



Grounding conceptual knowledge in modality-specific systems

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The human conceptual system contains knowledge that supports all cognitive activities, including perception, memory, language and thought. According to most current theories, states in modality-specific systems for perception, action and emotion do not represent knowledge – rather, redescrptions of these states in amodal representational languages do. Increasingly, however, researchers report that re-enactments of states in modality-specific systems underlie conceptual processing. In behavioral experiments, perceptual and motor variables consistently produce effects in conceptual tasks. In brain imaging experiments, conceptual processing consistently activates modality-specific brain areas. Theoretical research shows how modality-specific re-enactments could produce basic conceptual functions, such as the type–token distinction, categorical inference, productivity, propositions and abstract concepts. Together these empirical results and theoretical analyses implicate modality-specific systems in the representation and use of conceptual knowledge.

The human conceptual system contains people's knowledge of the world. In most theories, the basic unit of knowledge is the concept. This construct is highly contentious, however (see [Box 1](#)). Following psychological theories, we assume that a concept, roughly speaking, is knowledge about a particular category (e.g. *birds*, *eating*, *happiness*). Thus knowledge about *birds* represents the bodies, behaviors and origins of the respective entities. Knowledge plays a central role throughout the spectrum of cognitive activities. In on-line processing of the environment, knowledge guides perception, categorization and inference. In off-line processing of non-present situations, knowledge reconstructs memories, underlies the meanings of linguistic expressions, and provides the representations manipulated in thought.

Theories generally assume that knowledge resides in a modular semantic system separate from episodic memory and modality-specific systems for perception, action and emotion [1–4]. These theories further assume that conceptual representations are amodal – unlike representations in modality-specific systems – and operate according to different principles.

Here we review emerging evidence for an alternative view. Increasingly, researchers propose that conceptual representations are grounded in the modalities [5–10]. We

first present the underlying distinction that distinguishes amodal and modal approaches: transduction versus re-enactment. We then review recent empirical evidence for modal approaches [11]. Finally, we address theoretical issues and summarize a representative theory – perceptual symbol systems [10]. Amodal theories and the arguments for them lie beyond the scope of this review.

Box 1. What is a concept?

Cognitive scientists continue to argue about the construct of concept. For example, Platonists propose that concepts exist independently of minds, whereas naturalists argue that concepts are causal relations between the world and the mind [a–c]. From these two perspectives, the study of concepts constitutes a referential problem, namely, how do mental states refer to categories outside the mind? Many other cognitive scientists – especially psychologists – focus on the cognitive side of this relationship, assessing the structure, format and content of conceptual representations [d,e].

In the approach we take here, nothing is explicitly called a concept [f]. Instead our goal is to articulate specific mechanisms that produce conceptual processing. In the section on theoretical issues, one central mechanism is a simulator, namely, a skill for producing context-specific representations of a category. Most theorists would view such skills as peripheral to concepts. They would similarly consider the modality-specific information in simulators as peripheral, and also the extensive knowledge that supports situated action [g].

The difficulty of defining concept raises the issue of whether it is a useful scientific construct. Perhaps no discrete entity or event constitutes a concept. Perhaps conceptual functions emerge from a complex configuration of mechanisms in both the world and the brain. Thus, knowledge of *car* objects per se resides in the *car* simulator, but much other relevant knowledge resides in associated simulators, such as those for *road* and *travel*. Furthermore, referents in the world play a key role in producing and controlling this knowledge. The study of conceptual processing will be best served by discovering and describing the relevant mechanisms, rather than arguing about the meaning of lay terms such as concept.

