoughts, expectations, beliefs, emotions and reflexes. Perceptual learning, in contrast, refers to actual changes in *perception*. For example, a cup of coffee is placed in front of you and you are asked to indicate where it is located. You correctly indicate that the cup is waist-high and straight ahead of you, an ability useful for obtaining the cup if you want to drink from it, or avoid knocking it over if you don't. Suppose I now present your senses with certain experiences for 10 minutes. Afterwards, the cup is placed in exactly the same location. You perceive the cup to be at the same height, but insist you see the cup about six inches to your right. Experience with the world brought about an actual change in the visual perception of an object's location. If such a change occurred in any modality, it would be an example of perceptual learning, as broadly defined.

But do such changes occur? Change in perceived location was demonstrated in the laboratory 100 years ago^{1,2}, and is now the classic effect known as 'prism adaptation'. The 10 minutes of experience mentioned above involves looking at the world through a wedge prism. A wedge prism is a transparent object that is thicker at one edge and thinner at the other; light passing through the prism is bent, causing the visual world to appear displaced to one side of where it would appear without the prism. Experience with this distorted world leads to changes in the perception of location³⁻⁵ that have been reported to last more than two years⁶. (For a demonstration of a change to a different perceptual feature, see Box 1.)

How does one bring about changes in perception? We would not expect perception to change with every new experience. If perception changed that readily, the world would be chaotic, with objects and environments transforming almost continuously. Perhaps the world would look to adults as William James thought the world looked to infants: a blooming buzzing confusion⁷. For a consistent sensory world, perception should change only when the underlying processes giving rise to that perception are not functioning properly or could be improved upon. Otherwise, there would not be a need for perception to change; moreover, change could be harmful. Consequently, the experiences that lead to perceptual learning must imply that perceptual systems are not functioning correctly. However, if we try to analyse what kind of information would fit that description, we encounter a vexing puzzle.

Perceptual paradox

Learning is driven by experience with the world. Experience with the world comes through our sense modalities. In order for perceptual learning to occur, there must be evidence of an internal error. But how can information that comes through the senses possibly indicate that those very senses are incorrect? Why wouldn't that information simply be interpreted as reflecting something new about the world?

The answer to the apparent paradox is that not all knowledge about the world comes through our senses; some of it comes through our genes. Innate knowledge about the way the world works is available before any personal experience with the world. If sensory information appears to differ from that knowledge, we conclude that there is something

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Box 1. 'McCollough effect' and Pavlovian associations

An elusive phenomenon discovered in the 1960's (Ref. a) can also be understood within the current framework of perceptual correction. Viewing magenta vertical lines alternating with green horizontal lines leads to illusory color perception where white vertical lines look faintly green, and horizontal lines pink (see Fig. 1). This is no ordinary afterimage. The illusion persists for days, implicating adaptive learning of some sort. But if this is perceptual learning, what is it about these displays that indicates that our perceptual systems are malfunctioning?

The vertical and horizontal displays indicate that a single object – a grating of lines – changes color when the orientation of the object with respect to the observer changes. Yet an object should not change color when its orientation changes! To allow this to happen would undermine perceptual constancy (Ref. b). Consequently, the change of color is ascribed to a perceptual error, and the 'aftereffect' observed reflects the resulting perceptual tweaking (Ref. c). This view is contrary to a prevailing theory that the long-term after-effects result from Pavlovian conditioning, in which a simultaneous association is formed between magenta and vertical (and green and horizontal) because of their repeated co-occurrence in the visual world provided by the McCollough stimuli (Ref. d).

