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The Contribution of Sensorimotor Experience to the Mind and Brain

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Abstract

How does sensorimotor experience shape the human mind? This question has been of interest to thinkers for thousands of years, from Plato to the British empiricists. This chapter highlights insights into this puzzle from psychology and cognitive neuroscience. In what ways do knowledge and the functional organization of the cortex arise from sensory experiences? A key source of evidence comes from studies with individuals who have altered sensory experience from birth: those who are congenitally blind, deaf, or missing limbs. Such studies demonstrate that changes in early sensory experience dramatically alter the function of sensory cortices. In congenital blindness, “visual” cortices take on higher cognitive functions, including language and number. This plasticity is believed to occur as a result of top-down input from higher cognitive systems into “visual” cortices. In contrast to these dramatic change in the “deprived” sensory systems, the neural basis of concepts is largely unchanged in sensory loss. The cognitive and neural basis of concrete objects, events, and properties is similar in congenitally blind and sighted individuals. Insights from developmental psychology further suggest that human concepts are not constructed from sensations. Even seemingly sensory concepts such as “blue” have a rich abstract structure early in life. At the same time, studies of training and expertise show that sensorimotor experience does influence our knowledge of what things look like and how to motorically interact with objects. Semantic knowledge broadly construed includes both abstract conceptual and sensorimotor representations. These different types of information are represented in different cortical systems, each of which is sensitive to different aspects of our experience.

Introduction

How do sensory experiences contribute to the mind? In what sense do our experiences of seeing, hearing, and touching give rise to concepts such as *tiger*, *chair*, and *running*? Such questions have puzzled thinkers for thousands of years, dating back to Plato, who held that we are born knowing everything we will ever know, and the role of experience is merely to awaken this knowledge. By contrast, empiricist philosophers such as Locke and Hume proposed that all concepts are built out of sensorimotor experiences and are represented in their terms (Hume, 1748; Locke, 1690; Plato, 1961). Empirically disentangling the contributions of nature and nurture has proven a daunting task since humans share much of their genetic makeup as well as important aspects of experience—for example, vision, audition, motor experience, and the presence of objects, agents, and events in the environment.

A key source of insight comes from studies with individuals who have drastically different sensorimotor histories from birth: individuals who are blind, deaf, or have altered motor experiences. Studies of sensory loss provide a unique window into how the mind and brain responds to alterations in *species typical* or *expected* experiences, i.e. experiences that were ubiquitous to the species during our evolutionary history. As a result, the brain may plausibly have evolved to "expect" such experiences (Greenough, Black, & Wallace, 1987). How does the human brain and mind develop when such experiences are absent? This chapter reviews research examining the effects of sensory loss on different cognitive systems. To set the stage, I begin by describing the effects of sensory loss on the cortical systems that typically support sensory perception in the "deprived" modality, focusing on how congenital blindness influences the visual system. Next, I turn to the effect of sensory loss on conceptual representations of objects and events. By comparing how sensorimotor experience affects these different types of representations, we can better understand which experiences are most relevant to which cognitive systems. To complement these findings, I highlight insights from studies of cognitive development. Finally, I discuss findings from studies of sensorimotor expertise and training. Together, these data provide insights into how sensorimotor experience does and does not contribute to conceptual representations. I end by discussing implications for cognitive neuroscience theories of concepts.

Large-Scale Change to the Function of Sensorimotor Systems in Sensory Loss

Early imaging studies with blind and deaf humans provided some of the first demonstrations that early sensory experience changes cortical function. The “visual” cortices of individuals who are blind from birth are highly active during tactile and auditory tasks (Sadato et al., 1996). Analogously, the “auditory” cortices of deaf individuals show robust responses to visual stimuli (Finney, Fine, & Dobkins, 2001). In *cross-modal* plasticity, apart from changing their preferred modality of input, cortices change their sensitivity to information. For example, in blind but not sighted participants, parts of the dorsal “visual” stream respond to moving sounds and are active during sound localization (Collignon et al., 2011). Dorsal “visual” areas thus enhance their sensitivity to auditory information that comes from an analogous domain to the original visual function (i.e., spatial/motion).

