



Decision-making in a social world: Integrating cognitive ecology and social neuroscience

Kelly J. Wallace^a and Hans A. Hofmann^{a,b}

Abstract

Understanding animal decision-making involves simultaneously dissecting and reconstructing processes across levels of biological organization, such as behavior, physiology, and brain function, as well as considering the environment in which decisions are made. Over the past few decades, foundational breakthroughs originating from a variety of model systems and disciplines have painted an increasingly comprehensive picture of how individuals sense information, process it, and subsequently modify behavior or states. Still, our understanding of decision-making in social contexts is far from complete and requires integrating novel approaches and perspectives. The fields of social neuroscience and cognitive ecology have approached social decision-making from orthogonal perspectives. The integration of these perspectives (and fields) is critical in developing comprehensive and testable theories of the brain.

Addresses

^a Department of Integrative Biology, University of Texas, Austin, TX, 78712, USA

^b Institute for Neuroscience, University of Texas, Austin, TX, 78712, USA

Corresponding authors: Hofmann, Hans A. (hans@utexas.edu); Wallace, Kelly J. (kwallace@utexas.edu)

Current Opinion in Neurobiology 2021, **68**:152–158

This review comes from a themed issue on **The Social Brain**

Edited by **Hailan Hu** and **Michael Brecht**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 26 April 2021

<https://doi.org/10.1016/j.conb.2021.03.009>

0959-4388/© 2021 Elsevier Ltd. All rights reserved.

Social neuroscience has made great strides in understanding the key pathways and neuromodulators of important social, behavioral processes like affiliation, reproduction, and aggression. Independently, cognitive ecology has examined a diverse set of taxa to analyze behavior in social groups, determine decision-making rules and the factors that modulate them, and contextualize these processes in naturalistic scenarios to understand their adaptive value. The integration of these perspectives (and fields) is critical in developing comprehensive and testable theories of the brain

[5,31,14]. Here we review complementary insights into social decision-making from the perspectives of both social neuroscience and cognitive ecology. We describe each area of research and its development in recent decades, including a brief discussion of studies that have attempted to integrate both fields. We then outline several steps to further integrate social neuroscience and cognitive ecology toward a complete understanding of social decision-making.

What is social neuroscience?

Social neuroscience is the study of the neural mechanisms of social behavior, and as such, is situated within the tradition of neuroethology [66,65], which historically has included the study of social behavior, as well as investigations of reward, motivation, and decision-making (e.g. Ref. [56]). From this foundation, social neuroscience emerged as an independent field of research in the early 1990s [6] with the aim of understanding the neural, hormonal, cellular, and genetic underpinnings of social behavior [7]. It is this integration across levels of biological organization, and how they relate to the social realm, that separates social neuroscience from the more reductionist approaches in much of modern neuroscience (where behavior is often an afterthought, see Ref. [22]) and from the organism-level outlook characteristic of animal behavior research and psychology [17]. Importantly, almost from its inception, social neuroscience has embraced a diversity of model systems and attempted to infer evolutionary insights.

Current research in social neuroscience primarily stems from two areas of research [17]: a neuroethological perspective on sensory processing and a neuroendocrinological perspective on suites of social behaviors such as sexual behavior (including sexual signaling, mate choice, and courtship), aggression (including dominance, competition, and territoriality), parental care, and affiliation/avoidance (including cooperation and prosociality) (see Refs. [49,58]). Research on sensory processing has amassed a comprehensive and detailed inventory of the pathways, cells, and circuits that process social information from a multitude of modes (e.g. pheromones, acoustic, and visual courtship signals and cues) [53]. Conversely, research in the neuroendocrinology realm has demonstrated how remarkably conserved (in form, function, and occasionally both) the

mechanisms of social behaviors are across taxa, from sex steroids to nonapeptides to reward neuromodulators (dopamine, serotonin), to stress modulators (cortisol) [13,25,26,21,52].

A decade ago, Adolphs [1] proposed a set of ‘next steps’ in research on social neuroscience. These included new model systems, an emphasis on region mapping of socio-cognitive processing in the brain, and investigating generality versus domain-specificity in social information processing. All these suggestions reflected a need to more closely integrate a more naturalistic (or ecological) perspective into the field, as we discuss later. More specifically, Adolphs [1] identified that one strength of social neuroscience is its grounding in animal studies, then *subsequent* extension to humans, rather than the other way around. This is one challenge that social neuroscience encounters: studies amass a vast and often bewildering array of relationships between mechanisms and complex behavior, emotion, or personality traits, yet it only rarely addresses the functional implications, evolutionary constraints, or fitness consequences of the identified relationships [25,7]. We posit that a cognitive ecology framework will prove beneficial in contextualizing the results within a larger evolutionary framework.