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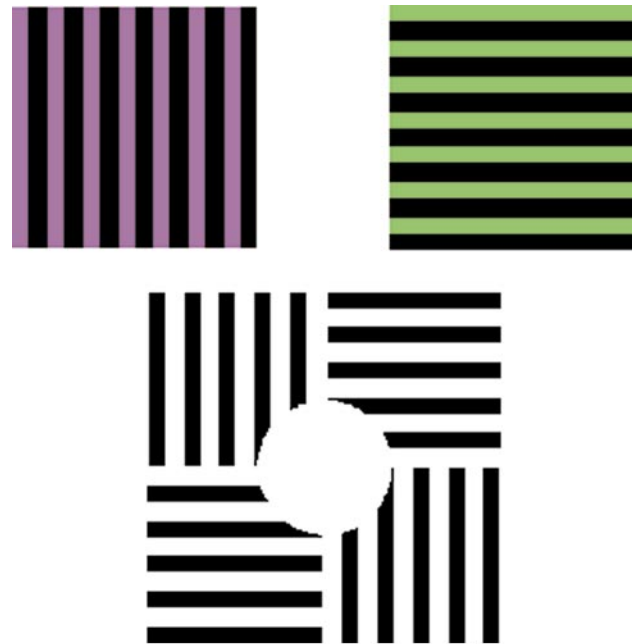


Fig. 1. The McCollough Effect. Cover the test pattern (bottom), and look at the pattern on the left for a few seconds. Do not fixate on any one place, but allow your eyes to wander around the whole pattern. Then shift your gaze to the pattern on the right and repeat. Switch between the two patterns every few seconds for two or more minutes. Close your eyes or look at something neutral for a few seconds to allow any simple afterimages to fade. Finally, look at the test pattern. You should see color contingent on the orientation of the bars.

wrong with the sensory systems. Otherwise, there would not be a way to know that our sensory systems are not working properly. The kinds of innate knowledge that are relevant are internal 'constraints' that have been found to affect perception and cognition. Spelke has found that infants already know that the world is constrained to behave in certain ways^{8,9}. Many of these constraints focus on properties of objects; for instance, objects travel on continuous paths and cannot pass through one another. Shepard has argued that properties that have been true of the world throughout our evolutionary history are candidates for internal constraints that affect what we see^{10,11}. For instance, most objects maintain their rigid structure over time rather than undergo plastic deformations. 'Internalization' of this fact has led to the perception of rigidity when viewing underdetermined, information-poor displays¹¹, such as when a polygon appears to rotate rigidly rather than deform, in an apparent motion paradigm¹². Another source of constraints, besides genetic internalization over evolutionary history, might arise from early internal developmental changes that are not dependent on environmental input. Such structures would presumably be innate, but not derived from genetic encoding^{13,14}.

Constraints are essential for allowing any perceptual learning to occur. In addition, consideration of perceptual learning suggests an important new reason for the existence of such constraints: detecting and fixing errors in perceptual mechanisms would be impossible without independent knowledge of how some aspects of the world work. And without finely tuned perceptual machinery, we would be

unable to gather veridical information about how the remaining aspects of the world work.

What about initiating changes specifically in the perception of location? The critical part of the experience with the prism-distorted world was identified to be a discrepancy between two different modalities, usually vision and touch. If you hold a pen and look at it at the same time through a visually displacing medium, the pen will be perceived to be in one location through the sense of vision, but will be perceived in a different location through the sense of touch/proprioception. In addition, it has been noted that this situation differs from the usual state of affairs, where vision and touch agree^{15,16}. While both of these ideas are important, they are also insufficient to account for why a change in perceived location occurs. Discrepancy or surprise is the input to all learning processes. What makes this discrepancy lead to a genuine change in *perception*? Consider the following three different possible consequences when confronted with a disagreement between vision and touch concerning location.

(1) 'Oh-Wow': 'Hey, I'll be darned. An object can be in two places at the same time. Better note that.'

(2) 'Ho-Hum': 'Vision and touch come up with two different locations because they are referring to different objects. Nothing new there.'

(3) 'Uh-Oh': 'Vision and touch localize the same object in two different places. I know that is impossible; therefore, there must be something wrong with me.'

Any of these three responses is logically possible. If the first alternative occurs, the observer will learn something

Box 2. Object identity

Object identity refers to the perception and knowledge that an object is the same object as one encountered previously, despite change (e.g. Ref. a). If a car disappears in a tunnel and later exits from the other side, you believe it is the same car despite the different spatial locations, but would not if it was a coupé that entered and a truck that emerged. In addition, an object-identity decision applies not only to samples from different times, but also to samples from different modalities (vision, audition, touch), spatial locations, and eyes (left eye, right eye) (F. Bedford, unpublished manuscript and Refs b,c). For instance, how do you know that the pen you are looking at and the pen you are holding are the same pen? A 'same object' decision is critical in order that such diverse phenomena as prism adaptation, apparent motion, Gestalt grouping, priming, and ventriloquism are obtained.

