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

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Highlights

- Social neuroscientists and cognitive ecologists study animal decision-making
- We retrace the development and current state of integration of the two fields
- We propose several approaches toward further integration
- We highlight exemplary model systems that are flourishing at this junction

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.

Social neuroscience has made great strides in understanding the key pathways and neuromodulators of important social behavioral processes like affiliation, reproduction, and aggression. Conversely, 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 (Buzsáki 2020, Poeppel & Alolfi 2020, Hofmann et al. 2014). 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 integrated both fields. We then outline several steps to further integrate social neuroscience and cognitive ecology towards a more 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 (Zupanc 2010; Zilkha et al. 2016), which historically has included the study of social behavior as well as investigations of reward, motivation, and decision-making (e.g. Watson & Platt 2008). From this foundation, social neuroscience emerged as an independent field of research in the early 19990's (Cacioppo and Berntson 1992) with the aim of understanding the neural, hormonal, cellular, and genetic underpinnings of social behavior (Cacioppo & Decety 2011). 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 Krakauer et al. 2017) and from the organism-level outlook characteristic of animal behavior research and psychology (Insel 2010). Importantly, almost from its inception social neuroscience has also embraced a diversity of model systems and attempted to infer evolutionary insights.

Current research in social neuroscience primarily stem from two areas of research (Insel 2010): 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 Taborsky & Oliveira 2012, Weitekamp & Hofmann 2016). 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) (Traniello et al. 2019) 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) (Goodson 2005, O'Connell & Hofmann 2011, 2012, Kanwisher 2006, Toth & Robinson 2007).

A decade ago, Adolphs (2010) 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 (2010) 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 (O'Connell & Hofmann 2011, Cacioppo & Decety 2011). 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 (Tinbergen 1963). The distinction of cognitive ecology from neuroethology and behavioral ecology was articulated by Real (1993), who put forward a "cognitive approach" towards 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 (Real, 1993). Shettleworth later defined cognition as "*all [the] ways in which animals take in information through the senses, process, retain and decide to act on it.*" (Shettleworth 2001). 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 (Dukas 1998). Cognitive ecology has oscillated between a more ecological and a more psychological perspective (Hulse 1993, Kamil 1998*)*. The ecological approach has proven invaluable in structuring testable and discrete hypotheses for cognitive processes (e.g. bird food caching (Sonnenberg et al. 2019), fish transitivity in mate choice decisions (Reding & Cummings 2018), bat prey cue assessment (Page & Ryan 2005)). In contrast, a psychological approach has increased our understanding of the cognitive processes that human and non-human animals share, primarily through assessment of primate cognition (Wellman & Gelman 1992).

Different cognitive domains are those that require different types of cognitive performance (Deary et al. 2010). 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. Cognitive test batteries are studies that employ multiple cognitive assays to compare performance across domains, and there has been a recent call to improve the universality of cognitive test batteries (as well as expand this type of testing to additional animal models) (Shaw & Schmelz 2017).

Model systems in cognitive ecology have been selected based on their unique behavioral repertoire (e.g. cleaner mutualism in fish and shrimp (Soares et al., 2017; Vaughan et al. 2017), bats navigating via echolocation (Spanjer Wright et al. 2011), vocal learning in songbirds (Searcy & Nowicki 2019). 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 (Pollen & Hofmann 2008). Designing an experimental paradigm that is ‘fair’, i.e., not biased towards 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 non-obvious 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 (Odling-Smee & Braithwaite 2003). 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 (Shettleworth 2001). 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 (Weitekamp & Hofmann 2017). Integrating proximate mechanisms into the research agenda of cognitive ecology has long been seen as critical (Shettleworth 2001), 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 1,068 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 take off 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 (2,564 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.

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, 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 often rely on cognitive processes. When possible, assessing the same individuals in social behavior assays *and* cognitive tasks can facilitate a better understanding of which social factors 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 (Donaldson & Young 2008), and spatial memory (Rice et al. 2017). 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. Okhovat et al. 2015). The evolution of our understanding of the function of the nonapeptides (Donaldson and Young 2008; Goodson 2005, Robinson et al. 2019) 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) (Shamay-Tsoory & Abu-Akel 2016, Beery & Kaufer 2015). It is important that mechanisms are not pigeon-holed into investigation only within traditional contexts and traditional model organisms. It is also important to record non-cognitive behavioral traits during assays, as they may be influencing the perceived cognitive performance (Van Horik et al. 2018).

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/non-parenting, 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* is a fish species that has emerged as a model system in social neuroscience (Maruska & Fernald 2018). Studies have disentangled the relevant modalities and social information males 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 (Rodriguez-Santiago et al. 2019).

Social neuroscience has extensively studied developmental aspects of social behavior and trajectories, a perspective cognitive ecologists can benefit from. 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 (Riede & Olson 2020).

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 non-traditional model systems can be particularly fruitful. Often, model systems are chosen due to a complex behavior or extreme social phenotype that they exhibit such as archerfish or naked mole rats. 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 (Menzel 2012; Zayed &

Robinson 2012). 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 (Wilson 2016, Snyder-Mackler et al. 2019, Jablonski 2020). Importantly, research on primates has been instrumental in building our understanding of higher-order cognitive processes, such as 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 (Kabelik & Hofmann 2018), longstanding biomedical model systems (e.g., the nematode worm *Caenorhabditis elegans*, the fruitfly *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. Taborsky et al. 2015; Williamson et al. 2016).