In other examples of cross-modal plasticity, the degree of functional reorganization is still more dramatic. Large swaths of “visual” cortices respond to linguistic information in blindness. This includes not only portions of the ventral and lateral occipital cortex but also parts of V1 (Lane, Kanjlia, Omaki, & Bedny, 2015; Röder, Stock, Bien, Neville, & Rösler, 2002). Responses are observed both to spoken and written (Braille) language and occipital activity is sensitive to high-level linguistic content (e.g., the grammar and meaning of sentences). For example, “visual” language areas respond more to sentences than to lists of words, more to jabberwocky than lists of nonwords, and more to grammatically complex sentences than to simple ones (Lane et al., 2015; Röder et al., 2002). There is also some evidence that these responses are behaviorally relevant. TMS to the occipital pole causes blind but not sighted participants to make semantic errors during verb generation (Amedi, Floel, Knecht, Zohary, & Cohen, 2004).

Language is not the only higher-cognitive function that invades the deafferented visual system. Other parts of “visual” cortices acquire responses to numerical information and still others to executive load in nonverbal tasks (figure 68.1*A*; Kanjlia, Lane, Feigenson, & Bedny, 2016; Loiotile & Bedny, 2018). According to one hypothesis, the invasion of “visual” networks by higher cognitive information in blindness occurs through input from frontoparietal and frontotemporal networks (Amedi, Hofstetter, Maidenbaum, & Heimler, 2017; Bedny, 2017). In the absence of bottom-up information from the retinogeniculate pathway, top-down frontoparietal connectivity takes over “visual” circuits. Consistent with this idea, studies of resting-state connectivity find that in blindness visual areas become more functionally coupled with multiple higher cognitive circuits in frontal and parietal cortices in a functionally specific way (figure 68.1*B*; Deen, Saxe, & Bedny, 2015; Kanjlia et al., 2016). Interestingly, this extreme functional reorganization is curtailed to sensitive periods of development. Although “visual” cortices of adult-onset blind individuals also respond to sound and touch, these responses seem to lack the kind of cognitive specificity observed in congenital blindness (Bedny, Pascual-Leone, Dravida, & Saxe, 2011; Collignon et al., 2013).

The studies reviewed above suggest that early sensory loss has the capacity to profoundly change the function of cortical systems. Even sensory systems believed to be predisposed by evolution for specific sensory processes undergo substantial functional reorganization when the type of experience they have evolved to “expect” is absent during early development (Greenough, Black, & Wallace, 1987).

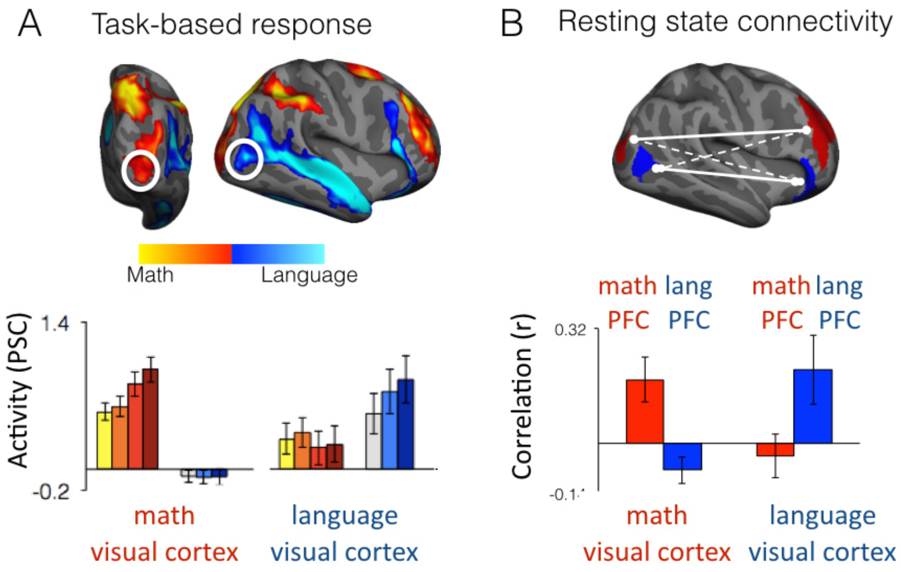

Figure 68.1 Responses to language and number in visual cortices of congenitally blind individuals. A, Math-responsive “visual” areas (*red*) show an effect of math equation difficulty (i*ncreasingly dark-red bars*). Language-responsive “visual” areas show an effect of grammatical complexity: lists of nonwords (*gray*), grammatically simple sentences (*light blue*), and complex (*dark blue*) sentences. *B,* Stronger resting-state correlations with language-responsive PFC in language-responsive visual cortex and with math-responsive PFC in math-responsive visual cortex.

