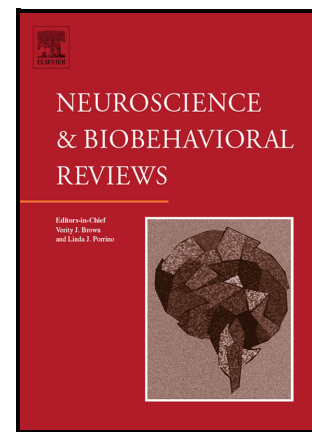# Journal Pre-proof

Animal Play and Evolution: Seven Timely Research Questions about Enigmatic Phenomena

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Animal Play and Evolution: Seven Timely Research Questions about Enigmatic Phenomena

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Abstract

The nature of play in animals has been long debated, but progress is being made in characterizing play and its variants, documenting its distribution across vertebrate and invertebrate taxa, describing its mechanisms and development, and proposing testable theories about its origins, evolution, and adaptive functions. To achieve a deeper understanding of the functions and evolution of play, integrative and conceptual advances are needed in neuroscience, computer modeling, phylogenetics, experimental techniques, behavior development, and inter- and intra-specific variation. The special issue contains papers documenting many of these advances. Here, we describe seven timely areas where further research is needed to understand this still enigmatic class of phenomena more fully. Growing empirical and theoretical evidence reveals that play has been crucial in the evolution of behavior and psychology but has been underestimated, if not ignored, in both empirical and theoretical areas of evolutionary biology and neuroscience. Play research has important ramifications for understanding the evolution of cognition, emotion, and culture, and research on animals can be both informative and transformative.

Highlights

- Play is important for understanding biological and cultural evolution but has largely been ignored by evolutionary and neuroscience researchers.

- We identify critical issues that can advance our understanding of the evolutionary processes and physiological bases underlying play phenomena

- We describe seven timely areas where further research is needed to fully understand this enigmatic class of phenomena.

- To achieve a deeper evolutionary understanding of play requires integrative and conceptual advances in neuroscience, computer modeling, phylogenetics, and experimental techniques.

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- The special issue documents many of these advances.

Introduction

Phenomena classified as *play* are likely important for understanding biological and cultural evolution but have long been ignored by many evolutionary biology and neuroscience researchers and scholars. We think serious attention should be directed toward integrating play phenomena into modern evolutionary thinking, including their applications to critical aspects of human life and societal functioning. We advance here some critical issues requiring additional attention and outline approaches that can advance our understanding of the role of play in evolutionary processes and their physiological and neuroscience bases. Although play in humans has been classified in many ways (e.g., Henricks, 2015; Johnson et al., 2015; Smith and Roopnarine, 2019), in nonhuman animals, the three categories typically employed are solitary/rotational play, object play, and, most studied, social play. The latter often involves wrestling and chasing but can also involve objects (e.g., tug-of-war) and socially coordinated locomotion. Other types of play have also been studied occasionally—including pretense, parallel, construction, teasing, courtship, socio-dramatic, creativity, flow, imagination, and others—but these three categories, especially social play, have received the most research attention in nonhuman animals, as they are directly focused on observable behavior.

We begin by placing play research in historical context. Play behavior in animals, especially in domesticated animals and primates (including humans), has fascinated people for a long time (Fagen, 1981; Burghardt, 2005; *Current Biology* vol 25(1), 2015). In the 19th century, several theories and approaches were advanced in the wake of Darwin's writings. Reviewed in some detail elsewhere (e.g., Burghardt, 2005; Henricks, 2015), these included the surplus energy,

recapitulation, instinct practice, exercise, semblance (cognitive), recreation, diversion, and recuperation (stress reduction) views. Initially severely criticized, all these are found in current research if unacknowledged. Among research scientists, however, play has been of sporadic interest to biologists and psychologists for decades, although the role of play in early learning and education is receiving much recent interest (Pellegrini, 2009, 2011; Smith, 2010; Johnson et al., 2015). Play has been viewed as prominent in only a few groups of mammals (e.g., primates, canids, cats, otters, cetaceans) and birds (e.g., parrots, corvids) (Bekoff and Byers, 1981; Fagen, 1981), lacking strong empirical evidence of adaptive and functional significance, and therefore downplayed as a major area of scientific interest. Few evolutionary biology or neuroscience textbooks include play in their indexes or as phenomena worth discussing. Darwin delighted in observing animal play as a measure of happiness, but play did not figure in his evolutionary thinking. Although Lorenz (1956) discussed play in relation to his ethological formulations, it was a side interest. Tinbergen (1963), in his seminal paper on the aims and methods of ethology, dismissed play as too 'subjective' to be a scientific topic. In comparative psychology, the leading proponent of the field in the post-war period, Frank Beach, wrote a critique (Beach 1945) that would, and apparently did, dampen comparative interest in the topic. For example, he attacked reports of play in fishes with alternative explanations for which he had no supporting evidence.

Research on human play has met less resistance. Educators often discuss play as a vital component in the early grades and kindergarten, and this goes back to the first kindergartens in the 19th century established by Frederick Froebel in Germany, who developed a standard set of materials ('gifts') by which children could learn about the activities promoted by everyday items via play (Kuschner, 2015). About 100 years later, developmental psychologists and educators, influenced by Piaget (1962) and Vygotsky (1967), more formally incorporated play as an

indicator of cognitive development, but their theories were largely untouched by evolutionary and ethological ideas that, admittedly, had little conceptually useful to say about play until later. Although play was frequently mentioned in monographs and descriptions of behavior in non-human mammals (e.g., Ewer, 1968), its theoretical import also received little critical attention. The comparative psychologist Harvey Carr (1902) did an admirable evolutionary and functional treatment of play, but it was rarely cited, although his ideas were insightful and surprisingly modern (Burghardt, 2005).