What is cognitive ecology?

Cognitive ecology has its roots in classical ethology’s emphasis on an integrative understanding of *natural* behavior [51]. The distinction of cognitive ecology from neuroethology and behavioral ecology was articulated by Real [33], who put forward a ‘cognitive approach’ toward understanding animal decision-making. Intended as an alternative to a strictly behaviorist/adaptationist approach, an individual’s decision is no longer seen as an objective weighing of external stimuli but rather a product of a series of processes (perception, encoding, storage, and representation) that are the product of evolution [33]. Later, Shettleworth defined cognition as “*all [the] ways in which animals take in information through the senses, process, retain and decide to act on it.*” [43]. Behavioral ecologists have increasingly embraced the implications of cognitive processes in their experimental designs, thus integrating research into animal cognition with behavioral ecology, a research field now often referred to as cognitive ecology [12]. Cognitive ecology has oscillated between a more ecological and a more psychological perspective [16,20]. The ecological approach has proven invaluable in structuring testable and discrete hypotheses for cognitive processes (e.g. bird food caching [47], fish transitivity in mate choice decisions [34], bat prey cue assessment [29]). In contrast, a psychological approach has increased our understanding of the cognitive processes that human and nonhuman animals share, primarily through the assessment of primate cognition [60].

Different cognitive domains are those that require different types of cognitive performance [9]. Common domains assessed in cognitive ecology literature include spatial learning, associative learning (including discrimination learning), cognitive flexibility (such as inhibitory control and reversal learning), and innovative problem solving/novel motor learning. Many studies employ multiple cognitive assays to compare performance across domains, and there has been a recent call to improve the universality of such cognitive test batteries (as well as expand this type of testing to additional animal models) [42].

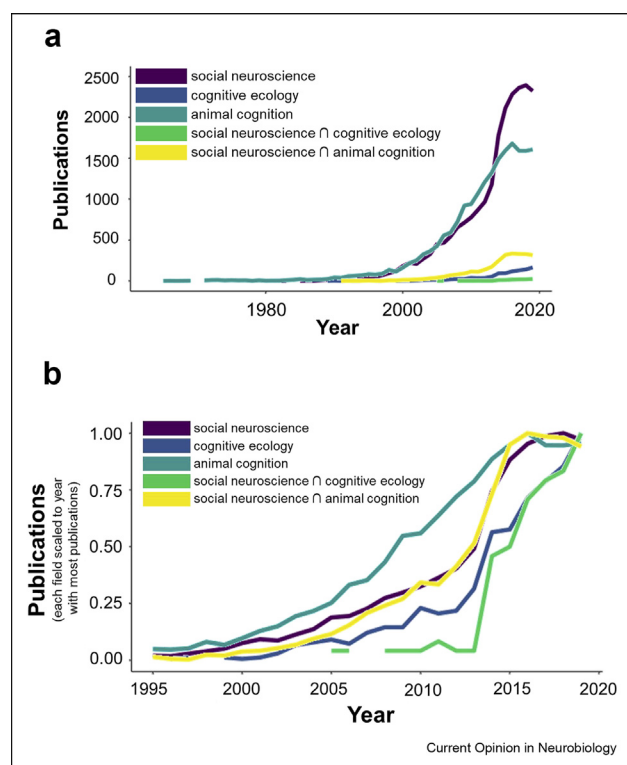
Model systems in cognitive ecology are often selected based on their unique behavioral repertoire (e.g. cleaner mutualism in fish and shrimp [46,55], bats navigating via echolocation [48], vocal learning in songbirds [41]). Given the diverse species studied, numerous often ingenious assays have been developed to assess cognition in a manner most appropriate for and relevant to the model system. However, examining cognitive behavior in a way that is efficient, robust, and relevant across species given their differences in natural and evolutionary history poses another great challenge [32]. Designing an experimental paradigm that is ‘fair’, i.e., not biased toward any one of the species under investigation, is difficult as species differences that are not directly relevant to the behavior under study might interfere in nonobvious ways. For example, in studies on spatial learning using a food reward, one species might simply be more motivated by the food reward used and yet would appear to be superior at spatial learning [27]. Nevertheless, the diversity of model systems has been an obvious boon for the field, yet inferring the mental processes taking place inside an animal’s brain from behavioral observations alone remains another major challenge [43]. This is particularly true when we consider different social environments where cognitive processes — such as the assessment of valence and salience, associative learning and memory retention, and the speed and accuracy of decision making — can change dynamically across social contexts [59]. Integrating proximate mechanisms into the research agenda of cognitive ecology has long been seen as critical [43], yet progress in this direction is ripe for additional exploration.