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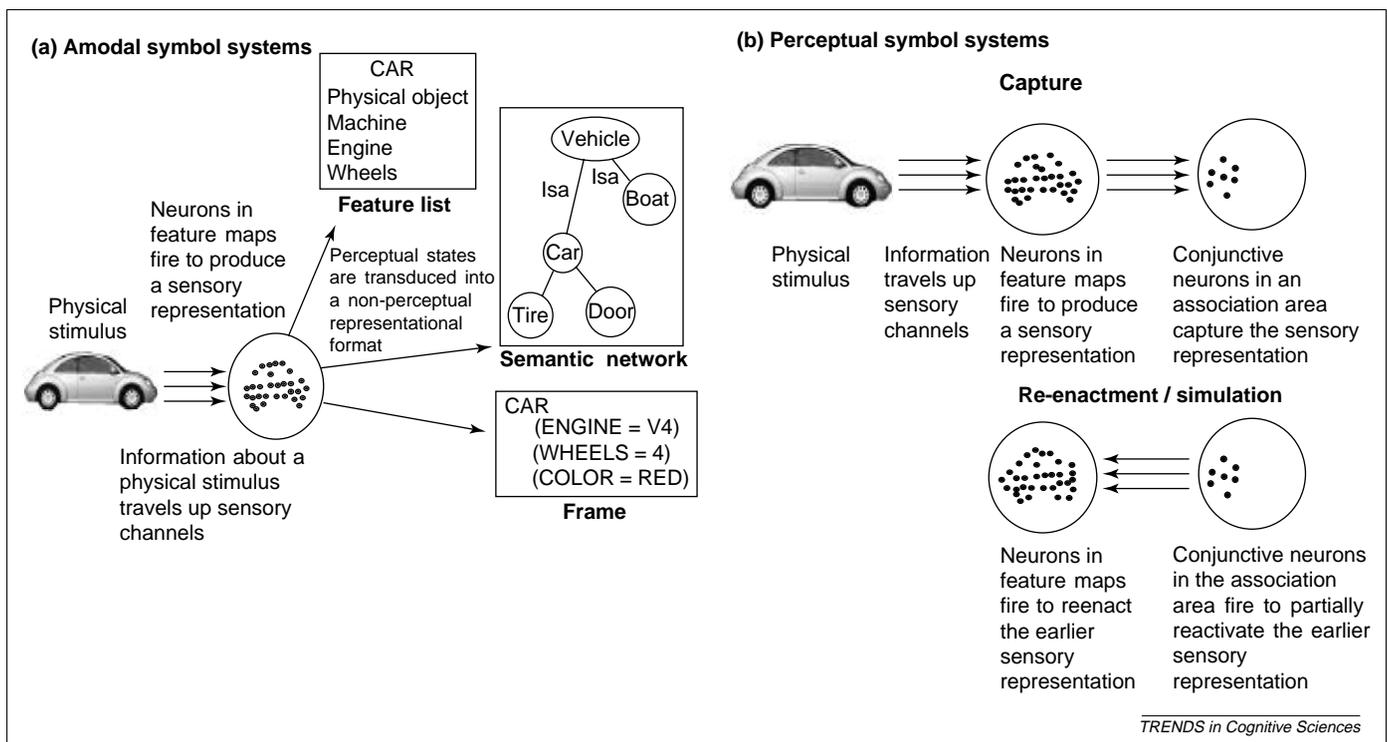


Fig. 1. (a) In amodal symbol systems, neural representations are established initially to represent objects in vision. Subsequently, however, these neural representations are transduced into another representation language that is amodal, such as a feature list, semantic network or frame. Once established, these amodal descriptions provide the knowledge used in cognitive processes, such as memory, language and thought. (b) In perceptual symbol systems, neural representations similarly represent objects in vision. Rather than being transduced into amodal descriptions, however, visual representations are partially captured by conjunctive neurons in nearby association areas. Later, in the absence of sensory input, activating these conjunctive neurons partially re-enacts the earlier visual states. These re-enactments contribute to the knowledge that supports memory, language and thought. This figure illustrates knowledge acquired through vision, but analogous accounts exist for acquiring knowledge in the other modalities (e.g. audition, action, emotion).

Transduction versus re-enactment

In a highly simplified and schematic manner, Fig. 1 illustrates the fundamental difference between amodal and modal approaches to representing knowledge. In amodal approaches, sensorimotor representations are transduced into an amodal representation, such as a feature list, semantic network, or frame (Fig. 1a). Amodal representations that reside outside sensorimotor systems redescribe sensorimotor states. Once amodal descriptions of sensorimotor states exist, all cognitive processes operate on them to achieve their functions – not on memories of the original sensorimotor states.

Modal approaches represent knowledge very differently. Rather than being transduced into amodal symbols, modality-specific states are captured by adjacent memory systems. Consider visual states (analogous accounts exist for states on other modalities). When a car is perceived visually, a set of neural feature detectors becomes active in the visual system (Fig. 1b). Conjunctive neurons in a nearby association area then conjoin the active features and store them in memory. Later, in the absence of visual input, these conjunctive neurons partially reactivate the original set of feature detectors to represent the car visually. Such re-enactments or simulations are never complete and might be biased. Nevertheless they provide the cognitive-level representations that support memory, language and thought.