The Abstractness of Blue: Resilience of Concepts to Congenital Sensory Loss

Early sensory loss leads to large-scale plasticity in “deprived” sensory cortices. Do these changes carry forward into conceptual systems? Are the cognitive and neural bases of concepts of concrete properties (e.g., blue), entities (e.g., dog), and events (e.g., run) very different in people who are blind from birth? The evidence reviewed below suggests that this is not the case. Even for seemingly purely “visual” concepts, such as *look* and *blue*, blind and sighted people’s concepts turn out to have a lot in common. Blind children acquire “visual” words at around the same time as sighted children and use them in appropriate ways, making subtle distinctions between the meanings of words such as *look* and *see*— you can look without seeing. Blind children and adults have a coherent understanding of how color works. By the preschool years, blind children understand that a car can be blue but a thunderstorm and an idea cannot (Landau & Gleitman, 1985). Blind adults know the similarity structure of color space, that orange is more similar to red than to blue—although this knowledge is more variable across blind than sighted subjects (Shepard & Cooper, 1992). Blind people are less likely to know object color pairings (e.g. elephants are grey) and less likely to automatically use object color when sorting fruits and vegetables but nevertheless have preserved understanding of the relationship between object kind (natural kind vs. artifact) and color (Kim, Elli & Bedny, 2019; Elli, Lane & Bedny, 2019; Connolly, Gleitman, & Thompson-Schill, 2007).

Analogous evidence comes from studies with individuals who are born without hands. Amelic individuals show typical categorization and perception of hand actions (e.g., typing, playing a guitar). Both reasoning about and perception of actions is intact. Individuals who themselves have never thrown a ball can nevertheless tell when a basketball throw is likely to hit its mark and are sensitive to whether a hand movement is or isn't awkward to perform (Vannuscorps & Caramazza, 2016). Thus, neither visual nor motor experience is necessary for the development of fine-grained reasoning about seemingly sensorimotor information, such as actions, perceptual experiences, light, and color. Even for concrete concepts, sensory loss does not substantially change what we know.

Consistent with the behavioral literature, the neural basis of concrete concepts is resilient to congenital sensory loss. Many cortical areas that are active during conceptual tasks in the sighted and were once thought to represent "visual" modality-specific information turn out to be preserved in congenital blindness. When sighted subjects make semantic judgments about concrete objects, they activate a distributed network of regions, including parts of the medial and lateral ventral occipitotemporal cortex (Martin, 2016). One interpretation of this ventral occipitotemporal activation is that it involves the retrieval of modality-specific visual representations of appearance-related knowledge (e.g., of color and shape). However, a number of studies have identified similar ventral occipitotemporal responses in people who are blind. Those parts of the mediate occipitotemporal and parietal cortex that preferentially respond to nonliving entities in sighted participants (medial occipitotemporal and inferior parietal) also prefer inanimate entities in blind participants (Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009; Wang, Peelen, Han, Caramazza, & Bi, 2016). When blind individuals listen to the characteristic sounds of entities (e.g., of people or artifacts), patterns of activity in ventral occipitotemporal cortex can be used to decode among the classes of entities (van den Hurk, Van Baelen, & Op de Beeck, 2017). Category-specific responses to concrete objects elsewhere in the brain are also preserved in blindness. For example, a recent study finds that different parts of the anterior temporal lobe (ATL) are involved in retrieving knowledge about concrete (e.g., dog) and abstract entities (e.g., idea) in sighted and blind participants alike, although some words, such as "rainbow", appear to activate different parts of the ATL across groups (Striem-Amit, Wang, Bi, &

Caramazza, 2018). In sum, a distributed but clearly defined network of cortical areas involved in representing knowledge about entities is shared among sighted and congenitally blind individuals.