Integrating social neuroscience and cognitive ecology

To assess where integration between social neuroscience and cognitive ecology is already occurring, we conducted a quantitative literature search in both [Google Scholar](#) and [PubMed](#), using representative search terms (see [Figure 1](#) legend for details). Here, we only report the analysis for PubMed as the two databases yielded concordant results. We identified 19,669 publications for the search term ‘social neuroscience,’ 17,883

publications for ‘animal cognition,’ and 1068 publications for ‘cognitive ecology.’ The fields of social neuroscience and animal cognition have been growing steadily since the mid-1990s, with the latter initially outpacing the former (Figure 1a). In contrast, cognitive ecology began to accelerate only about 15 years ago, albeit at a slower pace. To examine the state of integration of these fields, we then scaled each separately to its respective year with the most publications (Figure 1b). Interestingly, the intersection of social neuroscience and animal cognition (2564 publications) largely follows the trajectory of social neuroscience, while the intersection between social neuroscience and cognitive ecology (113 publications) began to accelerate only in the last decade (Figure 1b). Our analysis shows that both social neuroscience and cognitive ecology are thriving disciplines and that the very recent and ongoing integration of cognitive ecology and social neuroscience is an exciting and promising frontier.

Figure 1



Quantitative analysis of the publication effort in Social Neuroscience, Animal Cognition, and Cognitive Ecology. Three searches were conducted in PubMed (selecting ‘all fields’ and restricting the year to before and including 2019): ‘(social neuroscience) AND (animal)’, ‘(cognitive ecology) AND (animal)’, and ‘(animal cognition)’. Two additional searches assessed the intersections between the fields: ‘(social neuroscience) AND (cognitive ecology) AND (animal)’, and ‘(social neuroscience) AND (animal cognition)’. Shown are total research effort over time (a) and scaled research effort to facilitate comparison (b). Primary data and analysis code can be found at: https://github.com/kellyjwallace/Wallace_Hofmann_literature_analysis.

Promising approaches for further integration

We propose four approaches that cognitive ecologists and social neuroscientists may want to consider as they conduct integrative work between these two areas. These suggestions are not meant to be exclusive, and rather they reflect research directions that have already yielded novel insights — as demonstrated by the examples we provide — and are likely to play an important role in the future integration of these fields.

1) Assess social behavior and cognitive performance in the same subjects across cognitive and social domains.

The social environment is a rich landscape and individuals that navigate it rely on cognitive processes. When possible, assessing the same individuals in social behavior assays *and* cognitive tasks can facilitate a better understanding of the social factors that are relevant for certain cognitive abilities. The ability to correlate social factors with cognitive processes then allows researchers to generate specific hypotheses on how proximate mechanisms (such as neuromodulators) should vary across individuals and across these social factors.

For example, the prairie vole, *Microtus ochrogaster*, has become a model system for understanding social monogamy and the role of nonapeptides in social affiliation and salience. In this model system, a series of elegant studies of behavioral, neuromolecular, and genetic mechanisms have transformed our understanding of the role of nonapeptides in both social behavior [11], and spatial memory [35]. Further work comparing these social categories and cognitive domains is a critical step in identifying relationships between social behavior and cognition that can then be explored at a mechanistic level (e.g. Ref. [28]). The evolution of our understanding of the function of the nonapeptides [11,13,37] exemplifies the utility of investigating mechanisms in alternative contexts. Oxytocin was originally considered a neuromodulator of ‘social affiliation.’ But further exploration provided evidence for an expanded role, and now we more clearly understand its role in ‘social salience,’ or the orienting of responses to social cues. This expanded role explains the role of oxytocin in both the typical prosocial aspects of social behavior (such as trust and empathy), as well as antisocial aspects (such as aggression and envy) [44]. It is important that mechanisms are not pigeon-holed into the investigation only within traditional contexts and traditional model organisms. It is also important to record noncognitive behavioral traits during assays, as they may be influencing the perceived cognitive performance [54].

2) Compare social phenotypes over time and across developmental trajectories

As mentioned previously, study systems that display variation in a social attribute can be very useful for studies of cognitive ecology and social neuroscience, and this is even more the case when this variation can be organized into discrete phenotypes (e.g. male/female, parenting/nonparenting, dominant/subordinate, breeder/helper). Once the behavioral and mechanistic repertoires of social phenotypes are distinguished, it is then useful to employ repeated measures designs to understand the repeatability versus flexibility of the phenotypes. Employing repeated measures across contexts (e.g. across time or development) facilitates understanding the limits of phenotypic variation in behavior and underlying mechanisms.

The African cichlid fish *Astatotilapia burtoni* has emerged as a model system in social neuroscience [23]. Studies have disentangled the relevant modalities and social information males individuals use to ascend or descend in social dominance status, as well as detailing the physiological and neural transitions that parallel social change. Recent literature in this species has additionally disentangled how these social dominance phenotypes influence group learning [38].

