Continuity of the conceptual system across species

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In a recent neuroimaging study of macaque monkeys, Gil-da-Costa and colleagues reported that a distributed circuit of modality-specific properties represents macaques' conceptual knowledge of social situations. The circuit identified shows striking similarities to analogous circuits in humans that represent conceptual knowledge. This parallel suggests that a common architecture underlies the conceptual systems of different species, although with additional systems extending human conceptual abilities significantly.

The human conceptual system contains knowledge that supports the spectrum of cognitive activities from perception to thought. Standard accounts, such as semantic memory, view the conceptual system as modular and amodal. From this perspective, the conceptual system is modular because it is distinct from the brain's episodic memory and sensory-motor systems [1]. Its representations are amodal because they are symbolic descriptions that roughly mirror linguistic units [2]. Furthermore, it is often assumed implicitly that the human conceptual system differs significantly from the conceptual systems of other species because they lack our linguistic abilities.

An alternative view is that the conceptual system is non-modular and modal, using representational systems in the modalities to represent conceptual content [3–5]. Depending on the particular properties typically processed for a category, a distributed circuit across the relevant modalities represents them. Because this type of conceptual system could arise easily in non-human brains, it offers a continuous account of the conceptual system across species. In a recent experiment investigating the conceptual system of monkeys, Gil-da-Costa, Braun, Lopes, Hauser, Carson, Herscovitz and Martin offered evidence for this possibility [6].

Gil-da-Costa *et al.*'s findings
During PET scanning, rhesus macaques (*Macaca mulatta*) listened to two familiar macaque calls (coos and screams) and unfamiliar sounds (e.g. musical instruments). Whereas coos typically signal friendly approach, greeting or food, screams typically recruit coalition support during threat or attack, or they signal submission afterwards. Not surprisingly, both calls activated auditory processing areas. More significantly, both calls also activated a distributed circuit across other modality-specific areas that can be interpreted as representing associated situations. Specifically, both calls activated visual areas, suggesting that the macaques represented visual properties of other macaques who might be present (Figure 1a). Both calls also activated motion-processing areas in the temporal lobe often associated with facial expression and other visual motion (Figure 1b). Finally, areas associated with emotional processing became active in the ventromedial prefrontal cortex, amygdala and hippocampus. Notably, screams produced stronger activations in these three areas than did coos, consistent with the greater emotional intensity of scream situations (Figures 1c–e).

Distributed property circuits for conceptual knowledge of familiar situations
These findings suggest that macaques' knowledge of coo and scream situations is distributed across modality specific systems. As these situations are experienced, the neural systems that process their components become active. The auditory system processes the call, the visual system processes the faces and bodies of conspecifics, along with their expressions and actions, and the affective system processes emotional responses. Association areas capture these activations as they occur repeatedly, storing them for later representational use. When subsequent calls are encoded, they reactivate the auditory component of the resultant situational knowledge, which in turn activates the remaining components in other modalities. Thus the distributed property circuit that processed the original situation later represents it conceptually.

Continuity across species
This same basic architecture for representing knowledge is present in humans. Increasingly, studies show that knowledge about a particular category is distributed across the modality-specific systems that process its properties. When humans view a tool in isolation, visual, motor and spatial areas associated with using it become active [7]. Analogously, when humans view food in isolation, visual, taste and reward areas associated with consuming it are engaged [8]. When humans view a social entity, visual, motion, action and emotion systems that support interactions with it become active [9,10]. Finally, theories of selective deficits in category knowledge propose that focal lesions to distributed property circuits constitute one cause of these deficits [11,12].

The distributed property circuits identified in these human studies have roughly the same architecture as those identified by Gil-da-Costa and colleagues. In all cases, the modality-specific systems that process a category when its instances are actually present also represent the category when its instances are absent. Together, these findings suggest that a similar

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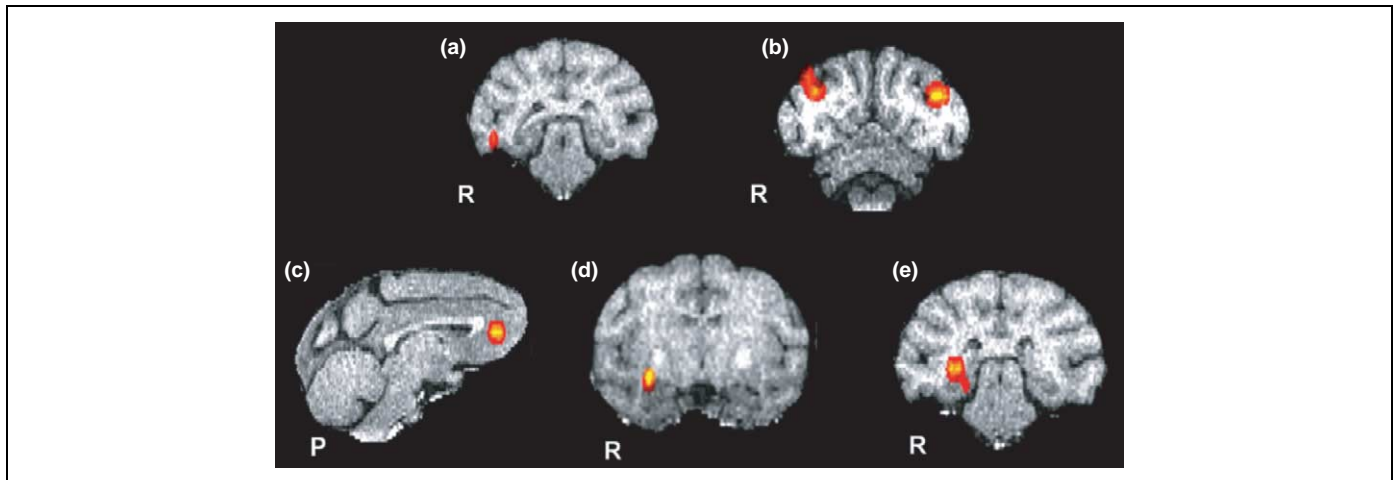*Corresponding author:* Barsalou, L.W. (barsalou@emory.edu).