An analogous picture of preservation has emerged from studies of concrete events. Secondary motor areas and parts of the frontoparietal cortices are active when subjects reason about actions (Hauk, Johnsrude, & Pulvermüller, 2004; Kemmerer & Gonzalez-Castillo, 2008). Such activations could in principle arise because of prior motor experiences of performing the actions. However, amelic individuals born without hands activate the same action-related neural systems when viewing videos of meaningful hand actions (e.g., taking a tea bag out of a cup, closing a sugar bowl), including regions within the frontoparietal *mirror neuron* system (Gazzola et al., 2007). Individuals who are blind from birth similarly activate frontoparietal circuits when listening to meaningful action sounds (Ricciardi et al., 2009).

Analogously, lateral temporal cortices (left middle temporal gyrus, or LMTG) that were originally thought to code visual motion features relevant to action verbs are active during verb comprehension in blind and sighted individuals alike (Bedny, Caramazza, Pascual-Leone, & Saxe, 2012; Noppeney, 2003; figure 68.2*A*). LMTG representations that are active during verb comprehension have turned out to be neither vision nor motion related, as was originally hypothesized, since even in the sighted the LMTG is equally responsive to abstract verbs that involve no motion at all, such as *believe* and *want* (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008). This suggests that the meanings of concrete verbs, such as *run*, are represented alongside the meanings of abstract verbs, such as *believe*. Spatial patterns of activity within the LMTG distinguish between different semantic categories of verbs, including the very types of verbs thought to dissociate within sensorimotor cortical systems. The LMTG distinguishes between hand (e.g., *slap*) and mouth (e.g., *chew*) actions, which in some views are distinguished based on patterns within motor cortex (Hauk, Johnsrude, & Pulvermüller, 2004). It also distinguishes between events of light (e.g., *sparkle*) versus those of sound (e.g., *boom*) emission (Elli, Lane, & Bedny, 2019), semantic features previously said to dissociate based on responses in visual and auditory cortices (figure 68.2*B*; e.g., Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008). Seemingly “sensory” features are represented in abstract conceptual systems.