Damasio's convergence zone theory offers one account of the re-enactment process, proposing that a hierarchical set of association areas (i.e. convergence zones) increasingly integrates modality-specific information across modalities [12]. Simmons and Barsalou develop this theory and use it to explain the conceptual deficits caused by brain lesions [13]. The construct of re-enactment/simulation is also viewed widely as the basis of mental imagery across the modalities [14–19]. Whereas mental imagery tends to be conscious, the re-enactments that underlie conceptual processing might often be unconscious [10].

Empirical evidence for re-enactment in the human conceptual system

A large empirical literature would be expected to assess whether knowledge is modal or amodal, given the importance of the issue. Surprisingly, however, researchers have adopted amodal approaches largely for theoretical reasons – relatively little direct empirical evidence exists for them [10]. Amodal theories have been attractive theoretically because they implement important conceptual functions, such as the type–token distinction, categorical inference, productivity and propositions. Amodal theories are also formalizable and can be implemented in computer hardware. Conversely, indirect empirical evidence has accumulated for modality-specific representations in working memory, long-term memory,

language and thought (see [11] for a review). In these studies, researchers typically address some other issue, but simultaneously obtain evidence for modality-specific representations.

Direct evidence from behavioral research

Researchers have designed experiments increasingly to assess directly whether conceptual representations are modality specific. One tack has been to compare the performance of participants asked to use imagery with the performance of neutral participants allowed to adopt whatever representations they choose. Amodal views predict that neutral participants should adopt amodal representations, whereas imagery participants should either run modal simulations or use tacit knowledge to behave as if they were. As a result, the performance of neutral and imagery participants should differ. Conversely, modal views predict that neutral participants adopt simulations spontaneously, and therefore perform similarly to imagery participants.

Two lines of work support the modal prediction [20]. In listing the features of a concept verbally, neutral participants produce the same complex distribution of features as imagery participants (both groups differ from subjects who produce word associations). Similarly, when subjects verify the properties of concepts linguistically (*mane* for *pony*), comparable regression equations explain the RTs (reaction times) and errors of neutral and imagery participants. The similarity of neutral and imagery participants in both lines of work suggests that neutral participants spontaneously simulate the referents of concepts.

Another tack in assessing modality-specific representations has been to manipulate sensorimotor variables and see if these affect performance (as in imagery research). If a representation is modality specific, then manipulating a variable on that modality should affect the representation's use.

Increasing evidence shows that perceptual variables affect conceptual processing [20]. In feature listing, a feature is produced less often when occluded than when unoccluded (e.g. participants produce *roots* less often for *lawn* than for *rolled-up lawn*). Participants simulate a referent of the target concept, with features visible in the initial simulation easier to report than occluded features. In property verification, perceptual variables capture large amounts of unique variance in RTs and errors. In particular, the larger a property, the longer it takes to verify, because larger regions of simulations must be processed.

In other property verification studies, participants verify a property on a particular modality (e.g. vision, audition, movement). On the preceding trial, participants verify a property on the same versus different modality. Similar to the psychophysical detection of sensory stimuli [21], a modality switching effect occurs [22]. Verifying *loud* (auditory) for *blender* is faster after previously verifying *rustling* (auditory) for *leaves* than after verifying *tart* (gustatory) for *cranberries*. Switching from one modality to another slows verification, thereby implicating modality-specific processing.

Perceptual similarity also affects property verification [23]. When participants verify *mane* for *pony*, they are faster if *mane* was verified previously for *horse* than for *lion*. Verifying *mane* for *horse* primes a perceptual form of *mane* that can be used later to verify *mane* for *pony*, whereas verifying *mane* for *lion* activates a different form that cannot be used. Control conditions rule out the explanation that similarity between concepts is responsible.

Perceptual simulation in language comprehension

When a text implies an object in a particular orientation, readers simulate the object in that orientation. On reading about a nail pounded into a wall, readers simulate a horizontal nail, whereas on reading about a nail pounded into the floor, readers simulate a vertical one. Evidence for this conclusion comes from observing that the subsequent processing of a nail in the implied orientation is faster than in an unimplied one [24]. Similar evidence exists for the implied shapes of objects. When a text implies a bird in flight, participants process pictures of birds with outstretched wings faster than birds with folded wings [25].