How do observers decide if two samples refer to the same object when they are not identical? A general solution for the establishment of object identity might be based on a hierarchy of geometries (F. Bedford, unpublished manuscript). In this theory, observers access a family of geometries, each a superset of the preceding one (derived from mathematician Felix Klein's transformation approach to geometry, Ref. d). Each geometry is defined by a group of transformations from one form to another that alter some properties of the original form (outside the geometry) and leave others unchanged (within the geometry). This leads to a natural ordering of 'shape' properties, such as location, size, parallelism, and order. The more geometric properties that are altered by a transformation between two samples, the less likely the two samples will be judged as originating from the same object.

The geometric view is consistent with recent research on object identity in infants. Shape is available to infants earlier in development than color or surface texture (T. Wilcox, 1997, poster presented at the Society for Research in Child Development, Washington, DC; see also Ref. e). In addition, some of the spatiotemporal properties preferred by infants (Refs a,f,g) might be equivalent to transformations in the geometric hierarchy from 'level 1', where preserving identity should be easiest. (For recent discussions on object perception in infants, see Refs h,i.)

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new about the world. Much discrepant and surprising information that we encounter in the world is handled in this way. But the ingredient that precludes learning about the world ('Oh-Wow') and produces instead a perceptual-error interpretation ('Uh-Oh') in this situation is the *a priori* knowledge that the world cannot be the way the sensory systems seem to suggest. The critical constraint is that an object cannot be in two places at the same time (Refs 17–20 and D. Narter, PhD thesis, University of Arizona, 1997). Only when the constraint contradicts the sensory information does the disagreement between the two modalities become a problem for perceptual mechanisms. If one is certain that an object cannot be in two places at the same time, but information received from the sensory systems indicates otherwise, then one deduces that there must be something wrong with the sensory systems. (See Box 1 for another example.) There must be an error in the chain of events that leads from the proximal stimulus (the retinal image in the case of vision) to the perceptual interpretation. The detected error leads both to a short-term resolution, where there is an immediate compromise between the two conflicting values or one value suppresses the other (called 'capture', e.g. Refs 21,22), and a long-term resolution where underlying changes will prevent conflicts in future situations ('adaptation').

Before proceeding, consider the second alternative where neither perceptual learning nor world learning occurs (the 'Ho-Hum' response). If the mismatch between the sensory systems is attributed to the existence of two different

objects, learning does not occur. There is no constraint that precludes different objects from being in different places at the same time. In addition, it is not an unusual occurrence: I may be looking at my pen while editing this manuscript but lifting the cup of coffee that is now of sight. The two different modalities must be judged to refer to the same object before any change in perception will occur^{23–26}. How does the perceptual system decide that the cup I am seeing and the cup I am feeling refer to the same object? Or that the pen that I am seeing and the cup that I am feeling are different objects? I believe that this is a question of fundamental importance that has not yet been completely answered (see Box 2).

A few rules

Getting perception to change is both difficult and easy. It is difficult because the information that drives perceptual learning must meet stringent criteria. It is easy because once those criteria are met, 5 or 10 minutes of concentrated training is all that is needed to produce simple changes. Consequently, many questions about the underlying mechanisms can be readily addressed in the laboratory.

We have conducted experiments that use modern variations on the 100-yr old paradigm involving prism-adaptation^{17,27,28}. A single red light, unilluminated at first, is attached to a subject's finger in a completely darkened room. When a visual target appears in the distance, the subject attempts to point to the target. If pointing is accurate, the light on the finger illuminates; if the subject strays as little as

Box 3. Cognitive impenetrability?

The pendulum has swung to an extreme. Pylyshyn argues that visual perception (specifically ‘early vision’) is prohibited from using any cognitive expectations or knowledge (Ref. a) and Radeau argues the same for crossmodal learning (Ref. b): However, earlier research suggests that changing an observer’s beliefs about whether they are in the presence of one or two objects changes the perceptual outcome of two modalities carrying conflicting information (Ref. c). One thing is clear: awareness of any type of conflict between modalities, error in pointing, discrepancy between values, or problem with perceptual systems is *unnecessary* to get perceptual learning. Training procedures that eliminate all awareness of errors do not preclude adaptation (‘concurrent display’, see Ref. d).