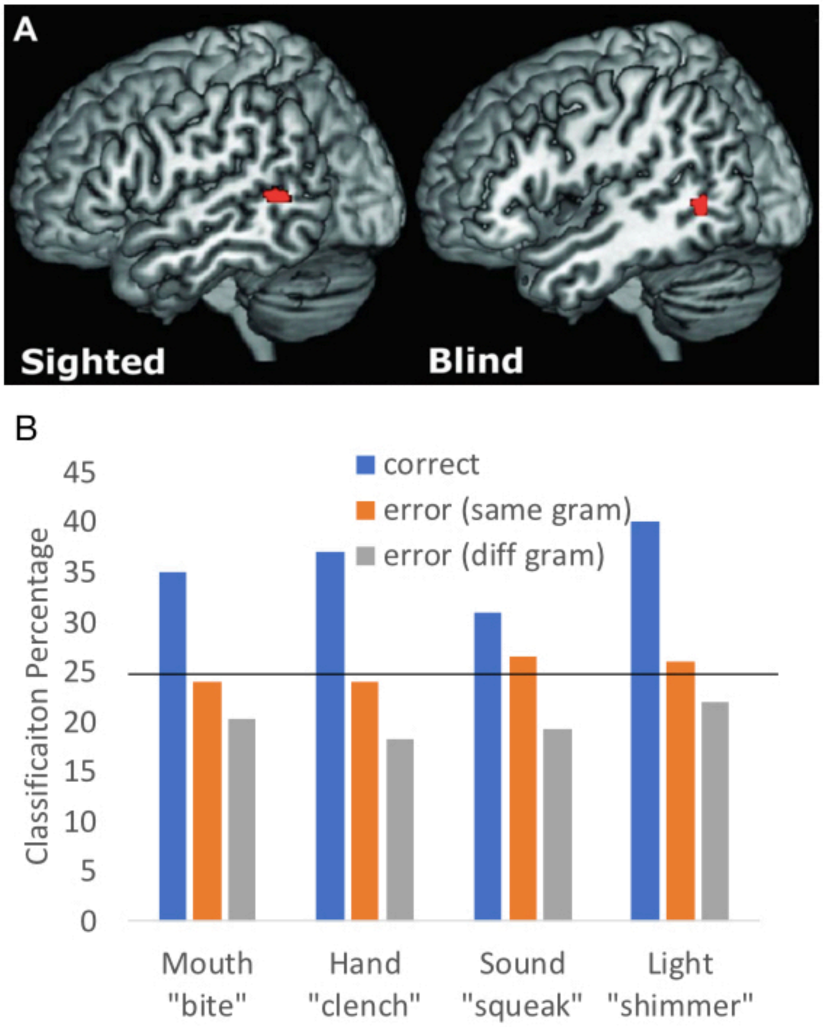

Figure 68.2 Representations of verb meanings in the left middle temporal gyrus (LMTG). *A,* Action verbs > object nouns in sighted (*left*) and congenitally blind individuals (*right*). Reprinted from Bedny et al. (2012). *B*, Performance of linear classifier distinguishing among four verb types based on patterns of activity in the LMTG of sighted individuals: transitive mouth and hand actions and intransitive light-and sound-emission events. The classifier successfully distinguished among mouth and hand actions and light-and sound-emission events. Errors across grammatical type (*white bars*; e.g., transitive mouth action mistaken for intransitive light-emission event) are less common than within grammatical type (*gray bars*; e.g., mouth action mistaken for hand action). From Elli, Lane, and Bedny (2019).

Converging evidence for the idea that rich semantic representations develop in the absence of first-person sensory access comes from studies of reasoning about the mental states. Neural population codes within the mentalizing network (e.g., the right temporoparietal junction) distinguish between beliefs based on seeing as opposed to hearing experiences (e.g., recognizing someone based on her handwriting versus her voice). And they do so equally in individuals who are sighted and in those who are congenitally blind (Koster-Hale, Bedny, & Saxe, 2014). Similarly, there is evidence that both the cognitive and neural architectures of numerical representations is preserved in blindness (Kanjlia et al., 2016). In sum, across a variety of conceptual domains and cortical systems, early and dramatic changes to sensory experience leave the cognitive and neural basis of concepts largely unchanged. This is true not only for abstract concepts such as *want* and *idea* but also for concrete ones such as *dog*, *run*, *see* and *sparkle*. Although sensorimotor experience changes sensory systems themselves, many conceptual representations of "sensory" knowledge are unchanged.

Insights into Origins of Concepts from Developmental Psychology

The evidence reviewed above suggests that a rich array of conceptual representations is independent from our sensorimotor experiences. This view is consistent with evidence from developmental psychology. Research with infants suggests that rather than beginning with sensory representations and gradually progressing toward abstract conceptual ones, children think abstractly from the beginning. Within the first few months of life, infants expect entities that look like agents (e.g., have arms or faces) to behave according to goals and intentions, even though goals are not directly observable (Woodward, 1998). Even without any perceptual evidence, preverbal infants infer the presence of intentional agents when things seem to have occurred "on purpose" (Saxe, Tenenbaum, & Carey, 2005). Infants show early sensitivity to the causal structure of events (Leslie & Keeble, 1987) and expect inanimate entities to obey the laws of intuitive physics (e.g., two things cannot be in the same place at once; Baillargeon, Spelke, & Wasserman, 1985; Saxe, Tenenbaum, & Carey, 2005). Children seek an underlying causal structure in the world around them. Preschoolers treat natural things (e.g., tigers and gold) as having an internal, unobservable essence that makes them what they are. A "three-legged, tame, toothless, albino tiger" is still a tiger because it came from a tiger mother (Armstrong, Gleitman, & Gleitman, 1983). Preschoolers recognize that the insides of objects are more important to determining kind than the observable outsides (e.g. pigs are more similar to cows than piggy banks) (Gelman & Wellman, 1991; Keil, Smith, Simons, & Levin, 1998). As noted above, studies with children who are blind further reveal abstract knowledge about seemingly sensory concepts, such *blue* and *see* (Landau & Gleitman, 1985).