Social neuroscience has extensively studied developmental aspects of social behavior and trajectories, a perspective cognitive that can benefit ecologists. Furthermore, investigating developmental trajectories can be a useful tool in understanding the evolutionary origins and conservation of social decision-making. In zebra finches (*Taeniopygia guttata*), as well as other songbird species, the neural circuits and critical developmental periods of song learning have been well characterized, as well as the ecological consequences (e.g. mate preference behavior). Care has been taken to disentangle the learned versus innate aspects of song and attention and interpretation of stimuli. Additionally, explorations on this topic have characterized the anatomical constraints of song production [36].

3) Increase the number of model systems studied in naturalistic communities.

As we noted above, diverse and unique study species have featured prominently in both social neuroscience and cognitive ecology, suggesting that investigating nontraditional model systems can be particularly fruitful. Often, model systems are chosen due to complex behavior or extreme social phenotypes that they exhibit, such as archerfish [39] or naked mole rats [15]. Additionally, species often vary considerably in social attributes (that potentially change over time), which allows

researchers to explicitly test evolutionary hypotheses and infer which mechanisms are similar (and possibly conserved) across species (see approach 4) below). This requires extensive knowledge of the social environment of the system. It is easy to overlook basic naturalistic characterizations, but the initial description of a species' life history, social organization, and naturalistic behavior is critical in establishing baseline predictions regarding cognitive performance. For example, in honeybees, studies of the relationship between spatial navigation and social communication, as well as the underlying neural mechanisms, have a rich history grounded in painstaking observations of behavior in nature [24,64]. Studies of primate societies, particularly geladas, rhesus macaques, and savannah baboons, have turned the limitations of studies conducted in the wild into a strength through detailed recording of social interactions paired with physiological and molecular assessments [62,45,18]. Importantly, research on primates has been instrumental in building our understanding of higher order cognitive processes, such as the theory of mind and subjective mental states, from an ecological rather than anthropocentric perspective. In addition to establishing new model systems via basic naturalistic characterizations [19], longstanding biomedical model systems (e.g., the nematode worm *Caenorhabditis elegans*, the fruit fly *Drosophila melanogaster*, and the mouse *Mus musculus*) will greatly benefit from more ecological perspectives that historically have not been central in their literature (e.g. Refs. [50,61]).

Importantly, new technologies such as automated tracking and machine learning have facilitated a renaissance of detailed behavioral observations, often in naturalistic contexts [10]. Scientists are also swiftly advancing neural recordings of freely interacting animals (e.g. Ref. [40]) as an alternative to more restrictive techniques that require animals to be fixed to a stage. Often, the analysis of these complex datasets requires new statistical approaches. Social network analysis, for example, has been a particularly fruitful subfield within the study of ecologically relevant social behavior. The observation of complex group social dynamics yields equally complex datasets and requires sophisticated statistical approaches [61,30]. These statistical approaches have undergone rapid development and have vastly improved our ability to interpret group social dynamics [57]. The rapid pace at which these technological and statistical advances occur provides exciting opportunities for the integration of social neuroscience and cognitive ecology [2].

4) Employ phylogenetic comparative analyses of mechanisms and behaviors

It is clear that for both social neuroscientists and cognitive ecologists, understanding animal behavior

(in particular social decision-making) requires an evolutionary framework. From the social neuroscience perspective, understanding the shared pathways and brain region homologies [13,25,26] is critical in determining the roles of key mechanisms and circuits. From the cognitive ecology perspective, understanding the fitness consequences of behavior provides insight into its maintenance in any given population.

Poeciliid fishes (a family of freshwater livebearing fish encompassing guppies, mollies, swordtails, and platys) initially became a model system for understanding life-history tradeoffs in response to predation, and have since emerged as a model system for mate choice, as closely related species vary in mating system. Studies on male visual ornaments and coloration paired with experience-dependent female mate choice and its neural mechanisms have all been grounded in an evolutionary framework of sexual conflict and alternative reproductive tactics [8].

There is a ripe opportunity for researchers of social behavior to employ more rigorous phylogenetic methods on large datasets across taxa to explicitly test observed conservation (see Ref. [63]). Phylogenetic analyses can more clearly paint an evolutionary trajectory of critical social attributes and their mechanisms across time. For example, many hypothalamic neuropeptides and releasing hormones are not only evolutionarily ancient but often show conserved functions, including their effects on behavior [37].

