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# Beyond Cognitive Templates: Re-Examining Template Metaphors Used for Animal Recognition and Navigation

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**Synopsis** The term "cognitive template" originated from work in human-based cognitive science to describe a literal, stored, neural representation used in recognition tasks. As the study of cognition has expanded to nonhuman animals, the term has diffused to describe a wider range of animal cognitive tools and strategies that guide action through the recognition of and discrimination between external states. One potential reason for this nonstandardized meaning and variable employment is that researchers interested in the broad range of animal recognition tasks enjoy the simplicity of the cognitive template concept and have allowed it to become shorthand for many dissimilar or unknown neural processes without deep scrutiny of how this metaphor might comport with underlying neurophysiology. We review the functional evidence for cognitive templates in fields such as perception, navigation, communication, and learning, highlighting any neural correlates identified by these studies. We find that the concept of cognitive templates has facilitated valuable exploration at the interface between animal behavior and cognition, but the quest for a literal template has failed to attain mechanistic support at the level of neurophysiology. This may be the result of a misled search for a single physical locus for the "template" itself. We argue that recognition and discrimination processes are best treated as emergent and, as such, may not be physically localized within single structures of the brain. Rather, current evidence suggests that such tasks are accomplished through synergies between multiple distributed processes in animal nervous systems. We thus advocate for researchers to move toward a more ecological, process-oriented conception, especially when discussing the neural underpinnings of recognition-based cognitive tasks.

## Introduction

A central goal across biological disciplines, from cognitive neuroscience to evolutionary ecology, is to better understand how animals experience the world around them. To be successful in a dynamic and complex environment, organisms must be able to perceive and interpret stimuli. Through each organism's sensory repertoire, a unique perceptual interpretation of the world emerges, and it is within this "perceptual space" that an animal interacts with its surroundings. Variations in sensory and perceptual abilities across the tree of life inspired pioneering investigators to better characterize these "perceptual spaces," leading to foundational concepts like von Uexküll's (1921; see Feiten 2020) *umwelt*, or "self-centered world." Since then, we have made enormous progress in studying the responses of organisms to their environments, with studies of animal behavior increasingly incorporating information about the mechanisms and evolution of animal

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sensory modalities, from vision to electromagnetic reception. However, our understanding of the mechanisms underlying higher-order cognitive processes that make use of these sensory modalities remains more rudimentary, despite growing work from neuroscience in a handful of human and model animal systems. For example, while we know that *Polistes* wasps can recognize individual conspecifics (Sheehan and Tibbetts 2011), we have little idea how they accomplish such recognition at the neural level (but see Jernigan et al. 2021). Without a clear understanding of mechanism, scientists have often adopted metaphorical language in order to continue conversations about the "black box" of cognition.

One obstacle to progress on cognitive mechanisms may be our metaphorical approach to comparative cognition itself. The metaphors we adopt can shape how research proceeds. As outlined by Brick et al. (2020), when creating such metaphors (e.g., labels, categories), any bias in the understanding of what constitutes the boundary between concepts (such as the assumption that an "essential" process generates a specific pattern) can lead to misunderstandings regarding the universality and/or variability of the phenomena in question (see also Kennedy 1992; Rendall et al. 2009). For example, in early neuroscience, technological achievements at the time gave rise to the "telegraph" metaphor for neuronal connectivity (Cobb 2020). Although the web-like nature of both telegraph lines and neurons is analogous, this metaphor was of limited utility except for describing structural aspects of the brain. As we began to obtain more functional data on neural substrates, researchers realized that the telegraph metaphor needed to be updated to better accommodate this new knowledge. This led to neuroscientists adopting the popular notion of "neural networks" from graph theory, thereby describing both the structure and function of the brain (Cobb 2020). Likewise, this conceptual shift marked a boon in research areas like computational neuroscience. Thus, by re-examining the conceptual ideologies that have given raise to prominent metaphors in science, we may better understand inadvertent limitations to our own scientific advancement.

A familiar concept in the exploration of animal perception and recognition is that of the *cognitive template*. Originating from work in human-based cognitive science (Selfridge and Neisser 1960), *cognitive templates* referred to a stored and literal representation of a stimulus that is compared with incoming stimuli for the purpose of recognition and/or discrimination of objects or states in the world. This original conception has been adopted by researchers studying a range of cognitive processes in nonhuman animals, from the formation of species-specific bird song during ontogeny (reviewed by Soha 2017) to the use of the so-called "mental maps" during foraging (reviewed by Asem and Fortin 2017). In these research contexts, the template concept became a working hypothesis for the mechanisms of cognition, motivating the search for literal neurons that store bird songs (reviewed by Bolhuis and Moorman 2015) or reference unique spatial locations (O'Keefe and Dostrovsky 1971). Once simply a metaphorical descriptor of how human and artificial intelligence might accomplish recognition tasks, this idea has evolved to become a mechanistic hypothesis used across multiple disciplines. In the process, the line between metaphor and mechanistic expectations has become blurred, often without asking whether one might reasonably expect a literal neural template to underly a given cognitive process. This has led us to ask whether invoking a *cognitive template* remains scientifically useful when weighed against available evidence for how animal nervous systems actually go about the tasks to which such templates are commonly ascribed.

In this article, we first examine the common terms used to describe recognition tasks—and specifically the contribution of the *cognitive template* concept when present—across nonhuman animal studies, including kin recognition, spatial cognition, mate selection, and other forms of object perception and recognition. In the process, we query whether the concept of the cognitive template has been useful, or whether it has limited empirical research. In particular, we assess the strength of current evidence for a localized, physical, stored neural representations associated with recognition tasks for which cognitive templates are often invoked. We find that although various versions of the concept are employed across fields, they are applied without consistency, and often without mechanistic insight. Ultimately, such inconsistency has led to an intellectually vague concept that has rarely been productive when interpreted literally. As such, we conclude by suggesting a reorientation away from template-based terminology to more process-based language. We argue that this process-based conceptualization of cognition, which emphasizes emergent synergies between multiple, physically distributed processes, is not only intellectually richer, but also more likely to resemble how animal bodies engage with their perceptual and physical worlds.