The claim that concepts are abstract from early infancy does not imply that concepts are hardwired fully formed into the brain and learning is unimportant. Children use their sensory systems to collect information from the environment, which enables them to elaborate and revise their representations (Carey, 2009). Importantly, learning itself does not appear to involve the gradual binding of sensations. With just a few examples and in some cases no sensory access to the thing being named, children learn labels for new categories and generalize these labels appropriately to novel instances. Children's learning appears to be a problem-solving process that involves hypothesis testing and revising theories (Gopnik & Meltzoff, 1998; Xu & Tenenbaum, 2007). From this perspective, it is not terribly surprising that concepts of people with altered sensory experience are not so different. The sophisticated learning devices that make up the human brain gather conceptually relevant information through various sensory channels (e.g., there are many clues to whether something is animate).

Sensorimotor Knowledge and Semantics: Insights from Studies of Expertise and Training

Not everything that we know about concrete entities and events is independent of the sensorimotor aspects of experience. Studies of expertise and training demonstrate that subtle and specific variation in sensorimotor experience in adulthood changes our long-term knowledge. Hockey experts (both players and fans) show differential priming effects when matching pictures of hockey actions to sentences that describe them ("The hockey player finished the stride”). When the same participants listen to these sentences in the scanner, experts (players and fans) activate left-lateralized secondary motor areas more than novices, and the degree of activation is correlated with priming effects outside the scanner (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008). Details of our sensorimotor experiences with objects are stored in long-term memory. When presented with photographs of objects, right-handers are faster at judging whether the object (e.g., a whisk) would be picked up by a “pinch” or a “clench” when its handle is oriented toward their own right hand. This effect reverses in patients who were previously right-handed but are now restricted to using their left hands due to brain injury (Chrysikou, Casasanto, & Thompson-Schill, 2017). Such evidence suggests that we acquire effector-specific information about canonical object-related motor actions and retrieve this information automatically, even when it is not required for the task.

Similar evidence comes from studies of color knowledge. For example, making detailed judgments about object color (e.g., Which is more similar to a school bus in color, egg yolk or butter?) activates cortical areas that partially overlap with those involved in color perception, particularly in people who report having a visual cognitive style (Hsu, Kraemer, Oliver, Schlichting, & Thompson-Schill, 2011). Such responses are influenced by training. Subjects who learn the diagnostic colors of novel objects over the course of a week activate color perception regions during recall, even when color is not relevant to the task (Hsu, Schlichting, & Thompson-Schill, 2014). Sensorimotor experience thus changes our reasoning about the physical world and changes representations in sensorimotor cortices.

At first glance, evidence from studies of sensory loss and sensorimotor expertise might seem contradictory. On the one hand, global and early changes to sensorimotor experience dramatically reorganize perceptual systems while leaving conceptual representations largely unchanged. Yet subtle alternations of sensorimotor experience in adulthood give rise to measurably different neural responses during conceptual tasks. How is it that blind and sighted people have similar representations of color, but the representations of sighted subjects trained on a color task for one week differ from those who have not been trained?

It is tempting to dismiss the findings from one of these literatures as “peripheral.” One might argue that the representations retrieved by sighted subjects while making cross-category color judgments and those used by blind individuals when thinking about color are shallow or “verbal” and therefore not truly conceptual. This argument, however, leaves us in the odd position of claiming that much of our linguistic communication and reasoning occurs without using concepts. On the other hand, we might suppose that sensorimotor representations retrieved during conceptual tasks are merely “sensory imagery” and not relevant to cognition and behavior. There is, however, evidence that such representations are behaviorally relevant.

Rather, different tasks engage different types of representations. Sighted people engage color-perception areas only when retrieving detailed information about color hue and saturation, i.e. when judging the colors of objects from the same color category (i.e., school buses, egg yolks, and butter.) No such activation is observed when deciding whether a strawberry is more similar in color to a lemon or a cherry (Hsu et al., 2011). This does not imply that the latter judgment is “shallow” or “verbal.” It still relies on abstract and detailed information about what color is and how it works (e.g., a physical property perceptible only with the eyes, comes in different types, varies across object types and within an object e.g. inside vs. outside) and knowledge of the color categories of specific objects (e.g., cherries are red). The within-category judgments additionally tap into perceptual knowledge of object colors (e.g., cherries are darker than strawberries). Even if we consider the perceptual knowledge of the color distinction between cherries and strawberries conceptual, it is a small fraction of conceptual color knowledge.