Conclusion

To understand how human and nonhuman animals make decisions in a social world, scientists must integrate across biological levels and diverse perspectives. This integrative approach is not a new concept, rather, integrative frameworks such as Tinbergen's four questions [51] have facilitated enormous conceptual progress in our understanding of animal behavior [3]. But given the recent advances in neuroscience and behavioral analyses [4], the ability to integrate these topics within single studies has become much more accessible [14]. We have described here the complementary approaches that social neuroscientists and cognitive ecologists have used to social decision-making, detailing their methodological strengths and weaknesses. The intersection of these two fields is ripe for more integration, which no doubt will yield important new insights.

Author contributions

HAH and KJW conceived of the study. KJW wrote the initial draft of the manuscript, and HAH provided feedback and comments during manuscript writing. All authors give final approval for publication.

Conflict of interest statement

Nothing declared.

Acknowledgements

We thank Hannah Chapman Tripp for assistance with the literature analysis. We thank Peter Dijkstra and May Dixon for their insightful comments on earlier versions of this manuscript, and we thank all members of the Hofmann Lab for their constructive advice and feedback. This work was supported by the National Science Foundation (NSF) Bio/computational Evolution in Action Consortium (BEACON) Center for the Study of Evolution in Action and NSF Grant IOS1354942 (to HAH); a National Academies of Sciences, Engineering, & Medicine Ford Foundation Pre-doctoral Fellowship, a UT Austin Graduate School Continuing Fellowship, the UT Austin Zoology Scholarship Endowment for Excellence, and a Department of Integrative Biology Doctoral Dissertation Improvement grant (to KJW).

References

Papers of particular interest, published within the period of review, have been highlighted as:

- * of special interest
- ** of outstanding interest

1. Adolphs R: **Conceptual challenges and directions for social neuroscience.** *Neuron* 2010, **65**:752–767, <https://doi.org/10.1016/j.neuron.2010.03.006>.
2. Amodio DM, Keysers C: **Editorial overview: new advances in social neuroscience: from neural computations to social structures.** *Curr Opin Psychol* 2018, **24**, <https://doi.org/10.1016/j.copsyc.2018.10.017>. iv-vi.
3. Bateson P, Laland KN: **Tinbergen's four questions: an appreciation and an update.** *Trends Ecol Evol* 2013, **28**:712–718.
4. Boender AJ, Young LJ: **Oxytocin, vasopressin and social behavior in the age of genome editing: a comparative perspective.** *Horm Behav* 2020, **124**:104780, <https://doi.org/10.1016/j.yhbeh.2020.104780>.
5. Buzsáki G: **The brain-cognitive behavior problem: a retrospective.** *eNeuro* 2020, **7**, <https://doi.org/10.1523/ENEURO.0069-20.2020>. 0069-20.2020.
- In contrast to many others, this author argues for brain mechanisms as a starting point of cognition studies as opposed to starting with (natural) behavior.
6. Cacioppo JT, Berntson GG: **Social psychological contributions to the decade of the brain: doctrine of multilevel analysis.** *Am Psychol* 1992, **47**:1019–1028, <https://doi.org/10.1037/0003-066X.47.8.1019>.
7. Cacioppo JT, Decety J: **Social neuroscience: challenges and opportunities in the study of complex behavior.** *Ann NY Acad Sci* 2011, **1224**:162–173, <https://doi.org/10.1111/j.1749-6632.2010.05858.x>.
8. Cummings ME: **Sexual conflict and sexually dimorphic cognition—reviewing their relationship in poeciliid fishes.** *Behav Ecol Sociobiol* 2018, **72**:73, <https://doi.org/10.1007/s00265-018-2483-9>.
9. Deary IJ, Penke L, Johnson W: **The neuroscience of human intelligence differences.** *Nat Rev Neurosci* 2010, **11**:201–211, <https://doi.org/10.1038/nrn2793>.
10. Dell AI, Bender JA, Branson K, Couzin ID, de Polaveja GG, Noldus LPJJ, Pérez-Escudero A, Perona P, Straw AD, Wikelski M, Brose U: **Automated image-based tracking and its application in ecology.** *Trends Ecol Evol* 2014, **29**:417–428, <https://doi.org/10.1016/j.tree.2014.05.004>.
11. Donaldson ZR, Young LJ: **Oxytocin, vasopressin, and the neurogenetics of sociality.** *Science* 2008, **322**:900–904, <https://doi.org/10.1126/science.1158668>.
12. Dukas R: *Cognitive ecology*. Chicago: Chicago University Press; 1998.