## The origin of the term cognitive template

Speculation about *cognitive templates* has been part of cognitive science and artificial intelligence ever

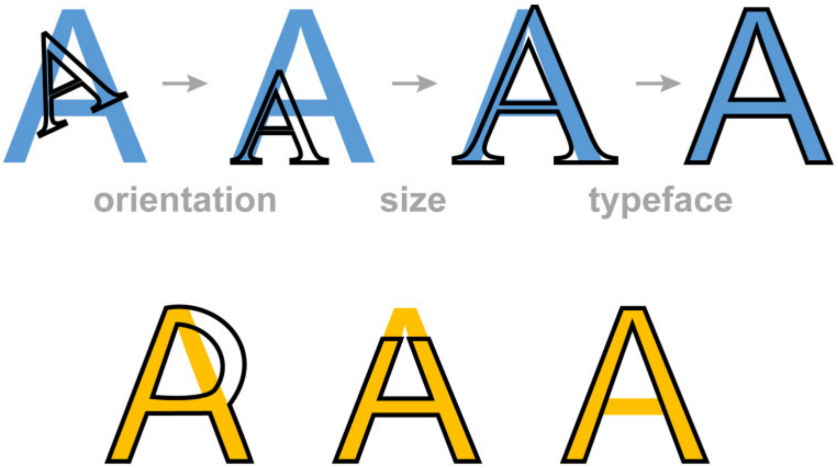

**Fig. 1** The letter "A" is classically used to exemplify the direct matching of the template (blue, yellow) and the input (black outline) given the correct orientation, size, typeface, and letter. However, difficulty in accurate matching for some letters (e.g., "R," "H," and "V" without orientation correction) suggests the need for the viewer to already know what every possible letter is beforehand

since these disciplines took form, used in explanations of both perception and action. The concept is borrowed from manufacturing, where a template is a model used to quickly mass-produce a product. Selfridge and Neisser (1960) realized that templates could serve both as models to produce and to recognize objects. Take printed letters, the classic example: the cognitive template for the letter "A" may be used to guide motor processes that enable the writing of the letter "A" (Fig. 1). The template may also recognize the letter: uninterpreted visual information in a sensory buffer would be compared with a series of templates and found to match that for the letter "A." Almost immediately, however, cognitive scientists realized that there were difficulties with this concept. For example, practiced readers can recognize the letter "A" in a variety of different orientations, whether upside down or rotated by any number of degrees, and in a variety of font sizes and typefaces. This led to a proposed two-step process for letter perception: first, correct the letter's orientation, size, and typeface to some standard, then see which templates apply. This could be supplemented by a learning process in which the letter's template is enriched by adding the newly recognized, pre-corrected letter to the old template. Even with this elaboration, issues remain with this concept. The first possibly surmountable issue is that the templates themselves would become complex and unwieldy; the second, probably insurmountable, issue is that it is hard to see how to correct the orientation, size, and typeface of the letter if the viewer does not already know what the letter is. For this reason (and others), Selfridge and Neisser abandoned the idea of *cognitive templates*. They called the two-step process inadequate and replaced templates with sets of features processed according to Selfridge's "pandemonium model."

This introductory history of the cognitive sciences illustrates that at a time when the discipline was brand new, the idea of *cognitive templates* was already considered inadequate and unworkable. Yet, the concept is still widely used in the cognitive sciences, including when the methods of the cognitive sciences are applied to study nonhuman behaviors. When adopted by biologists for use in animal cognition and behavior, the concept has been applied to a wide variety of cognitive processes in multiple subfields, resulting in several variations in terminology (Table 1). Though slightly different in name, the core concept of a *cognitive template* remains well conserved and is most often employed by biologists as a metaphorical description of mental representations.

## Bird song: a case study

A familiar use of *cognitive templates* is in the study of bird song. Early ethologists, such as Marler, Konishi, and Thorpe, demonstrated that birds have an innate (i.e., unlearned) song pattern that they listen for, filtering out inappropriate tutors, and selectively attending to species-specific song (Thorpe 1961; Konishi 1965; Marler 1970). This ability was explained with *cognitive templates* that are innate and specific to particular phrases in species-specific songs. As a male develops, through sensorimotor feedback and comparison to learned songs, the bird elaborates its species- and sex-typical song. The final, crystallized song pattern is a result of the innate

**Table 1** Glossary of terms used in different disciplines to invoke the *cognitive template* concept

| Term | Definition |
|---|---|
| Cognitive template | A stored, localized neural representation that is directly compared to incoming stimuli (after Selfridge and Neisser 1960) |
| Template matching | The process whereby recognition occurs "if there were sufficient overlap pattern between a novel pattern and template" that is "stored in long-term memory" (Bruce et al. 2003) |
| Phenotype matching | A process where internal representations of phenotypic states of individuals or objects are used to compare to external cues for recognition and discrimination tasks (e.g., "An individual learns and recalls its relatives' phenotypes or its own phenotype, and compares phenotypes of unfamiliar conspecifics to this learned 'template'" (Holmes and Sherman 1982) |
| Recognition template | "Internal representations of the characteristics of desirable or undesirable recipients. Recognition occurs when phenotypes of the recipients match these templates closely enough" (Sherman et al. 1997) |
| Cognitive map/Mental map | An allocentric representation of places in terms of distances and directions separating items in the environment that is stored in memory and matched to landmarks to orient an individual in space (O'Keefe and Nadel 1978) |
| Internal representation | In general usage, a structure of the nervous system that carries information about the environment. However, often described in template-like terms (e.g., "the characteristics of desirable and undesirable recipients which are to be compared against using a matching algorithm" (Sherman et al. 1997) |

template being continually edited by learned experience. Behavioral findings such as these suggested that the mechanism of song recognition and repetition was potentially underlain by a template—a blueprint innately programmed in the bird that is compared with songs heard and produced by the male. With emerging innovations in neurophysiology, scientists searched for the neural substrate of the "song template." Electrophysiology on anaesthetized birds demonstrated that some neural clusters exhibit increased firing in response to the species' song (e.g., Gentner and Margoliash 2003), and lesioning studies identified crucial neural junctions for normal song development (Fig. 2A; Bolhuis and Moorman 2015), providing promising support in the search for a *cognitive template*. The template was hypothesized to be in the caudomedial nidopallium or caudomedial mesopallium (Fig. 2A) responsible for perception and recognition of tutor songs, or the anterior forebrain pathway, a circuit crucial for sensorimotor learning, or the song motor pathway, which regulates song production (Mooney 2009; Bolhuis and Moorman 2015). Decades of work in search of the template have resulted in extensive mapping of pathways (Fig. 2A), but no template or "engram" (i.e., memory trace) has been found. Instead, the most consistent finding has been that the song system as a whole is a diffuse and integrative network from which birdsong emerges (Fig. 2A).

We use this particular example to illustrate what we believe to be the inevitable fate of the *cognitive template* hypothesis. Proposed as a literal, localized template, a schema to match to incoming songs and a standard against which to shape the acquisition of song production, the "song template" hypothesis motivated successful research into the neurobiology of learning and memory. However, after years of dedicated investigation, the field has arrived at the conclusion that a single "song template" cannot exist as originally hypothesized but is instead a network of interacting pathways that synergize to create typical song development. We suggest that the concept of *cognitive templates* will follow this same trajectory and is in the process of being repeated across the various fields in which it is employed, serving as a ladder to be kicked down once climbed.