But what happens if observers do become aware of some error? Conscious awareness leads to other ways to correct errors, such as a deliberate motor correction. Whether these other con-

current learning mechanisms indirectly affect perceptual learning, and/or whether conscious awareness itself directly influences perceptual learning is not yet known. Informal observations in our laboratory suggest that awareness of pointing errors leads to *less* perceptual learning (see also Ref. d), but the level of interaction is not yet clear.

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0.25 degree away, the light turns off. The task is initially challenging because the subject is looking through a prism: where the target appears is not where the target is actually located. Nonetheless, after a few seconds of trial and error exploration, a subject hones in on the true position of the target (does it matter what she is thinking? See Box 3) and the finger light illuminates (Fig. 1). But note that the subject is also looking at the finger through the prism. Consequently, the subject will feel the finger to be in one place, but will see it in a different place. At this moment, when the subject succeeds in illuminating the light on her finger, there is information about a new mapping at effectively only a single location in space. For instance, if the true location of the target is straight ahead, and the prism produces a 10 degree displacement, a single visual–motor (or visual–proprioceptive) pair of (10,0) has been created. The procedure allows for greater control of space than older procedures where a simple uniform shift of all of space was used almost exclusively. To create ‘complete’ mappings, different size shifts for different places in space are used. The different size shifts are created with a computer-driven variable prism, which allows a wide range of shifts in either direction to be selected.

When the world is ambiguous

What happens if we shift the visual world a few inches at only one location, without providing any information about any of the other locations? Repeated training with a single visual–proprioceptive pair (e.g. 10°, 0°) leads to a change at the trained location²⁷. Previously, we did not know that such limited exposure could even drive the perceptual machinery. Of special interest is how this information generalizes to other locations. A familiar type of generalization would be if the impact of that training declined as the distance from the trained location increased. However, a seemingly complete generalization extending at least 20 degrees in either direction is observed²⁷ (Fig. 2). This was the first indication that a mapping between two dimensions should not be thought of as a set of independent visual–motor pairs as simple associative models would predict. Instead, locations

are linked to one another. Changes in one region have substantial impact throughout the connected dimension.

While investigations into the formation of associations have focused extensively on representing individual connections, the issue of mappings between entire dimensions does resurface from time to time and further study may reveal new important ideas about learning.

Additional research demonstrates that equal-sized generalization can be prevented by adding training at a second location, whose shift is in the *opposite* direction to that of the first location^{27,28}. This results in a uniform expansion (or contraction) of one modality with respect to the other for all of space, despite training at only two locations of space (Fig. 2). Training with two new visual–motor pairs (e.g. 15, 25; –15, –25) is ambiguous and does not specify what the mapping should be elsewhere. An infinite number of mappings would be consistent with any two pairs. However, the data suggest a mapping is nonetheless imposed from within such

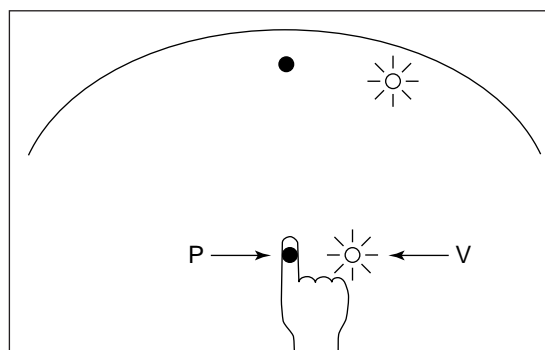


Fig. 1. Perceptual learning. Illustration of the training condition used to initiate changes in the perception of location. Subjects look at a single illuminated target in space in a completely darkened room and try to point accurately at the target while looking through prisms that shift the visual image. The actual position of the target in space is shown by the small filled circle. The position as it appears through the prism is shown by the open circle with ‘sunburst’. Also shown are the visual position (V) and the felt position (P) of a small light worn on the finger at the point when the subject has succeeded at pointing to the actual location of the target. Note how V and P are different.