13. Goodson JL: **The vertebrate social behavior network: evolutionary themes and variations.** *Horm Behav* 2005, **48**:11–22, <https://doi.org/10.1016/j.yhbeh.2005.02.003>.
14. Hofmann HA, Beery AK, Blumstein DT, Couzin ID, Earley RL, Hayes LD, Hurd PL, Lacey EA, Phelps SM, Solomon NG, Taborsky M, Young LJ, Rubenstein DR: **An evolutionary framework for studying mechanisms of social behavior.** *Trends Ecol Evol* 2014, **29**:581–589, <https://doi.org/10.1016/j.tree.2014.07.008>.
15. Holmes MM, Goldman BD, Goldman SL, Seney ML, Forger NG: **Neuroendocrinology and sexual differentiation in eusocial mammals.** *Front Neuroendocrinol* 2009, **30**:519–533, <https://doi.org/10.1016/j.yfrne.2009.04.010>.
16. Hulse SH: **The present status of animal cognition: an introduction.** *Psychol Sci* 1993, **4**:154–155, <https://doi.org/10.1111/j.1467-9280.1993.tb00479.x>.
17. Insel TR: **The challenge of translation in social neuroscience: a review of oxytocin, vasopressin, and affiliative behavior.** *Neuron* 2010, **65**:768–779, <https://doi.org/10.1016/j.neuron.2010.03.005>.
18. Jablonski NG: **Social and affective touch in primates and its role of skin in the evolution of social cohesion.** *Neuroscience* 2020, <https://doi.org/10.1016/j.neuroscience.2020.11.024> (in press).
19. Kabelik, Hofmann: **Comparative neuroendocrinology: a call for more study of reptiles!** *Horm Behav* 2018, **106**:189–192, <https://doi.org/10.1016/j.yhbeh.2018.10.005>.
20. Kamil AC: *On the proper definition of cognitive ethology. Animal cognition in nature: the convergence of psychology and Biology in laboratory and field.* Academic Press; 1998, <https://doi.org/10.1016/b978-012077030-4/50053-2>.
21. Kanwisher N: **What's in a face?** *Science* 2006, **311**:617–618, <https://doi.org/10.1126/science.1123983>.
22. Krakauer JW, Ghazanfar AA, Gomez-Marin A, MacIver MA, Poeppel D: **Neuroscience needs behavior: correcting a reductionist bias.** *Neuron* 2017, **93**:480–490, <https://doi.org/10.1016/j.neuron.2016.12.041>.
23. Maruska KP, Fernald RD: **Astatotilapia burtoni: a model system for analyzing the neurobiology of behavior.** *ACS Chem Neurosci* 2018, **9**:1951–1962, <https://doi.org/10.1021/acchemneuro.7b00496>.
24. Menzel R: **The honeybee as a model for understanding the basis of cognition.** *Nat Rev Neurosci* 2012, **13**:758–768, <https://doi.org/10.1038/nrn3357>.
25. O'Connell LA, Hofmann HA: **The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis.** *J Comp Neurol* 2011, **519**:3599–3639, <https://doi.org/10.1002/cne.22735>.
26. O'Connell LA, Hofmann HA: **Evolution of a vertebrate social decision-making network.** *Science* 2012, **336**:1154–1157, <https://doi.org/10.1126/science.1218889>.
27. Odling-Smee L, Braithwaite V: **The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback.** *Anim Behav* 2003, **65**:701–707, <https://doi.org/10.1006/anbe.2003.2082>.
28. Okhovat M, Berrio A, Wallace G, Ophir AG, Phelps SM: **Sexual fidelity trade-offs promote regulatory variation in the prairie vole brain.** *Science* 2015, **350**:1371–1374.
29. Page RL, Ryan MJ: **Flexibility in assessment of prey-cues: frog-eating bats and frog calls.** *Proc R Soc B* 2005, **272**:841–847, <https://doi.org/10.1098/rspb.2004.2998>.
30. Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, de Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, Fewell J, McDonald DB: **The dynamics of animal social networks: analytical, conceptual, and theoretical advances.** *Behav Ecol* 2014, **25**:242–255, <https://doi.org/10.1093/beheco/art047>.
31. Poeppel D, Alolfi F: **Against the epistemological primacy of the hardware: the brain from inside out, turned upside down.** *eNeuro* 2020, **7**, <https://doi.org/10.1523/ENEURO.0215-20.2020.0215-20.2020>.