Research on language comprehension has further shown that readers compute the functional affordances of perceptual simulations. In one study, participants assessed whether a novel object could serve a needed function (e.g. whether a sweater filled with leaves versus water could serve as a pillow) [26]. Readers computed these functions rapidly. Because prior knowledge and linguistic representations do not seem to be adequate to compute these functions, it seems that perceptual simulations are responsible. Readers similarly understand the functions of novel actions immediately, such as using a crutch to bat a ball [27].

Bodily states in conceptual processing

Viewing an object immediately activates the appropriate hand shape for using it [28]. Seeing a car key activates a precision grip for grasping and turning. Knowledge of these hand shapes later interacts with motor responses for making unrelated judgments [29]. For example, judging whether a key is manufactured versus natural is faster when the response is made with a precision grip than with a power grip. Object concepts similarly activate arm movements. When verifying that '*Open the drawer*' is a sensible sentence (as opposed to an anomalous one), responses are faster when the response action is a pulling motion instead of a pushing one [30]. Setting concepts similarly activate eye movements. On hearing a description about the top of a building, participants are more likely to look up than in other directions [31]. Similarly, when participants remember something that occurred in a spatial location, their eyes are more likely to revisit that location than others [32].

The social psychology literature demonstrates a plethora of embodiment effects [33]. Some studies demonstrate that social stimuli induce bodily states, including postures, arm movements and facial expressions. Others show that bodily states produce emotions (e.g. a pushing movement

associated with avoidance produces negative affect). Further work shows that when bodily states are compatible with cognitive states, processing is optimal. For example, processing a positively valenced stimulus (e.g. *baby*) is faster when performing an approach arm movement (pulling) than an avoidance movement (pushing). Together these effects indicate a tight coupling between the cognitive and motor systems.

Evidence from neuroscience

Brain research provides increasing evidence for modality-specific representations in the conceptual system. Neuropsychologists report that lesion patients exhibit category-specific deficits for specific categories (e.g. *animals*). Many researchers argue that these deficits arise because lesions in modality-specific areas disrupt conceptual knowledge stored there [34–36]. Alternative views stress other mechanisms [37,38]. All these mechanisms seem to be important and can be integrated into a single account, with modality-specific mechanisms playing a major role [13].

Using neuroimaging techniques, Martin and his colleagues have localized various forms of conceptual processing in modality-specific areas [39–41]. Conceptualizing the colors of objects activates a brain area near V4, the area that processes color sensations. Conceptualizing object form activates areas near brain centers for perceiving form. Conceptualizing object motion activates areas near brain centers for perceiving motion. Conceptualizing actions that an agent could take on an object activates the motor system. At the categorical level, categories with mostly visual properties activate visual areas. Analogously, functional categories with many motor properties activate motor areas, whereas social categories with emotion properties activate emotion areas. In our own work, verifying visual properties in concepts activates visual areas [42]. As Box 2 describes, the interpretation of this functional magnetic resonance imaging (fMRI) activation in all these studies is far from settled.

Is amodal mimicry possible?

Some readers are undoubtedly thinking that classic amodal theories can explain modality-specific effects in conceptual processing. Technically, they are correct. Increasingly, however, the amodal position faces challenges [7,8,10,43]. One problem is that amodal theories can explain modality-specific effects because, in principle, they can explain anything. As often noted, amodal theories have Turing machine power, which means that they can express any describable pattern [44,45]. The power to mimic any empirical result, however, comes at the cost of unfalsifiability. Because these theories explain anything, no result can disconfirm them. From this perspective, the ability to explain modality-specific effects is not particularly impressive.

An unfalsifiable theory gains stature if it predicts important findings *a priori*. To our knowledge, however, predictions of modality-specific effects have come from modal theories, not from amodal ones. Modality-specific effects do not seem to be readily compatible with amodal

Box 2. What does brain activation in conceptual tasks mean?

Imaging researchers report increasingly that modality-specific brain areas become active during conceptual processing [a,b]. This activation is often interpreted as evidence that modality-specific representations underlie conceptual knowledge. Although this interpretation might be correct, alternative explanations exist.