Implications for Cognitive Neuroscience Theories of Concepts

Where are concepts in the brain? The answer to this question depends on what one means by the term *concept*. If what we mean are the representations that enable us to judge whether something is or is not a dog, then concepts are represented in amodal cortical systems. Such representations enable us to say that a dog that looks like a cat is still a dog, as long as it has dog DNA. These abstract representations play a crucial role in reasoning, even for seemingly “sensory” categories (e.g., *blue*). This is why people who are blind have a similar concept of *blue* to people who are sighted, while those fish, birds, and insects that perceive blue, nevertheless, do not. If instead by *concept* one means everything we know about a category, then not only amodal representations of what something is but also sensorimotor representations of what it looks like, sounds like, and smells like are included.

Different aspects of our semantic knowledge have distinct developmental origins and are represented in different cortical systems. Experience affects these systems in different ways. Seeing a dog, hearing it bark, and even hearing someone say “dog” are qualitatively different experiences from the perspective of our sensory systems in that they modify different neural circuits (i.e., visual vs. auditory cortices). These experiences are equivalent, however, from the perspective of the abstract conceptual system that represents animate entities: they provide evidence for the existence of an animal of the type dog. Our abstract conceptual knowledge depends on the information the senses convey but not on the modality-specific aspects of experience. This perspective on the origins of knowledge has implications for cognitive neuroscience theories of concepts.

A prominent view is that concepts are distributed across sensorimotor cortical systems (Barsalou, Kyle Simmons, Barbey, & Wilson, 2003). In recent years there has been increasing evidence that modality-independent cortical areas (e.g., the anterior temporal and inferior parietal lobes) play a role in conceptual processes (Binder & Desai, 2011). One construal of this evidence is that the neural basis of human semantic memory consists of sensorimotor features represented in sensorimotor cortices plus the domain-general binding hubs that bind and weigh these features. The evidence reviewed in this chapter does not favor this view. Modality-independent cortical areas *represent* abstract conceptual information, rather than binding sensory features elsewhere.

Moreover, conceptual modality-independent cortical areas are numerous, heterogeneous among themselves, and, in some cases, organized at the regional scale by cognitive domain (entity vs. event; Leshinskaya & Caramazza, 2016). The list of these areas continues to grow, and multivariate methods are beginning to uncover neural population codes within them (Fairhall & Caramazza, 2013). These population codes make explicit those aspects of objects, events, and properties that are causally central and relevant to category membership (e.g., agent/object, artifact/natural kind, intentional/accidental), including information about seemingly sensory categories (e.g., blue is a physical property perceptible with the eyes). These abstract conceptual systems interact with modality-specific sensory cortical systems when we think, talk about and act on the world (Mahon & Caramazza, 2008).

Conclusions

Evidence from studies of sensory loss demonstrates that the human cortex is functionally flexible early in life. Early changes in experience can alter the representational content of cortical networks dramatically—for example, from low-level vision to linguistic processing (Bedny, 2017). Yet cortical systems are also remarkably specific in the type of experience to which they are sensitive. The same experience that reorganizes sensory systems has little effect on abstract conceptual ones. Innate connectivity patterns constrain which part of experience a given cortical system will be sensitive to (Mahon & Caramazza, 2011; Saygin et al., 2016). Each cortical system can be thought of as a powerful learning device with a particular window onto the world (Gallistel, Brown, Carey, Gelman, & Keil, 1991). Abstract conceptual systems for representing entities, properties, and events are examples of such specialized neural learning devices, each of which only "sees" a particular part of our experience. An important goal for future research is to uncover the physiological properties that make neurocognitive systems so good at learning in general, as well as properties that prepare each system for representing and learning specific types of information. One prediction of such a "specialized learning systems" view is that although abstract conceptual systems do not change much in sensory loss, they would change if information available about objects, entities, and events were altered early in development.

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