32. Pollen AA, Hofmann HA: **Beyond neuroanatomy: novel approaches to studying brain evolution.** *Brain Behav Evol* 2008, **72**:145–158, <https://doi.org/10.1159/000151474>.
33. Real LA: **Towards a cognitive ecology.** *Trends Ecol Evol* 1993, **8**:413–417, [https://doi.org/10.1016/0169-5347\(93\)90044-P](https://doi.org/10.1016/0169-5347(93)90044-P).
34. Reding LP, Cummings ME: **Rational mate choice decisions vary with female age and multidimensional male signals in swordtails.** *Ethology* 2018, **124**:641–649, <https://doi.org/10.1111/eth.12769>.
35. Rice MA, Hobbs LE, Wallace KJ, Ophir AG: **Cryptic sexual dimorphism in spatial memory and hippocampal oxytocin receptors in prairie voles (Microtus ochrogaster).** *Horm Behav* 2017, **95**:94–102, <https://doi.org/10.1016/j.yhbeh.2017.08.003>.
36. Riede T, Olson CR: **The vocal organ of hummingbirds shows convergence with songbirds.** *Sci Rep* 2020, **10**:2007, <https://doi.org/10.1038/s41598-020-58843-5>.
37. Robinson KJ, Bosch OJ, Levkowitz G, Emanuel Busch K, Jarman AP, Ludwig M: **Social creatives: model animal systems for studying the neuroendocrine mechanisms of social behavior.** *J Neuroendocrinol* 2019, **31**:1–12, <https://doi.org/10.1111/jne.12807>.
38. Rodriguez-Santiago M, Nührenberg P, Derry J, Deussen O, Francisco FA, Garrison LK, Garza SF, Hofmann HA, Jordan A: **Behavioral traits that define social dominance are the same that reduce social influence in a consensus task.** *Proc Natl Acad Sci USA* 2019, **117**:18566–18573, <https://doi.org/10.1073/pnas.2000158117>.
- In this important study, the authors combine machine learning with careful experimentation to show that socially dominant animals are poor demonstrators of a learned task although they are in the center of attention.
39. Schuster S, Wöhl S, Griebisch M, Klostermeier I: **Animal cognition: how archer fish learn to down rapidly moving targets.** *Curr Bio* 2006, **16**:378–383, <https://doi.org/10.1016/j.cub.2005.12.037>.
40. Scribner JL, Vance EA, Protter DSW, Sheeran WM, Saslow E, Cameron RT, Klein EM, Jimenez JC, Kheirbek MA, Donaldson ZR: **A neuronal signature for monogamous reunion.** *Proc Natl Acad Sci USA* 2020, **117**:11076–11084, <https://doi.org/10.1073/pnas.1917287117>.
41. Searcy WA, Nowicki S: **Birdsong learning, avian cognition and the evolution of language.** *Anim Behav* 2019, **151**:217–227, <https://doi.org/10.1016/j.anbehav.2019.01.015>.
42. Shaw RC, Schmelz M: **Cognitive test batteries in animal cognition research: evaluating the past, present and future of comparative psychometrics.** *Anim Cognit* 2017, **20**:1003–1018, <https://doi.org/10.1007/s10071-017-1135-1>.
43. Shettleworth SJ: **Animal cognition and animal behaviour.** *Anim Behav* 2001, **61**:277–286, <https://doi.org/10.1006/anbe.2000.1606>.
44. Shamay-Tsoory S, Abu-Akel A: **The social salience hypothesis of oxytocin.** *Biol Psychiatr* 2015, **79**:194–202, <https://doi.org/10.1016/j.biopsych.2015.07.020>.
45. Snyder-Mackler N, Sanz J, Kohn JN, Voyles TN, Pique-Regi R, Wilson ME, Barreiro LB, Tung J: **Social status alters chromatin accessibility and the gene regulatory response to glucocorticoid stimulation in rhesus macaques.** *Proc Natl Acad Sci USA* 2019, <https://doi.org/10.1073/pnas.1811758115>.
- This study exemplifies the integration of modern technology with natural history by examining the genomic mechanisms by which social rank affects behavior and health in a primate species.
46. Soares MC: **The neurobiology of mutualistic behavior: the cleaner fish swims into the spotlight.** *Front Behav Neurosci* 2017, **11**:191, <https://doi.org/10.3389/fnbeh.2017.00191>.
47. Sonnenberg BR, Branch CL, Pitera AM, Bridge E, Pravosudov VV: **Natural selection and spatial cognition in wild food-caching mountain chickadees.** *Curr Bio* 2019, **29**:670–676, <https://doi.org/10.1016/j.cub.2019.01.006>.