## Kin recognition

Researchers studying kin recognition have eagerly invoked the notion of a *cognitive template*, often called a *recognition template*, as a key part in the process of discriminating between kin and nonkin. For example, Tsutsui et al. (2003), in their work on kin recognition in social Hymenoptera, note that these insects "form a recognition template against which it compares labels of conspecifics. A mismatch between an individual's template and the label of another individual generally triggers rejection". Such statements are commonplace in the kin recognition literature, appearing in studies focused on nestmate recognition in ants, kin recognition in mammals, and maternal recognition of eggs in birds. However, these researchers are often swift to point out that evidence for a literal template remains elusive. Hauber and Sherman (2001) state, "How the recognition template develops, exactly where it is stored, and how cue-template similarity is assessed are the interesting, open questions". Thus, the impression left by many publications seeking to explain

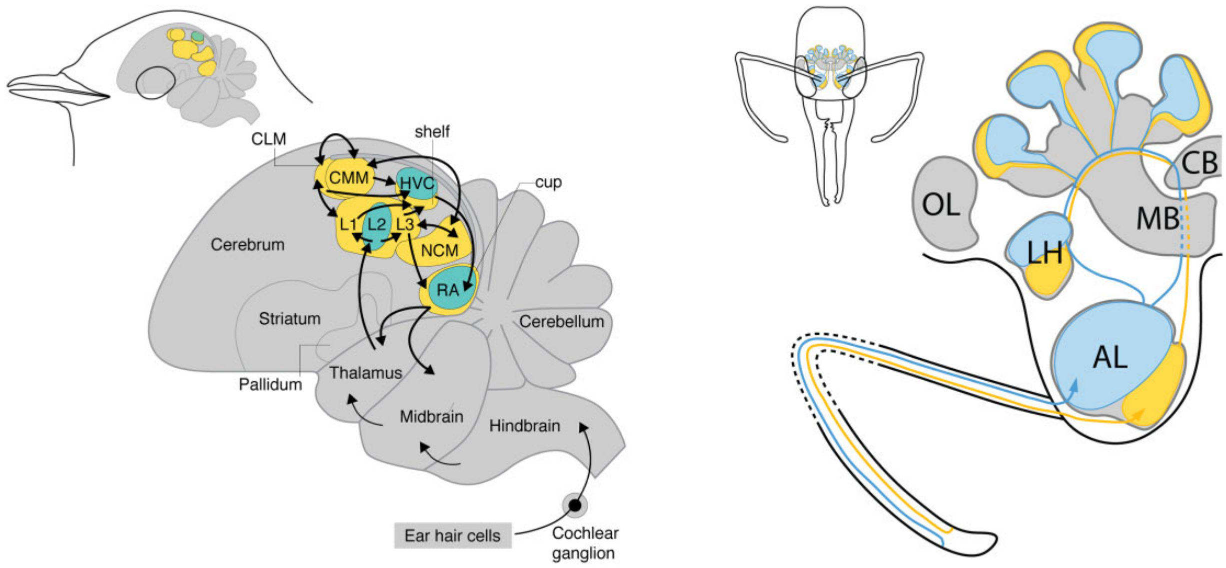

**Fig. 2** Schematic depictions of brain regions involved in recognition tasks in birds and ants. (A) Auditory pathways involved in song learning and recognition in the songbird brain. Regions in yellow increase neuronal activation following song reception, including the caudolateral mesopallium (CLM), caudomedial mesopallium (CMM), caudomedial nidopallium (NCM), and L1 and L3 subdivisions of Field L. Regions in green also respond during song reception, but with variable activation, including the HVC (former acronym now recognized as the official name of this brain region), the robust nucleus of the arcopallium (RA), and the L2 subdivision of Field L. Arrows show known connections between these nuclei and with other brain regions. Redrawn with permission from Bolhuis and Moorman (2015). (B) Brain regions involved in olfactory processing in the ant brain. Brain regions colored in yellow were originally thought to comprise a subsystem dedicated to nestmate discrimination, whereas those colored in blue were thought to function in general odorant discrimination. However, recent work (e.g., Slone, et al., 2017) indicates that both sets of regions are involved in a variety of odorant discrimination tasks, including both nestmate and general odorant discrimination. Labeled brain regions include the lateral horn (LH), antennal lobe (AL), T6 glomerular cluster, optic lobe (OL), mushroom bodies (MB), and central body (CB). Redrawn with permission from d'Ettorre et al. (2017)

the mechanisms of kin recognition is that although a template must be involved, such "templates" have yet to be identified at the neural level.

Perhaps, the clearest opportunity for identifying a literal neural template comes from work on olfaction-based nestmate recognition in social Hymenoptera, where decades of research have identified cuticular hydrocarbons (CHCs) as the predominant molecular substrate involved in discrimination between nestmates and non-nestmates. Recent work on the ant *Camponotus floridanus* by Ferguson et al. (2020) highlights a central role for odorant receptor coding in the active discrimination of chemical signatures associated with nestmates and non-nestmates, a process which they argue involves precise matching between an odorant "key" and an odorant receptor "lock." Where might such a "lock" (i.e., neural template) reside? The most obvious answer would be to search for "nestmate recognition" glomeruli in the antennal lobes (Fig. 2B; Zube et al. 2008). Several lines of circumstantial evidence support this hypothesis, namely that glomeruli number has co-evolved with the expansion of odorant receptor complexity in ants (Zube et al. 2008; McKenzie et al. 2016), and that mutagenesis of *orco*, a gene required for odorant receptor function, results in significant (e.g., 82%) decreases in glomeruli number and antennal lobe volume (Trible et al. 2017). In addition, past work has implicated a particular cluster of glomeruli, termed the T6 cluster, in dedicated processing of CHCs (Fig. 2B; McKenzie et al. 2016; Sharma et al. 2015; Nakanishi et al. 2010). However, structure–function analyses of the ant central olfactory system indicate that specific odorants often induce responses in large numbers of glomeruli and that individual glomeruli often respond to multiple odorants (Zube et al. 2008). This lack of one-to-one correspondence between specific odorants and glomeruli responses in the antennal lobe implies that other brain regions are likely necessary for odorant decoding, pushing the search for the "lock" or neural template farther into the brain. Evidence for this more distributed view of CHC discrimination comes from work by Slone et al. (2017), who showed that non-T6-related olfactory receptors also respond to CHCs and may play a role in nestmate recognition (Fig. 2B), thus challenging the proposed role of T6 as a dedicated nestmate recognition system. To make matters more complicated, recent behavioral work has provided evidence that ants may use multiple "templates" when discriminating nestmates from non-nestmates, with some of these "templates" subject to modification via learning (Neupert et al. 2018). Thus, what researchers have classically referred to as a neural template for nestmate recognition may be a complex collection of overlapping neural processes involving temporally dynamic recruitment of suites of olfactory receptors, glomeruli, and upstream neural processing (Fig. 2B), rather than something resembling a singular, localized neural template or subsystem.