One possibility is that amodal symbols reside near modality-specific areas and become active during conceptual processing. Evidence against this interpretation is that perceptual variables affect behavioral performance on conceptual tasks (e.g. occlusion, size, shape, orientation). Reconciling such effects with the interpretation that only amodal symbols exist is difficult.

Another possibility is that amodal symbols are associated with modality-specific representations, and that amodal symbols serve some roles, whereas modal symbols serve others. Two factors suggest caution in adopting this view. First, if modal symbols can implement all necessary conceptual functions (see the section in main text on theoretical issues), then it is not clear why the brain would redundantly include amodal symbols [c]. Second, direct empirical evidence for amodal symbols is lacking (see the section on amodal mimicry). Until such support exists, we should remain cautious about the brain containing amodal symbols.

A final possibility – and the one we endorse – is that conjunctive neurons in convergence zones constitute a somewhat amodal mechanism for capturing and re-enacting modality-specific states [d,e]. We hasten to add, however, that conjunctive neurons generally seem to have modality-specific tunings. Furthermore, their primary role might be to reactivate modality-specific states that then support conceptual processing.

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theories for two further reasons. First, amodal theories assume that knowledge is separate from modality-specific systems. Second, amodal theories tend to assume that knowledge filters out the modality-specific details that produce modality-specific effects (e.g. a single symbol for *roof* represents all types of roofs) [23].

Another problem is that, so far, little empirical evidence exists for amodal symbols in the brain. Instead, theoretical factors have been responsible primarily for the widespread adoption of amodal symbols [10]. Clearly, however, strong empirical support would be expected for such an important theoretical assumption, and the lack of such support suggests caution.

Perhaps powerful amodal accounts of modality-specific phenomena will develop and motivate predictions confirmed in experimental studies. Perhaps amodal symbols will be found in neural systems. Nevertheless, modality-based theories explain a wide variety of behavioral and

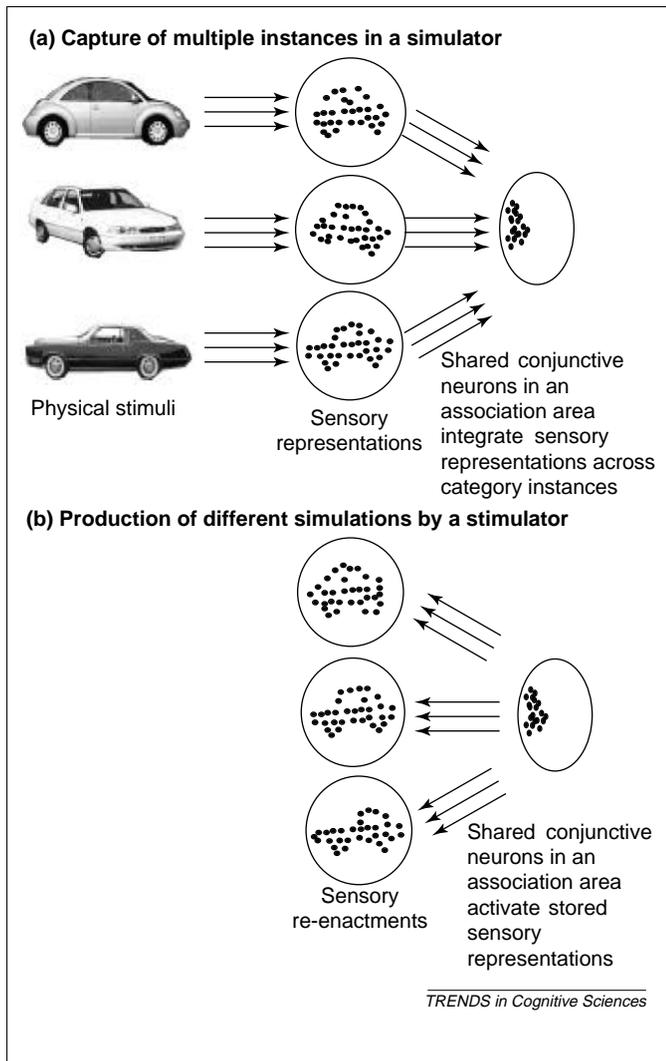


Fig. 2. (a) As multiple instances of a category are encountered, neural representations of them arise in vision. Because conjunctive neurons in visual association areas are tuned to particular conjunctions of visual features, a common set of conjunctive neurons captures the visual representations of the category's instances, which tend to share visual features. Sets of conjunctive neurons in other association areas (not shown) similarly capture a category's instances on other modalities (e.g. audition, action, emotion). In higher-order association areas (also not shown), common conjunctive neurons integrate modality-specific information for a category across modalities. (b) Once a simulator develops for a category, it later produces specific simulations of the category. On a given occasion, a subset of conjunctive neurons in the simulator produces one particular simulation in the visual system. This simulation could represent a given instance, an average of several instances, or a variety of other possibilities, depending on which subsets of stored information become active. Re-enactments typically occur on multiple modalities simultaneously, producing a multimodal simulation of the category, not just on vision (as shown).