This exemplary study employs spatial cognitive tasks to link cognitive performance with age and survival in a natural population of food-caching chickadees.

48. Spanjer Wright G, Wilkinson GS, Moss CF: **Social learning of a novel foraging task by big brown bats, *Eptesicus fuscus*.** *Anim Behav* 2011, **82**:1075–1083, <https://doi.org/10.1016/j.anbehav.2011.07.044>.
49. Taborsky B, Oliveira RF: **Social competence: an evolutionary approach.** *Trends Ecol Evol* 2012, **27**:679–688, <https://doi.org/10.1016/j.tree.2012.09.003>.
50. Taborsky M, Hofmann HA, Beery AK, Blumstein DT, Hayes LD, Lacey EA, Martins EP, Phelps SM, Solomon NG, Rubenstein DR: **Taxon matters: promoting integrative studies of social behavior: NESCent working group on integrative models of vertebrate sociality: evolution, mechanisms, and emergent properties.** *Trends Neurosci* 2015, **38**:189–191, <https://doi.org/10.1016/j.tins.2015.01.004>.
51. Tinbergen: **On aims and methods of ethology.** *J Anim Psychol* 1963, **20**:410–433, <https://doi.org/10.1111/j.1439-0310.1963.tb01161.x>.
52. Toth AL, Robinson GE: **Evo-devo and the evolution of social behavior.** *Trends Genet* 2007, **23**:334–341, <https://doi.org/10.1016/j.tig.2007.05.001>.
53. Traniello IM, Chen Z, Bagchi VA, Robinson GE: **Valence of social information is encoded in different subpopulations of the mushroom body Kenyon cells in the honeybee brain.** *Proc R Soc B* 2019, **286**:20190901, <https://doi.org/10.1098/rspb.2019.0901>.
54. Van Horik JO, Langley EJG, Whiteside MA, Larker PR, Beardsworth CE, Madden JR: **Group social rank is associated with performance on a spatial learning task.** *R Soc Open Sci* 2018, **285**:20180150, <https://doi.org/10.1098/rsos.171475>.
The authors demonstrate in male pheasants how cognitive performance in a learning task is related to an individual's social rank within a group.
55. Vaughan DB, Grutter AS, Costello MJ, Hutson KS: **Cleaner fishes and shrimp diversity and a re-evaluation of cleaning symbioses.** *Fish Fish* 2017, **18**:698–716, <https://doi.org/10.1111/faf.12198>.
56. Watson KK, Platt ML: **Neuroethology of reward and decision making.** *Philos Trans R Soc B Biol Sci* 2008, **363**:3825–3835, <https://doi.org/10.1098/rstb.2008.0159>.
57. Webber QMR, Vander Wal E: **Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach.** *Anim Behav* 2019, **149**:77–87, <https://doi.org/10.1016/j.anbehav.2019.01.010>.
58. Weitekamp CA, Hofmann HA: **Brain systems underlying social behavior. Evolution of Nervous Systems.** *Elsevier* 2016, <https://doi.org/10.1016/B978-0-12-804042-3.00025-7>. Second Edition.
59. Weitekamp CA, Hofmann HA: **Neuromolecular correlates of cooperation and conflict during territory defense in a cichlid fish.** *Horm Behav* 2017, **89**:145–156, <https://doi.org/10.1016/j.yhbeh.2017.01.001>.
60. Wellman HM, Gelman SA: **Cognitive development: foundational theories of core domains.** *Annu Rev Psychol* 1992, **43**:337–375, <https://doi.org/10.1146/annurev.ps.43.020192.002005>.
61. Williamson CM, Lee W, Curley JP: **Temporal dynamics of social hierarchy formation and maintenance in male mice.** *Anim Behav* 2016, **115**:259–272, <https://doi.org/10.1016/j.anbehav.2016.03.004>.
62. Wilson ME: *An introduction to the female macaque model of social subordination stress. Social Inequalities in Health in Nonhuman Primates.* Springer; 2016.
63. Young RL, Ferkin MH, Ockendon-Powell NF, Orr VN, Phelps SM, A Pogány, Richards-Zawacki CL, Summers K, Székely T, Trainor BC, Urrutia AO, Zachar G, O'Connell LA, Hofmann HA: **Conserved transcriptomic profiles underpin monogamy across vertebrates.** *Proc Natl Acad Sci USA* 2019, **116**:10186–10188, <https://doi.org/10.1073/pnas.1813775116>.
In this transformative study, the authors used comparative transcriptomics to show that similar brain gene expression profiles are associated with independent transitions to monogamy in five pairs of vertebrate species. By using phylogenetic comparative methods, they also demonstrate that a considerable fraction of the species variation in neural gene expression is explained by variation in the social system.
64. Zayed A, Robinson GE: **Understanding the relationship between brain gene expression and social behavior: lessons from the honey bee.** *Annu Rev Genet* 2012, **46**:591–615, <https://doi.org/10.1146/annurev-genet-110711-155517>.
65. Zilkha N, Sofer Y, Beny Y, Kimchi T: **From classic ethology to modern neuroethology: overcoming the three biases in social behavior research.** *Curr Opin Neurobiol* 2016, **38**:96–108, <https://doi.org/10.1016/j.conb.2016.04.014>.
66. Zupanc GK: *Behavioral neurobiology: an integrative approach.* Oxford University Press; 2010.