Less well characterized are the neural mechanisms involved in other more multivariate kin recognition tasks, such as those used by vertebrates involving olfactory, visual, and auditory cues. However, in a review of the literature on neural mechanisms of kin recognition in vertebrates, Tang-Martinez (2001) concluded that there was no evidence for the evolution of dedicated kin recognition neural systems, but rather that kin recognition was likely to have evolved as a product of other recognition tasks, such as species and sex recognition. Furthermore, Tang-Martinez (2001) concluded that vertebrate kin recognition has drawn opportunistically on a range of nonspecialized sensory and cognitive abilities, suggesting that the resulting neural processes are often distributed and prone to species specificity. Consistent with this, recent work by Gerlach et al. (2019) on larval zebrafish (*Danio rerio*) indicates that kin recognition and associated olfactory imprinting are not localized in the central nervous system, but rather involve key changes in gene expression and olfactory receptor sensitivity in the olfactory epithelium. Similar results have been reported for detection of major histocompatibility complex (MHC) peptides in mammals, which appears to rely on both combinatorial neural activities paired with changes in the peripheral olfactory system (Leinders-Zufall et al. 2004; Spehr et al. 2006).

Finally, a now-classic example of kin recognition involves egg recognition by bird species experiencing brood parasitism. Current evidence remains equivocal regarding whether hosts of nest parasites recognize parasitic eggs based on a mismatch between an internal reference (innate or learned) of what their own eggs should look like or an assessment of "which of these is not like the others" (Hauber and Sherman 2001). Nevertheless, researchers have often invoked the possibility of a referential template that is used to judge the size, color, and maculation of eggs in the nest (Rothstein 1975, 1978; Lyon 2006). In some species, these properties appear to be assessed all together, whereas in other species, a single metric appears dominant. Much of this work focuses at the level of behavior, rather than neurobiology, and no neural correlates have been identified that might mediate this process. Yet, the diversity of behavioral mechanisms identified, as well as the range of visual properties implicated in this discrimination process (e.g., egg size, shape, color, maculation), suggests that the neural processes involved in identification of parasitic eggs are likely to draw on a range of sensory and cognitive systems, often in a species-specific manner. Thus, this form of kin recognition seems likely to comport with Tang-Martinez's (2001) suggestion that such recognition processes may often arise through co-option of other (distributed) cognitive and sensory functions.

## Spatial cognition and navigation

Animal navigation and spatial orientation is a fundamental and cognitively challenging task for animals. At minimum, spatial cognition requires that an animal employs information about itself in relation to the physical layout of the environment. Many species, from arthropods to vertebrates, use celestial, magnetic, and/or gravitational cues to orient themselves in space (Asem and Fortin 2017). Path integration pairs orientation information with idiothetic recordings of distance, creating an egocentric navigation system that allows animals to travel between known locations, such as a nest or food source (McNaughton et al. 2006; Bird and Burgess 2008). As the environment or behavior becomes more complex, however, an animal might navigate between multiple locations or landmarks (Bird and Burgess 2008; Ekstrom and Ranganath 2018). These landmarks must then be identified and remembered, with associated information about a landmark's position in the environment and in relationship to other landmarks. Navigation and spatial cognition of this complexity has led researchers to the assumption that the layout of an area and the relevant landmarks or locations therein are represented and stored in the form of a *cognitive map*: an internal representation of the environment in which they can place themselves and landmarks of interest (Tolman 1948; Cruse and Wehner 2011; Asem and Fortin 2017). Proponents of the *cognitive map* hypothesis argue that path integration mechanisms cannot provide the allocentric spatial information needed for an animal to navigate via novel routes (Tolman 1948; Collett and Graham 2004; Poucet and Save 2009; Asem and Fortin 2017). Rather than solely encoding orientation and distance, as in path integration, *cognitive maps* are built by integrating the locations of multiple landmarks in an area to create a single spatial representation. This spatial representation can then be referenced by matching a landmark in the environment with its corresponding point in the map. Thus, cognitive maps are employed in the same manner as cognitive templates, as holistic neural representations, with correlating features and associated information, which are stored and consulted to guide behavior.

This spatial template has often been treated, at least conceptually, as a literal and localized neural unit. Attempts to locate the physical "map" began with O'Keefe and Dostrovsky (1971) with the identification of hippocampal "place" cells, neurons that exhibit increased firing at specific locations of an animal's environment. The hippocampus of rodents has also been shown to have "head direction" cells, which provide orientation information (Taube et al. 1990) and "grid" cells to create a triangular lattice of activation across physical space (Moser et al. 2008). Together, "place" cells, "head-direction" cells, and "grid" cells provide evidence for correlations between locations in the brain and locations in the physical world. As a result, the hippocampus has been repeatedly called the *cognitive map* of the mammalian brain, despite many unknowns regarding the processing and integration of spatial information (O'Keefe and Dostrovsky 1971; O'Keefe and Nadel 1978; O'Keefe 1990; Moser et al. 2008; Poucet and Save 2009; Asem and Fortin 2017; Ekstrom and Ranganath 2018).

The template metaphor becomes complicated, however, when the map is refreshed or replaced. Though multiple theoretical models differ on mechanism and ontogeny, it is generally thought that "grid" cells provide relatively stable scaffolding upon which spatial representations are built. For example, electrophysiological data from rats navigating a maze have demonstrated that when faced with a decision between known right and left turns, "place" cells associated with locations on both paths can be sequentially activated in the brain, suggesting place-based prediction and planning (Johnson and Redish 2007; Asem and Fortin 2017). This "place" cell activation is dependent on the experience, however. When the rat is removed from the maze and begins mapping a new environment, the same "place" cells become correlated with new features (Johnson and Redish 2007; Moser et al. 2008). Behavioral evidence suggests that rats can rapidly reorient to a familiar environment, presumably retrieving the template and resetting the cells in the grid to the remembered specifications. However, the neural mechanisms underlying this are unknown. This process of retrieval and reprogramming suggests that the networks of cells that create grids and place fields for active navigation are not responsible for encoding and storing the relationships between landmarks in an environment (Moser et al. 2008). Rather, the relationships between known landmarks are likely to be stored elsewhere in the nervous system and then projected onto a grid network when triggered by a familiar stimulus via pattern completion, with "place" cells flexibly taking on new relationships and spatial meaning (Nakazawa et al. 2002; Moser et al. 2008). As such, "place" cells and "grid" cells do not record and store environmental templates, but rather act as a generic substrate upon which such maps might be used. Though these are, as of yet, the closest evidence for a physical "mental map," because these cells are rewritten and refreshed to fit instantaneous navigational needs (i.e., "place" cells may be associated with landmark A one moment, then landmark B, then landmark C, perhaps even returning to referencing landmark A later), they depart significantly from the conventional meaning of a *cognitive template*, functioning more like "working memory" than a fixed template. Additionally, the existence of "place" and "grid" cells is not fully sufficient to explain "map"-based behaviors because the involvement of other brain regions is also required.