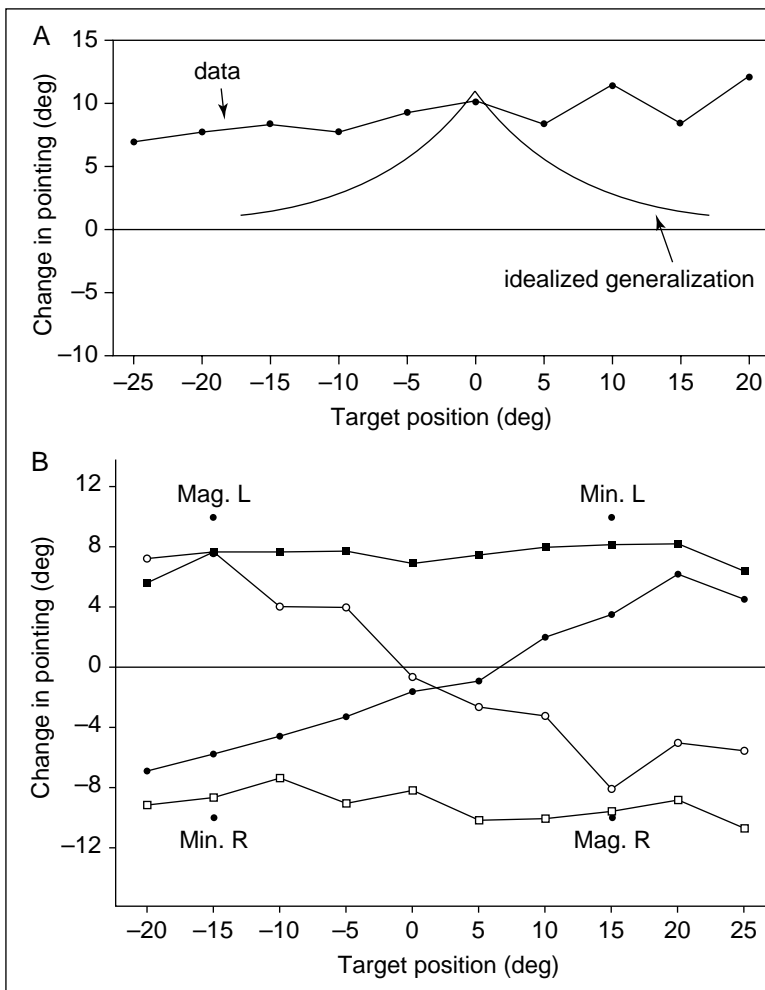


Fig. 2. Ambiguous input. The graphs show generalization to untrained locations following training at only one location (A) or two locations (B). An experiment consisted of three parts: pre-test, in which normal pointing to visual targets was assessed before training; training, in which subjects received the new mappings between modalities; and post-test, in which pointing to visual targets was reassessed. Data shown are mean differences in pointing to visual targets before and after training (post-test minus pre-test) as a function of target position (0 = straight ahead of subject, minus directions = left of straight ahead.) Thus, if training was ineffective, data shown would be always be at zero. (A) An idealized generalization gradient and the actual data following repeated training trials at the visual position -1.3 degrees. The position was shifted 11.3 degrees to produce a single visual-proprioceptive pair of locations at $(V,P) = (-1.3, 10)$. This differs from the normal mapping where values of the V-P pair would be identical to each other $(-1.3, -1.3)$. Note how the data show a rigid shift for all of space despite the limited training, and contrary to an idealized generalization decrement surrounding the trained location. (B) Four groups of subjects are shown. Each group received training with two visual-proprioceptive pairs. Two of the groups received training in which there were 10 degree shifts for the two pairs in the same direction $[(V,P) = (-15, -5), (15, 25)]$ for the 'left displacement' group, filled squares; $(-15, -25), (15, 5)$ for 'right displacement', open squares] and the other two groups received training with 10 degree shifts that were in opposite directions $[(15, -25), (15, 25)]$ for the 'minification' group, filled circles; $(-15, -5), (15, 5)$ for the 'magnification' group, open circles]. The locations of training positions are shown on the graphs as the unconnected filled circles. (L = left displacement, R = right displacement, Mag. = magnification, Min. = minification.) Note how the data show *linear* generalization to untrained positions in all 4 groups.

that all positions between the two trained locations change in accord with a linear function. This result is consistent with the view noted above that a dimension is not a set of independent locations (see also Refs 24,27-29) and further suggests that linearity (uniform shifts leftward or rightward, and uniform stretches or squashes) might be an internal bias for correcting perceptual errors.