neural results and generate many new ideas for research. At a minimum, they force a more careful examination of the role of modalities in knowledge.

Theoretical issues

Computational power

Modern cognitive scientists tend to believe that modality-specific representations lack the computational power to implement a fully functional conceptual system [46]. Theorists have assumed that these representations are undifferentiated holistic recordings, such as those captured by a camera or an audio-recorder [47,48]. An

image of a scene, for example, does not identify objects in it – the image is simply an undifferentiated bitmap. Problematically, such representations cannot implement basic conceptual functions, such as distinguishing types and tokens, producing categorical inferences, combining concepts productively, and constructing propositions that interpret the world. The apparent inability of modality-specific representations to implement these functions has peripheralized their role in theories of knowledge. The theory of perceptual symbol systems (PSS) described next was developed to show that modality-specific representations can implement a fully functional conceptual system [10].

Attention and integration

Earlier we presented the construct of re-enactment as the underlying mechanism in modality-specific approaches (Fig. 1b). This simple construct is not sufficient to implement a fully functional conceptual system. Re-enactment alone simply implements a recording system that partially reproduces experienced states. PSS uses two further mechanisms – selective attention and memory integration – to achieve full functionality. First, the capture process in Fig. 1b does not operate on entire perceptual states but only on components of them. On viewing a street scene, for example, the brain does not capture the entire scene. Instead, as attention focuses on a scene component, such as a car, an associative area captures the neural state that represents the component. Although components outside attention might be captured to some extent, much memory literature shows that where attention goes, memory follows [49]. Selective attention is also central in other modality-specific approaches to knowledge [6,50,51].

Once attention selects a component of experience, a memory of the component becomes integrated with memories of similar components, via content addressable memory. When focusing attention on a car, for example, the active neural state in the visual system becomes integrated with similar visual patterns captured previously. Because conjunctive neurons are tuned to specific feature sets, the same neurons tend to capture the same visual experiences [13]. Language might also play a central role in causing people to integrate two memories from the same category, even when their surface similarities differ [52]. Most importantly, memories for the same category become integrated over time, such as multiple memories for cars. Because conjunctive areas are organized hierarchically to integrate information across modalities, multimodal representations of categories develop [12,13]. For cars, such knowledge includes not only how they look but also how they sound, smell and feel, how to operate them, and emotions they arouse.

Simulators and simulations

A simulator is a distributed collection of modality-specific memories captured across a category's instances (illustrated in Fig. 2 in a highly simplified and schematic manner). When the category is processed on a given occasion, only a small subset of this information becomes active – not the

entire simulator. The active subset is then run as a simulation that functions as one of infinitely many conceptualizations for the category [53–55]. Thus the simulator for *car* can produce indefinitely many simulations of different cars, in many situations, from different perspectives. Again such simulations are multimodal, containing not only sensory states but also motor and mental states.

Simulators develop for any component of experience (or configuration of components) processed repeatedly by attention. Thus simulators develop for objects, actions, events, settings, mental states, features, relations, and so on. In all cases, integrated information about the processed component(s) accrues in a simulator that later produces specific simulations. Simulations are never complete re-enactments of the original modality-specific states, but are always partial and might contain distortions. The open-endedness of the simulators that are possible reflects attention's tremendous flexibility to focus on myriad aspects of experience [56].

Achieving a fully functional conceptual system

By breaking holistic perceptual experience into components and integrating memories of each component, a conceptual system emerges [10]. Rather than memory containing holistic representations of scenes, as in a recording system, memory contains categorical knowledge that can subsequently interpret the components of experience.

Types and tokens are realized by simulators and simulations, respectively. Because a simulator integrates conceptual content about a category across instances, it constitutes a type that represents the category as a whole. Because a simulation represents one particular form that a category can take, it constitutes a token.