Importantly, new technologies such as automated tracking and machine learning have facilitated a renaissance of detailed behavioral observations, often in naturalistic contexts (Dell et al. 2014). Scientists are also swiftly advancing neural recordings of freely-interacting animals (e.g. Scribner et al. 2020) 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 ecologically-relevant social behavior. The observation of complex group social dynamics yields equally complex datasets and require sophisticated statistical approaches (Williamson et al. 2016, Pinter-Wollman et al. 2014). These statistical approaches have undergone rapid development and have vastly improved our ability to interpret group social dynamics (Webber & Vander Wal 2019). The rapid pace at which these technological and statistical advances occur provides exciting opportunities for the integration of social neuroscience and cognitive ecology (Amodio & Keysers 2018).

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 homology (Goodson, 2005; O'Connell & Hofmann 2011, 2012) is critical in determining the roles of key mechanisms and circuits. From the cognitive ecology perspective, understanding the fitness consequences of a 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 systems for understanding life history tradeoffs in response to predation, and since have emerged as a model 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 (Cummings 2018).

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 Young et al. 2019). 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 (Robinson et al. 2019).

Conclusion

To understand how human and non-human 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 (Tinbergen 1963) have facilitated enormous conceptual progress in our understanding of animal behavior (Bateson & Laland 2013). But given the recent advances in neuroscience and behavioral analyses (Boender & Young 2020), the ability to integrate these topics within single studies has become much more accessible (Hofmann et al. 2014). 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.

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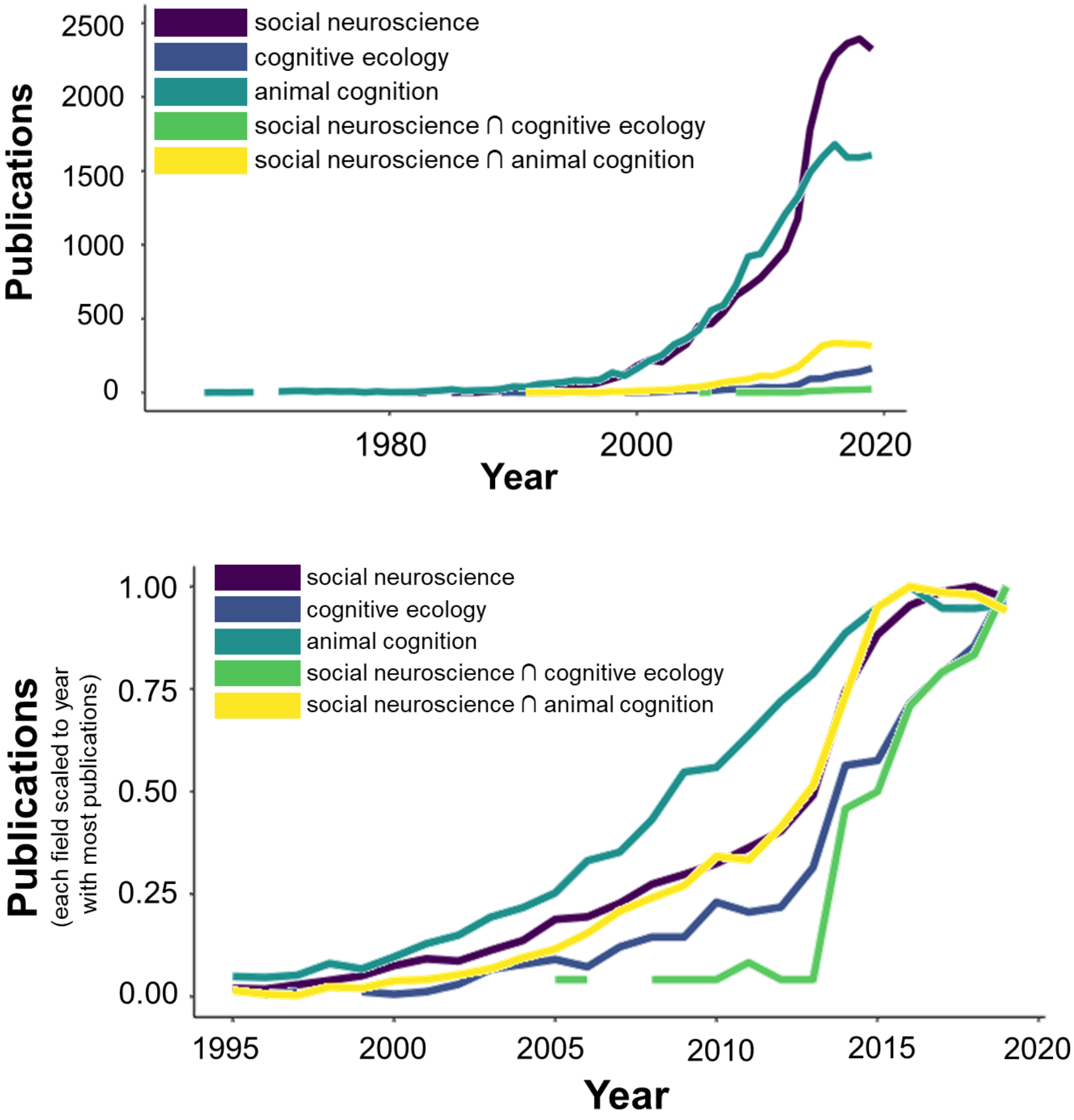
Fig 1. Quantitative analysis of the publication effort in Social Neuroscience, Animal Cognition, and Cognitive Ecology. Three searches were conducted in PubMed (selecting "all fields" and restricting the year to before and including 2019): "(social neuroscience) AND (animal)", "(cognitive ecology) AND (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.



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