The study of path integration has produced decades of compelling behavioral and neurological evidence that support much more parsimonious navigational mechanisms, especially in non-hippocampal systems. The same infrastructures used as evidence for *cognitive maps* (i.e., "head-direction" cells, "place" cells, and "grid" cells) have been well documented as necessary and sufficient properties of path integration without the expectation of a singular "map-like" locus stored in memory (Cruse and Wehner 2011; Turner-Evans et al. 2020). Invertebrates have been shown to execute remarkably complex navigational tasks without the assumption of a centralized neural representation (Fig. 3). Ring attractors in *Drosophila* operate as "head direction" cells (Turner-Evans et al. 2020), angle-specific polarized-light neurons are used for direction orientation in insects (Labhart and Meyer 2002; Heinze 2017), and a decentralized neural network can still execute the novel shortcuts that were thought to set cognitive maps apart from simpler mechanisms (Cruse and Wehner 2011).

As such, the *cognitive map* remains a working hypothesis without a specific mechanistic grounding, much like that of the cognitive template. Although the "mental map" metaphor has remained a compelling tool for investigating the decisions animals make when navigating complex environments, its empirical value has been challenged several times before

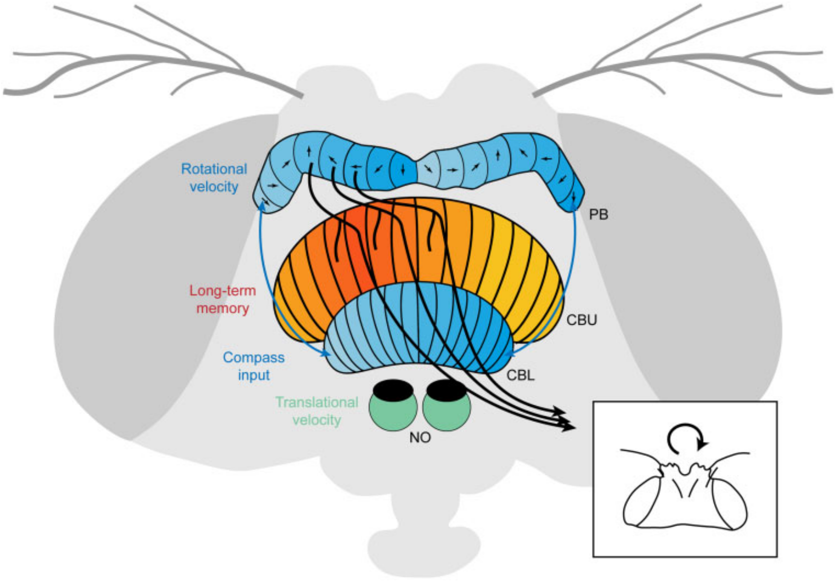

**Fig. 3** Navigation control processes model for insects. Direction encoding occurs in the lower central body (CBL) or ellipsoid body (EB), protocerebral bridge (PB), and the noduli (NO). Compass information in integrated with direction and rotational velocity vectors with a proposed feedback mechanism from previous direction vectors stored in memory centers of the upper central body (CBU) or fanshaped body. After collaborative processing through the PB, NO, and both divisions of the central body, neural projections into the lateral accessory lobes compare current and desired heading information to drive motor control of flight. Redrawn with permission from Heinze (2017)

(Bennett 1996; Cruse and Wehner 2011; Asem and Fortin 2017). The assumption of a literal map led to greater understanding of specific cell types in the hippocampus and their relationship to navigational behaviors, but it also narrowed the scope of investigation to primarily hippocampal organisms. Current understanding of the diverse cell types and diffuse processing sites suggests a less localized organization of a cognitive map, such that it is more similar to an active process of spatial sense-making rather than a physicalized neural object (Johnson and Redish 2007). The search for a physical map/template thus may have distracted researchers from the emergent way-finding behaviors that we now know many animals exhibit.

## Mate choice and species recognition

During mate choice, individuals must recognize and/or discriminate among other individuals to guide mating behaviors that increase fitness. The use of a "stored representation" of an appropriate mate seems intuitive and therefore has been commonly assumed, referenced to variously as *internal recognition template* (Pfennig 1998), *template matching* (Sherman et al. 1997), or even *cross-correlation* (Hennig 2003). Darwin himself in *The Descent of Man* used a highly anthropomorphized description of mate choice in female ducks—and their inner sense of "aesthetic" beauty—to propose the importance of sexual selection in the evolution of biodiversity, his language evoking template-like reasoning (Darwin 1871). Despite a reliance on such variable language and associated "template-like" assumptions, a review of the evidence for neural correlates in mate choice reveals a more distributed process. The mechanisms of recognition during mate choice have been extensively studied in frogs, where males produce species-specific songs to attract females. Modeling of recognition and discrimination tasks showed that tungará frogs (*Engystomops pustulosus*) may use a generalized cognitive framework for recognizing mating calls in different choice contexts (Ryan et al. 2003; Phelps et al. 2006), and females categorically discriminate against conspecific versus heterospecific calls (Baugh et al. 2008). Together, these behaviors could depend on the use of a species-specific "template" although this has not explicitly been tested. At the neurological level, however, mating decisions involve multiple brain regions, or at least the coordinated activity of many neurons. This is contrary to the original interpretation of a template as a singular, stored locus recalled during stimulus comparison. Multiple regions of the torus semicircularis (a region critical to auditory integration and phonotaxis) were most responsive while listening to rival mating calls in male tungará frogs (Hoke et al. 2004). Although the laminar subdivision showed the greatest difference in neural activity when listening to conspecifics, changes occurred across the entire brain region, and the response in aggregate across subdivisions was a better predictor of conspecific signals than changes in any one brain subdivision. Furthermore, functional connectivity between hypothalamic nuclei changed in female frogs exposed to songs of different social valence (Hoke et al. 2005). In tree frogs (genus *Hyla*), "interval counting" neurons in the midbrain are most responsive to species-specific rates of song calling. Different populations of these "interval counting" neurons respond to different temporal properties of acoustic stimuli, and changes in sensitivity correlate with differences in song rate or song onset between species (e.g., pulse rate, pulse rise; Rose et al. 2015). Yet, other neurons in the same region are responsible for integrating inhibition and excitation to respond to changes in song duration (Leary et al. 2008; reviewed in Rose 2018). These cases demonstrate that mate choice is most likely distributed across neural populations, even if behavioral data make no specific delineations of the neural mechanisms.