When the world is unambiguous but strange

Underdetermined situations cause internal biases to reveal themselves in patterns of generalization to novel locations. One can also ask: what are the limits of perceptual correction? Consider the two mappings shown in Fig. 3. The first distorts space by taking all positions to the left of straight ahead and pulling them further to the left by the same amount, and all the positions to the right of straight ahead and pulling them to the right by the same amount. The second mapping does the reverse: all the positions to the left of straight ahead are shifted rightward, and all positions to the right of straight ahead are shifted leftward. Both mappings use the same visual positions and the same size distortions. However, the second mapping violates the *topology* of space. Note how the mapping is many-to-one; that is, points distinct in the visual dimension are fused together in the motor/proprioceptive dimension. This implies that two different visual locations could be touched by pointing to a single location! Note also how the original *order* of the points is disrupted when they are mapped from one modality to the other.

How are these bizarre modality mismatches accommodated? Roughly twice as much perceptual change occurs for the mapping that does not destroy the topological properties¹⁷. Note that a linear bias by itself is insufficient to account for this difference because both mappings are non-linear (neither mapping uniformly shifts or uniformly changes the scale of all of space.) In addition, while there was some adaptive change even to the non-topological mapping, none

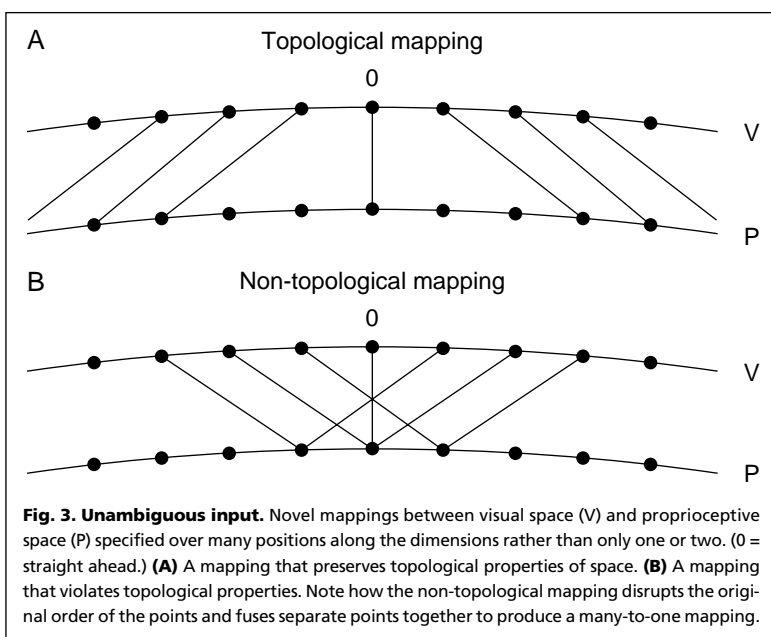


Fig. 3. Unambiguous input. Novel mappings between visual space (V) and proprioceptive space (P) specified over many positions along the dimensions rather than only one or two. (0 = straight ahead.) (A) A mapping that preserves topological properties of space. (B) A mapping that violates topological properties. Note how the non-topological mapping disrupts the original order of the points and fuses separate points together to produce a many-to-one mapping.

Box 4. When is it perceptual learning?

Figure 1 illustrates a paradigm that involves locations, pointing, errors, and novel mappings – yet is not perceptual learning. Subjects see a target in the distance, in an otherwise completely dark room, and are instructed to illuminate an LED on their finger by pointing and moving their hand around. Like our prism adaptation paradigm, the LED is programmed to turn on when the hand is to one side of where the subject sees the target, but subjects do not look through a prism (Ref. a). Although the mapping between the target in the distance and the location of the hand is identical to the prism adaptation paradigm (compare with Fig. 1 in the main text), here the subject sees the hand and feels the hand in the *same* position. Because there is no single object localized in different places by different modalities, there is no violation of an internal constraint, no indication of a problem with the perceptual machinery, and therefore no reason to change perception.