Figure 1. Coronal slices from Subject 1 in Gil-da-Costa *et al.*'s study [6] illustrate the location of enhanced activity for conspecific vocalizations (coos and screams) versus non-biological sounds in areas TE/TEO (**a**) and MT/MST/STS (**b**). Sagital and coronal slices from Subject 1 illustrate the location of enhanced activity for screams versus coos and for screams versus non-biological sounds in ventromedial prefrontal cortex (**c**), amygdala (**d**), and hippocampus (**e**). R is right hemisphere; P is posterior. Parts of Figures 2 and 3 from [6] reproduced by permission of the National Academy of Sciences.

architecture for representing category knowledge exists across species.

Pattern completion inferences in situated action

Why might the conceptual systems of different species be grounded in this common architecture? One possibility is because it supports situated action. When an animal enters a situation, the ability to predict likely entities and events is useful for leveraging environmental resources, as are the abilities to activate relevant goals, actions and emotions.

The distributed property circuits that underlie categories support prediction in situations. When something from a familiar situation is perceived, the relevant perceptual system becomes active to process it. As a result, the associated pattern of distributed property information entrenched across previous occasions becomes active to represent the situation conceptually. Even though many corresponding aspects of the situation might not have yet been perceived, representations of them establish inferences about what is likely to occur. If an organism encounters a smell associated with a food it consumes frequently, a circuit of property representations across other modalities represents the food's appearance and taste, along with how to eat it, and the likely emotional response.

This type of inference via situational pattern completion appears central to the cognitive system [13]. An animal simulates the situation that it predicts is about to unfold, thereby preparing itself for action that will achieve its goals. Because this pattern completion process is probably essential for the survival of all species, it makes sense that a common architecture for implementing it exists.

Future issues

Other species

If situational pattern completion is important across species, then distributed property circuits should be observed in other species besides humans and macaques.

Clearly, the specific forms of these circuits should vary widely. Depending on the modalities central to a species' interactions with its environment, different types of property circuits should develop. The importance of sonar in bat cognition, for example, should produce a property circuit for representing moths that differs considerably from the circuits that represent moths in primates.

Nevertheless, important commonalities should arise. Because all animal species sense and act, distributed property circuits should generally include properties from sensory and motor systems. Because many species additionally have intentional states and affective systems, their distributed property circuits should typically include goals and emotions.

In species such as insects, genetics probably largely determine the distributed property circuits that represent relevant categories, although some adaptation is likely to occur. As species become increasingly adaptive, however, greater potential for acquiring these circuits exists. Nevertheless, substantial genetic contributions constrain the structure of the modality-specific systems that create these circuits.

Extensions to other processes

Distributed property circuits might support a variety of other intelligent processes besides situational pattern completion. For example, these circuits might provide the computational processes that underlie classical conditioning across species. Initially, hardwired neural connections link sensory representations for unconditioned stimuli (e.g. food) to unconditioned responses (e.g. salivation). Later, when a conditioned stimulus comes to predict the unconditioned stimulus, property information about the conditioned stimulus is added to the distributed property circuit. Operant conditioning can be viewed similarly.

Distributed property circuits also appear relevant to episodic memory [14] and working memory [15]. Increasing research shows that the modality-specific systems used to process a stimulus at encoding later represent it at

retrieval. For example, a stimulus encoded visually reactivates visual areas when retrieved, whereas auditory stimuli reactivate auditory areas. Lesions in modality-specific areas that produce amnesia further implicate the modalities in representing memories [16].

Extensions of the conceptual system in humans

Clearly the human conceptual system differs substantially from the conceptual systems of other species. One account suggests that the conceptual systems of non-humans primarily serve to process current situations [17]. Perceiving a predator, for example, produces a simulation of an impending attack that motivates escape behavior. Feeling hungry produces a simulation of food that motivates foraging.

By contrast, humans represent situations that are completely unrelated to the current situation. Greater frontal lobe development might support the abilities to attenuate current sensory-motor processing and then to simulate non-present situations. By simulating past situations, learning occurs that enhances future performance. By simulating future situations, plans develop that maximize goal achievement. The same circuits that simulate current situations also simulate non-present situations, under greater frontal control.

Other relevant developments in humans are the cognitive abilities that support social coordination, such as joint attention and perspective taking [18]. Brain systems that implement these abilities might have significantly extended the human ability to conceptualize situations. Nevertheless, these new abilities complement the same basic architecture for representing categories that exists in other species.

Finally, language is obviously another important development in humans that extends conceptual processing significantly. One possibility is that the linguistic system provides exquisite control over the simulation system as it represents non-present situations. By associating words and grammatical structures with components and configurations of multi-modal information, linguistic expressions control the simulation process compositionally [19]. Again, greater frontal control could be essential to this process, along with mechanisms that support social coordination. What results is control of the distributed property architecture to represent components of situations and to combine them in novel ways. This system might also allow humans to focus on mental states and their relations to events, thereby supporting the semantics of abstract concepts [20].

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