In addition to amphibians, specific investigations into neural mechanisms of mate choice come from literature across diverse taxa. These studies have uncovered evidence for multiple neurons or brain regions associated with choice. Within finches, two new areas have been identified as responsive in female brains while listening to preferred male songs over unpreferred noises (Van Ruijssevelt et al. 2018), in addition to the classically characterized auditory regions of the avian forebrain (see above and Fig. 2A). Recent research in fishes, specifically swordtails (genus *Xiphophorus*) and Trinidadian guppies (*Poecilia reticulata*), showed that distinct brain regions including the optic tectum and the telencephalon both show transcriptional responses after exposure to males (Lynch et al. 2012; Bloch et al. 2018). These changes in gene expression between different brain regions also changed after exposure to an attractive male versus unattractive male or conspecific female, highlighting connectivity between brain regions and variability associated with mate choice as a social interaction (Bloch et al. 2021). Outside of vertebrates, in the cricket *Gryllus bimaculatus*, Schöneich et al. (2015) described how relative rates of inhibition and excitation of five neurons create a microcircuit for a temporal feature detection sensitive to changes in male song rate. Researchers have called this a "template" while acknowledging "that inhibitory and excitatory inputs from the presynaptic auditory network shape its activity" (Kostarakos and Hedwig 2012). And in *Drosophila melanogaster*, changes in the propagation of signals to P1 neurons (responsible for promoting courtship behaviors) switch affiliative behaviors toward conspecific female signals to aversive behaviors, despite conserved peripheral neurological responses between species and similar structural connections in central circuits (Seeholzer et al. 2018). In fact, recent work in *Drosophila* has shown widespread neural responses to courtship song throughout the central brain (Pacheco et al. 2021). Cumulatively, these studies indicate that a diverse set of neural substrates and the relative valence of connectivity between them (e.g., interregional activity, construction of neural circuits) are used in mating decisions, not just a single locus as predicted by a cognitive template. If we were to expand our definition of what a *cognitive template* is or where it could be to include all the circuitry used during mate detection, then it is not clear what scientific work is provided by invoking a mate template in the first place. In other words, if anything we find in the nervous system involved in a recognition task is *the* template, no matter how complex or distributed, then the utility of invoking a template is lost.

One caveat to our review of the behavioral evidence for the use of a *cognitive template* in mate choice is that researchers have used a wide range of stimulus types when exploring behavioral and neural responses to sexual signaling, including both intra- and intersexual signals as well as intra- and interspecific trait comparisons. For example, because of the prominent role sexual selection may play in speciation (Ritchie 2007; Ellis and Oakley 2016), many studies looking at the neurological basis of female preferences have tested female responses to conspecific versus heterospecific signals. This comparison only considers two points along a continuum of signals elaborated during speciation. Such experimental designs ignore the possibility that conspecific and heterospecific signal processing are handled via different neurological mechanisms (as recently reviewed in birds; Louder et al. 2019) because some signals or complex displays may contain both species-specific information (Baugh et al. 2008) and traits used for intraspecific comparisons of mate appropriateness. On the other hand, some researchers have argued that species labeling and mate choice need not be separate evaluative processes (Mendelson and Shaw 2012), and behavioral evidence in frogs demonstrates that recognition processes may be shared across these inter- and intraspecific signaling contexts (Ryan et al. 2003; Phelps et al. 2006). However, at the neurobiological level, female frogs exposed to either intra- or interspecific signals do show differences in immediate early gene expression across the brain (Chakraborty et al. 2010; Mangiamele and Burmeister 2011). Such results indicate that animal brains may interact with intra- and interspecific signals in a more complex manner than binary categorization would imply. From an experimental standpoint, we argue it is best to keep in mind that inter- and intraspecific signaling *may or may not* be processed separately. In addition, evolutionary history should be explicitly considered during stimulus selection when investigating the neural basis of mate choice (Mendelson 2015). We thus suggest more caution when interpreting how neural responses correlate with the behavioral labeling of species and population boundaries in order to reduce assumptions and risk overlooking interesting biological phenomena.

In our survey of the literature, we have noted that research groups studying a wide range of animal taxa have increasingly moved toward using process-based language when discussing mating decisions. We feel this could be an excellent example to other fields of cognition. Although the idea of a *cognitive template* during mating decisions does exist in the literature, its evidence is scant. Instead, recent work in vertebrates discusses how a subset of the social decision making network (SDMN) may be actively involved during mate choice (DeAngelis and Hofmann 2020). This discussion has evolved from a "stored representation" hidden deep within the brain to how peripheral sensory inputs are modulated, integrated, and lead to activation of other pathways, thereby playing a role in a complex set of connected feedback processes (e.g., Hoke et al. 2007). In the context of mating decisions, such process-oriented language has two advantages: (1) the proposed connections of networks like the SDMN align more readily with the plasticity observed in mating preferences, such as incorporating variation in environment, internal states, and behavioral contexts and (2) this allows for the development of mechanistic hypotheses regarding the broader set of neural, molecular, and regulatory substrates involved in these behaviors, hypotheses that are unconstrained by the implied localization of a "cognitive template."

## Animal perception and object recognition

In addition to recognizing kin, mates, and locations in the environment, many animal behaviors rely on detection and recognition of particular objects (e.g., food, host plants). For visual object recognition, a well-supported approach involves studying the perceptual processes that parse visual complexity in "pattern space" (Stoddard and Osorio 2019), including edge detection, local feature detection, and recognition of more complex visual objects (e.g., faces). These levels of processing are also commonly described in the literature on predation and camouflage as low- and high-level figure-ground processing (Troscianko et al. 2009), and the existence of such processing distinctions is supported by behavioral evidence across animal systems. First, behavioral orientation toward visual edges (such as those created by chromatic or achromatic contrasts) has been found across arthropod and vertebrate species (Lehrer et al. 1990; Bhagavatula et al. 2009), and computational models have shown how camouflage that obscures edges disrupts prey recognition (Stevens and Cuthill 2006). Second, local feature detection (e.g., of visual "parts," as in parts-based processing) was even reported in Tinbergen's (1951) classic studies using three-spined sticklebacks, where males readily attacked crude, unrealistic models of conspecific males with the distinct red belly (a territorial signal) over more detailed and realistic models. Similarly, the jumping spider *Evarcha culicivora* more often attacks modified lures, models, and abstract images that show specific characteristics of its preferred prey, blood-fed female mosquitos (e.g., engorged red/darker colored abdomen, female head and thorax, leg-resting position), over realistic representations of male mosquitos, honey-fed females, and other less-preferred prey (Nelson and Jackson 2012; Dolev and Nelson 2014).