But note that there is a reason to change *something*. Subjects become aware of a mismatch between the target and where they point and moreover, they must learn – and do learn – to point to the new location specified by training. What kind of learning is this? Perhaps it has something to do with the acquisition of new motor skills, or with some type of conscious, cognitive problem solving. Whatever learning process this situation invokes, it does not meet the criteria for leading to changes in perception. And in fact, training of this sort leads to different outcomes: there are more local effects and more typical generalization decrements than with the prism adaptation paradigm (Ref. a).

It remains an exciting and open question as to the whether several new and recently used learning paradigms (Refs b–f) meet the error-triggering criteria to elicit genuine perceptual learning or instead lead to some other learning process. These new paradigms and outcomes include: (1) altered visual–motor mappings, using a computer screen for visual targets and a mouse-like tablet for motor responses (Refs b,c); (2) disruption of arm movements while pointing using a force field (Ref. d); (3) altered relationship between position of a target on the screen and position of a key press for both Huntington's patients and normal observers (Ref. e); and (4) apparent improvement in visual identification

with extensive practice (K. Reinke, PhD thesis, University of Arizona, 1998, and Ref. f).

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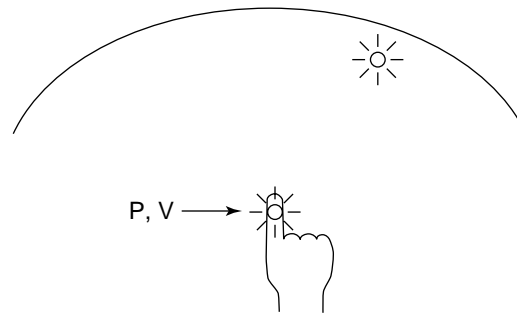


Fig. 1. Not perceptual learning. (Compare with Fig. 1 in main text.) Training condition in which the relation between the visual position of the target in space and the position of the hand is identical to that depicted in Fig. 1, but does not create the conditions necessary to initiate perceptual learning. The difference between the location of the visual target and the location of the hand that results in illumination of the finger LED was produced through computer software rather than prism-distorted vision. Note how V and P of the hand are the same. (V = visual position of the finger LED; P = felt position of the finger LED.)

of the non-topological *features* was accommodated; distinct positions in space did not fuse nor cross over one another, at least in the training time allotted. These experiments help explore the limits and unique rules of perceptual plasticity (see Box 4) and further investigations are warranted.

What is the function of perceptual learning?

The function of much of the learning we do is to acquire knowledge about the way the world works. However, the function of perceptual learning is to correct internal errors^{17,24}. As shown, a combination of sensory information from the world and *a priori* knowledge of the world is needed to set the process in motion. Once begun, some of the rules involve efficacy of limited input, a bias towards uniform shifts, followed by a bias for scale changes, followed by a sensitivity to topological properties. But why have *a priori* knowledge of the world that an object cannot be in two places at the same time, if in fact objects never do occur in two places at the same time? Why have a perceptual mechanism designed to deal with the event that an object appears to be localized in different places, when such an event is

impossible? There must be a naturally occurring situation where an object could erroneously appear to be in two different places because of a frequent universal perceptual problem. Without the internal constraint about the behavior of objects, we would never know we had a perceptual problem, and could easily come to the wrong conclusion about the world. Without the machinery, we would be unable to fix the problem.