Categorical inference results in many ways. Most basically, perceiving a category instance activates the best fitting simulation in a simulator (e.g. a perceived car activating a *car* simulation). Once a simulation becomes active, it typically carries inferences beyond the information given in the perceived instance. Thus, if a car is perceived from the side, a simulation could produce inferences about unperceived components through pattern completion (e.g. *headlights*, *engine*, *speedometer*) [33].

Productivity – the combination of existing concepts to form complex new ones – arises through the ability to embed simulations in one another [10,51]. Once an initial simulation has been constructed, one or more of its regions can be instantiated systematically with contrasting simulations to form new concepts (e.g. varying the contents of a simulated box).

PSS implements classic propositions by binding simulators to perceived category instances, thereby creating type–token relationships [10,57]. On binding the *car* simulator to a perceived car, an implicit type–token claim is made, namely, that the perceived car is an instance of the *car* type. Because such bindings might be mistaken, false propositions can result (e.g. mistakenly binding the *student* simulator to a scruffy young

Box 3. Questions for future research

- Is 'concept' a useful scientific construct, or should it be replaced with specific mechanisms?
- At a detailed computational level, what does a simulator contain, and how does it work?
- At a detailed computational level, how would productivity, propositions and abstract concepts be implemented in a modality-based conceptual system?
- In brain imaging experiments on conceptual tasks, what does brain activation in modality-specific areas mean?
- Is the convergence zone idea correct, namely, that conjunctive neurons partially re-enact states in feature maps to represent entities and events in their absence?
- What are the genetic contributions to a modality-specific conceptual system?
- How well does the modality-specific approach to concepts describe non-human conceptual systems, and help to establish the continuity of conceptual systems across evolution?
- In the face of increasing behavioral and neural evidence for modality-specific effects in conceptual processing, how do amodal symbol systems fare?
- Will either modal or amodal systems alone turn out to provide a complete account of the conceptual system, or will a mixed model be required?
- Will direct evidence be found for amodal symbols in the brain?

professor). Through productivity, complex hierarchical propositions can be implemented and mapped into structured sets of individuals.

Applications of PSS

The PSS framework is being extended increasingly in new theoretical directions. One application is to the problem of abstraction; specifically, how summary representations develop that can then be used to interpret a category's instances propositionally [57]. Summary abstractions exist in PSS at two levels. First, simulators that represent the properties and relations for a category constitute abstractions about its instances (e.g. *wings* and *flies* for *birds*). Second, property and relation simulators are assembled productively into structured on-line abstractions that interpret particular instances propositionally.

Another extension of PSS is to situated cognition [8,9,11,58]. On this view, conceptual knowledge is not a global description of a category that functions as a detached database about its instances. Instead, conceptual knowledge is the ability to construct situated conceptualizations of the category that serve agents in particular situations. Thus, the *car* simulator does not deliver a global car description across all situations, but tailors specific simulations to current situations, such as driving a car, refueling one, and so forth. Furthermore, these simulations include agent actions and mental states, thereby creating the experience of 'being there' in the respective situations.

Situated simulations have also been used to provide accounts of abstract concepts and function. From this perspective, abstract concepts are complex configurations of components in simulated situations, especially mental states [10,59,60]. Similarly, functions are complex configurations of situational components that represent affordances and designer intentions [61,62].

The need for computational models

Computational implementations of PSS need to be developed. Because re-enactment is a neural process, neural nets constitute a natural approach. Such implementations, however, face many challenges. Although preliminary sketches of mechanisms and architectures exist [10,13], much new computational machinery seems to be required [59]. It will be necessary to implement not only modality-specific circuits from sensation, action and emotion but also a powerful attentional mechanism and a spatial-temporal framework in which simulations can run, combine productively, and map propositionally onto individuals.

Conclusion

Although amodal approaches to knowledge have dominated cognitive science since the cognitive revolution, researchers increasingly find fault with them [7–10,43]. The lack of direct empirical evidence for amodal symbols is also a problem. Conversely, researchers increasingly report evidence that knowledge is grounded in modality-specific systems, and see how these systems could help to implement a fully functional conceptual system. Clearly, much further work is necessary to establish these claims. Not only is further behavioral and neural evidence required, so are computational implementations (see Box 3). A broad cognitive science approach is essential to understanding the conceptual system.

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