Third, for visual recognition studies of more complex objects, facial recognition has been the subject of intensive investigation. Attentiveness to eyes and eye-like patterns is broadly observed across all major, extant vertebrate taxa (regardless of differences in social communication behavior). As a result, researchers studying facial recognition have theorized that animals initially evolved mechanisms for identifying eye-like stimuli to aid in predator detection and avoidance, with facial recognition evolving secondarily as an exaptation for intraspecific communication (Leopold and Rhodes 2010). The use of facial discrimination is now known to be taxonomically widespread. For example, in nonhuman primates, rhesus macaques and chimpanzees can use facial cues to discriminate between unfamiliar conspecific individuals, while chimpanzees can additionally discriminate between unfamiliar heterospecifics (Parr et al. 2000; Wilson and Tomonaga 2018). Similarly, species of guenon monkeys use variations in facial ornaments to identify conspecifics (Winters et al. 2020), and species across this tribe of primates have evolved visually distinct species-specific facial patterns within multispecies communities, presumably to facilitate species recognition (Allen et al. 2014). While we know less about how invertebrates may interact with faces, there are still several compelling cases. Many paper wasp species use simple facial markings to communicate social status (Tibbetts and Lindsay 2008; Baracchi et al. 2013). Female *Polistes fuscatus* paper wasps can even discriminate between faces of individuals in order to navigate their complex social hierarchies (Sheehan and Tibbetts 2011). In the context of predation, the araneophagic jumping spiders *Portia fimbriata* can discriminate between spider prey types by using only differences in facial features and adopts a specific stalking strategy when viewing salticid prey faces (Harland and Jackson 2002).

But how do animals recognize objects and faces at the neural level? Work on the neural basis of these visual processing mechanisms has provided evidence for the involvement of a number of neural loci, from edge detection in the retina or early visual processing centers to deeper-level brain regions involved in recognition of complex objects like faces. However, such work has rarely identified a single, distinct brain region used for any particular visual recognition task, as might be predicted by the *cognitive template* concept. For example, edge orientation and detection behaviors in *Drosophila* begin in the photoreceptor cells in the retinae dedicated to achromatic vision (Zhou et al. 2012). Mammalian visual object detection also begins in the retina, with further visual processing engaging the lateral geniculate complex of the thalamus, superior colliculus of the midbrain, and other visual cortical areas (Masland and Martin 2007). For example, edge detection and line orientation occur early in the visual neural processing pathway, attributed largely to the primary visual cortex (V1) neurons, as shown by single-cellular recordings (Lamme 1995; Bruce et al. 2003). There are also retinal ganglion cells in the eyes with different sensitivities (e.g., toward directional stimuli) that are less well understood, as they occur in lesser numbers and thus are not easily evaluated by the common method of averaged single-cellular recordings (Masland and Martin 2007). Thus, the processing of visual functions such as edge and feature detection, visual memory, shape and motion, color perception, and attention occurs throughout multiple, parallel pathways with intercommunication between brain regions (Masland and Martin 2007). For example, in macaques, neural sensitivity to faces has been found across several areas in the temporal lobe of the brain with high levels of communication in between each and to other areas of the brain (Grimaldi et al. 2016). Furthermore, visual object recognition seems to be facilitated by bottom-up neural processes as well as and other top-down processes, such as attention and training conditions (Giurfa et al. 1999; Masland and Martin 2007).

Throughout these studies, authors primarily use process-oriented language (e.g., evaluating animal behaviors as "shape perception" and "shape discrimination"), and template terms are rarely used. In particular, studies that incorporate more neurological approaches tend to completely avoid using template-like terms, such as the evaluation of jumping spider visual perception of prey and other ecologically relevant stimuli through single-unit neural recordings (Menda et al. 2014). However, template ideas are sometimes mentioned informally in discussion of some higher-order object recognition. More broadly across theoretical and behavioral studies, terms analogous to *cognitive template* are sometimes adopted from classic human visual perception literature, including *template matching*, *feature matching*, and *structural descriptions* (Bruce et al. 2003). *Template matching* is defined similar to *cognitive template* and describes the matching of external patterns to a stored template, while *feature matching* describes matching of parts and combinations of an image. The related term *structural descriptions* (using a set of descriptive or relational values about the configuration of an object) also echoes some concepts of direct *template matching* through its invocation of a stored "structural description" placed somewhere in the brain (Bruce et al. 2003). Some of these human-centric terms and concepts were transferred into animal perception and behavioral studies as a starting point, though very often the specific terms are either not clearly defined, or the *template matching* concept is invoked in the discussion using template-like language. For example, researchers have invoked analogies between the flight patterns of honeybees and the visual scanning patterns of humans (Anderson 1979; Noton 1970) without scientifically developing this idea past the point of analogy.

Ecological experiments also primarily utilize process-oriented language (e.g., Wilkinson and Huber 2012). Work in foraging and predation contexts likewise does not utilize template-like terms, instead commonly using the term *search image* as first coined by Tinbergen (1960)—the theory describes selective attention to specific prey features and does not invoke any mechanistic assumptions (e.g., Jackson and Li 2004). However, some vertebrate and invertebrate cognition studies employ the term *phenotype matching* to describe internal templates used to compare to external cues when perceiving or recognizing stimuli (Gherardi et al. 2012). In many of these studies, the neural mechanisms of *phenotype matching* are not directly articulated. Thus, it remains ambiguous whether this term overall serves as a functional or mechanistic definition, though the first usage of the term specifies the comparison of external phenotypes to a learned template (Holmes and Sherman 1982). The function these terms serve (as illustrative metaphors or supported hypotheses) is not clearly articulated but would be a key in preventing inherent percolation of misinformation. For example, Gärdenfors (1996) states that *detached representations* may be used in animal cognition to allow for planning, but he explicitly emphasizes that the term is an untested "theoretical idealization" and only to be used as a metaphor to predict and test empirically. There is also a niche term, *mental template matching*, used to describe the learning of tool making in New Caledonian crows (Jelbert et al. 2018).