A universal perceptual problem arises from growth. Held suggested over 30 years ago that adaptation to prism-distorted vision in adults may reflect a corrective mechanism designed to deal with physical growth in infants and children³⁰. As the body grows, regardless of how gradually, mappings between the proximal stimulus and perception must change. For instance, as the head grows, a fixed difference in the time of arrival of a sound at the two ears, say 0.3 ms, will correspond to different locations of an auditory stimulus (see also Refs 31–33). Differences in the time of arrival of a sound at the two ears can be used to localize the direction of sound because different direction sounds produce different timing differences as sounds get relatively

Outstanding questions

- If the function of perceptual adaptation is to accommodate growth or drift, what are the exact transformations that would be needed for each of these problems, and do they match the rules so far discovered for adaptation?
- Entire dimensions of stimuli, rather than associations between individual stimuli, seem to play an important role in acquiring new perceptual mappings. Is this true of other learning mechanisms, or is this a unique feature of perceptual learning?
- Why should topological properties influence the type of mappings that can be learned?
- Can conscious awareness of an error affect changes in perception, and if so, at what level does the influence occur?
- How do observers 'decide' if an object they are seeing and an object they are feeling refer to the same object or to two different objects?

closer to one ear and further from the other. But the difference in the time of arrival is also dependent on the distance between the two ears, which changes with development. The scheduling and extent of growth is influenced by external factors and therefore cannot be compensated for in advance. If different modalities are affected by growth at even slightly different rates, crossmodal perception will give rise to objects that are detected in different places by different modalities, although the mismatch is likely to be smaller than the typical mismatch created experimentally. (See Refs 34,35 for recent issues in crossmodal perception.)

A second perceptual problem is 'drift'. A complex system can drift unpredictably from peak performance and corrective mechanisms can realign perception. An analogy to two modalities that drift out of alignment with each other is two clocks that are highly precise but will nonetheless fall out of synchrony with each other unless a signal is passed between them. Measurable drift would be expected if one modality operated without verifying feedback from another modality for an extended period of time. For instance, pointing to targets in space without sight of the hand should eventually lead to changes in where subjects point. If true, perceptual learning mechanisms might not simply reflect vestigial childhood flexibility, but rather the need to fine-tune our perceptual systems continuously. Neuroscience research showing rapid synaptic changes (e.g. Ref. 36) might be consistent with frequent perceptual adjustment.

Conclusion

Keeping perception accurate is essential. Without veridical perception, interacting with the world and learning about the world would be compromised. Many types of learning have an unstated premise that perception is unchanging and veridical throughout the learning. Yet perception itself must change to remain veridical. We have made progress towards understanding many of the unique challenges facing perceptual learning, including the kinds of experiences needed to initiate learning and the rules that operate once changes in perception are required.

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The functional neuroanatomy of emotion and affective style

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Recently, there has been a convergence in lesion and neuroimaging data in the identification of circuits underlying positive and negative emotion in the human brain. Emphasis is placed on the prefrontal cortex (PFC) and the amygdala as two key components of this circuitry. Emotion guides action and organizes behavior towards salient goals. To accomplish this, it is essential that the organism have a means of representing affect in the absence of immediate elicitors. It is proposed that the PFC plays a crucial role in affective working memory. The ventromedial sector of the PFC is most directly involved in the representation of elementary positive and negative emotional states while the dorsolateral PFC may be involved in the representation of the goal states towards which these elementary positive and negative states are directed. The amygdala has been consistently identified as playing a crucial role in both the perception of emotional cues and the production of emotional responses, with some evidence suggesting that it is particularly involved with fear-related negative affect. Individual differences in amygdala activation are implicated in dispositional affective styles and increased reactivity to negative incentives. The ventral striatum, anterior cingulate and insular cortex also provide unique contributions to emotional processing.

This article presents an overview of recent research on the functional neuroanatomy of human affective processes, focussing on studies using positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). Where relevant, some studies on patients with discrete lesions are also included, as well as animal studies that provide much of the foundation for the modern human work. Research on patients with mood and anxiety disorders is, for the most part, not included as such studies have been extensively reviewed in a number of recent publications^{1–6}. Over the past 10 years, there has been an enormous increase in animal research that has provided a detailed foundation for understanding the neural circuitry of several basic

emotional processes⁷. This corpus of literature has helped to make emotion a tractable problem in the neurosciences and has led to the development of affective neuroscience⁸. With recent advances in functional brain imaging, the circuitry underlying emotion in the human brain can now be studied with unprecedented precision (see Box 1).

The functional neuroanatomy of approach and withdrawal-related emotion

Two basic systems mediating different forms of motivation and emotion have been proposed^{9–12}. Although the descriptors chosen by different investigators varies and the specifics of the proposed anatomical circuitry is presented in varying

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