Outside of the visual perception studies, *internal recognition templates* and *odor templates* are commonplace in describing olfactory and chemosensory recognition of substrates for oviposition and food identification. Much like in kin recognition, olfactory and chemosensory cues are often referred to as matching an innate or acquired template for the identification of host plants, food odors, and pheromones (del Campo et al. 2001). Oftentimes, these *internal recognition templates* are presented as tuned to or induced by specific compounds, such as host plant recognition mediated by indioside D in *Manduca sexta* (del Campo et al. 2001) and oviposition site selection triggered by $\gamma$-octalactone in *Bactrocera dorsalis* (Damodaram et al. 2014). In the case of *B. dorsalis*, behavioral experiments demonstrated that recognition of appropriate site-selection was based on an innate response to $\gamma$-octalactone even when reared without exposure to the compound (Damodaram et al. 2014). These *odor templates* are thought to be based on the ratio of components in a signal (Martin and Hildebrand 2010) and firing synchrony (Sehdev et al. 2019). A common theme among these olfactory templates is the precision and specificity required for recognition, such that even "learned templates" become fixed after imprinting. This introduces complications in complex environments where odors are intermixed, requiring that odorant signatures be extracted and identified as unique object cues (Sehdev et al. 2019). Multiple insect studies have used electrophysiology to record activation in the olfactory bulbs in response to recognition cues (Freeman 1979; del Campo et al. 2001; Martin and Hildebrand 2010; Damodaram et al. 2014). Research in several moth species has suggested that both mate pheromone and food odor recognition are mediated by a common mechanism in which specific patterns of neural activity in the antennal lobe aid recognition (Martin and Hildebrand 2010). These neural signatures of odor recognition have been taken as evidence for the use of *odor templates*, as well as the location in which they reside in the nervous system. However, recent emphasis on the importance of firing synchrony for appropriate identification suggests feedback loops is employed in the recognition process (Sehdev et al. 2019; Sehdev and Szyszka 2019). Thus the specificity and precision of pheromone matching and host plant identification are the result of tight coevolutionary relationships and do not represent a global or flexible mechanism of all recognition behaviors.

## Discussion

Although acknowledged as mechanistically unworkable by the cognitive scientists who developed it, the concept of *cognitive templates* was nonetheless widely adopted by biologists as a convenient metaphor for the mechanisms underlying recognition tasks. With this expanding popularity came ever broader applications of the original concept, leading to a dissipation of its specific (and testable) implications as well as a proliferation of analogous terms and concepts (Table 1). However, a common finding from this work is a lack of empirical support at the neurological level for a central, stored location of a literal and direct template for such cognitive functions such as recognition or navigation. Thus, we argue that researchers would be well served by abandoning use of the "cognitive template" concept. An alternative to the use of template-like concepts would be to conceive of recognition tasks as the result of distributed cognitive processes involving not only multiple brain regions and circuits but also peripheral sensory systems and even the actions of body parts (e.g., movement of the eyes and limbs). Such a distributed view of cognition is supported by work in birdsong, kin recognition, and navigation. Other fields have approached decision-making behaviors without *a priori* assumptions of the underlying neural substrates and have found evidence for a more network-like process throughout the brain. For example, much of *Drosophila* neuroscience uses more process-oriented language without incorporating cognition and psychology metaphors. Searching for patterns of relational activity at all levels of a neural system (i.e., between receptors, cells, and regions) seems to more accurately mirror our current understanding of anatomy, chemistry, and electrophysiology.

This intellectual path, which emphasizes the emergent properties of complex relational networks over the search for singular physical loci, mirrors the historical trajectory of the field of genetics, which moved from a Mendelian emphasis on single genetic loci of large effect to a more nuanced understanding of quantitative traits caused by many interacting loci of variable (and often nonlinear) effect. We argue that a similar path may (and should) be in store for work on the mechanistic bases of recognition and discrimination behaviors, or indeed any field in cognitive science where stored representations are invoked. As the techniques of comparative neuroscience increase in sophistication, we may be able to test these more distributed models of cognitive processing across increasingly diverse systems, thereby building the infrastructure for deeper understanding of how such networks evolve over time in ways analogous to the study of gene regulatory networks.

We have been quite critical of some of the metaphors applied in animal recognition studies, especially *cognitive templates* and *cognitive maps*. These metaphors have inspired valuable empirical findings, but they have also at times misguided research to search for a direct neural correlate of a recognized external object or environment (Kennedy 1992; Rendall et al. 2009). We would be remiss if we did not offer a replacement for these metaphors. Our proposal is for researchers in nonhuman cognition to ally themselves with current research in ecological psychology (Gibson 1979; Chemero 2009; Gibson 2014). Ecological psychologists do not focus on the supposed computational abilities of brains as early cognitive scientists did. Instead, they take their subject matter to be emergent brain–body–environment coalitions. From this perspective, the activity of nervous systems is not to re-construct a copy of the environment inside the animal, but to help maintain the connection between the animal and relevant parts of its world. So far, ecological psychologists have focused primarily on humans (see Chiovaro and Paxton 2020 for an exception), but their approach is specifically designed to apply to any organism in its environment, even those without nervous systems. The ecological approach is well established, with sophisticated and rigorous experimental methods and modeling techniques that could easily be applied to nonhuman animals (e.g., Riley and Van Orden 2005; Kelso and Engstrom 2006; Riley and Holden 2012). Perhaps, most importantly, adopting the ecological approach enables us to recognize the role of not just brain areas for perception and cognition, but other parts of animals and parts of the environment as well. Just as Gibson (1966) pointed out that the human visual system is not just eyes and brain, but also includes the muscles that move the eyes and head and enable locomotion, we could see that, for example, a web-building spider's prey recognition does not occur only in the spider's brain, but also crucially involves other parts of the spider's body and the spider's web. We hope this emphasis on emergent animal–environment systems will promote study of all aspects of animal cognition without a narrowed assumption about localized mechanisms. At the very least, our review of the available evidence suggests that the related concepts of "cognitive templates" and "mental maps" have outlived their real utility and should be discarded in favor of a perspective that emphasizes cognition as the result of distributed and often nonlinear interactions between suites of neural and other bodily processes. In this way, we can step into a new era of inquiry into how and why animals have evolved their myriad and multifaceted perceptual worlds. Such was the motivation for invoking templates and maps in the first place. It just turns out that animals, their bodies, and their brains are even more wondrously complex than our sometimes-limited conceptions give them credit.

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## Conflict of interest statement

The authors have no conflicts of interest to declare.

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