Beginning in the 1970s, things began to change, coincident with the rise of cognitive, developmental, ethological, and ecological studies and the institutionalizing of research in zoos (see the pioneering volume published by the US National Academy of Sciences and edited by George Rabb [Anon, 1975]). Animal play, especially in monkeys, apes, canids, rodents, and ungulates, became the focus of research rather than a topic of peripheral or passing mention. In 1981, Fagen published the first comprehensive treatise devoted to play in almost a century (Groos, 1898, original German edition in 1895). Since then, there have been many hundreds of research articles and chapters devoted to play and many edited and single-authored books, including handbooks and encyclopedias, devoted to play (e.g., Smith, 1984, 2010; Sutton-Smith, 1997; Bekoff and Byers 1998; Power, 2000; Burghardt, 2005; Pellegrini and Smith, 2005; Brown and Vaughn, 2009; Pellis and Pellis, 2009; Pellegrini, 2009, 2011; Bateson and Martin, 2013; Henricks, 2015; Johnson et al., 2015; Smith and Roopnarine 2019). New journals devoted to play have been established (*American Journal of Play, International Journal of Play*), and an updated Oxford Bibliography of important sources has been published (Burghardt, 2018a). While many of these sources include both human and nonhuman play, treatments are generally more parallel than integrated.

Much research has accrued in recent decades on all aspects of animal play, including in humans (especially infants and children). They embrace topics such as detailed comparative description, characterization of the neural mechanisms involved in social play, development, ecological and social contexts for play, reproductive adaptiveness and evolution, mathematical models and computer simulations, and proximate functions in learning, education, therapy, and so on. Although Tinbergen criticized play as not a worthy topic in his influential paper on the aims of ethological research, the full gamut of research aims advocated by Tinbergen (1963) has, perhaps ironically, since been applied to play, and Tinbergen's reluctance to include the organism's experience (perceptions, emotions, feelings, motivations) into play research and animal behavior studies generally is no longer tenable (e.g., Burghardt, 1997; Himmler et al., 2016; Panksepp, 1998; de Waal, 2016, 2019). Leca (2023, this special issue) provides an evaluation and reworking of the aims of ethological research and their integration that can be fruitfully applied to the study of play.

Although the extensive work on play over the last few decades has led to increased understanding of its nature and evolutionary significance, much work remains. In the remainder of this paper, we outline what we see as the frontiers of research on play. We consider perspectives from animal behavior, evolutionary theory, neuroscience, genetics, robotics, and child development and lay out seven important research question for understanding what play is, how it evolved, its underlying mechanisms, and why it is important. To help readers gain a better understanding of these large research questions, we provide a series of more tractable questions for each showing where progress has been made and where more research is needed. The extensive research available on play, including that reported in this special issue on *The neurobiology of play: Comparative and evolutionary perspectives* (Schank et al., 2023), will be

reviewed here only as it relates to the areas we identify as ripe for current study of diverse play behavior as important biological phenomena of evolutionary significance. For a more thorough look at the biological research on play to date, in-addition to the papers in this issue, we direct the reader to a number of recent reviews (Pellis et al., 2019; Vanderschuren et al., 2016; Palagi et al., 2016; Palagi, 2018), especially the six chapters in Part I of Smith and Roopnarine (2019), and recent special issues of *The International Journal of Play*. We hope that readers will seriously consider play, in all its protean aspects, as central to many areas of biological research, from empirical science to philosophical reflection. We have organized our take on these broad questiond into seven major topics, but all should be viewed as mutually linked.

1. The Emergence of Play

- What are the conditions that have promoted the origin and emergence of play?

- How does the diversity of types of play vary across lineages?

Most scholars of play in the 20th century assumed that play was restricted to large-brained or highly social mammals such as primates, carnivores, and perhaps some birds, as illustrated by the major reviews of animal play in the 1980s (Bekoff and Byers, 1981; Fagen, 1981). Play in 'lower' vertebrates and invertebrates was long considered absent, and any claimed evidence was considered anecdotal, anthropomorphic, or misinterpreted. For example, putative play, as in birds, was dismissed as just maturationally incomplete instinctive behavior (Fagen, 1981; Williams, 1992). A major stumbling block was the lack of adequate criteria for play that could effectively help us identify play in species or contexts in which we did not already assume play was occurring.

The situation has changed in recent years for two reasons. First, an improved way of identifying play using five criteria advanced by Burghardt (Burghardt, 2005, 2011; Pellis and

Burghardt, 2017; Palagi and Pellis, 2023) has become widely adopted. In brief, a behavior is play if these five criteria are satisfied: a) the behavior appears incompletely functional in the context expressed; (b) it can be characterized as being voluntary, rewarding, pleasurable, or done for its own sake; (c) it is to some extent modified structurally or ontogenetically when compared to when it is performed in its normal, functional context; (d) it is performed repeatedly, but not necessarily in an invariant form; and (e) it is initiated in healthy animals free from more urgent motivational demands (e.g., hunger, fear) or conditions (e.g., inclement weather, illness, social upheaval), although lack of stimulation (boredom) or motivational conflicts are modest stressors that may facilitate play. All five criteria must be satisfied in at least one respect for a confident attribution of play. Second, better technology and increased access to it have led to the accumulation of observations, backed up by film and video recording, of behavior that would clearly be labeled playful in other species but hitherto not documented. Amateur videos on YouTube and other sites have facilitated these observations, as used extensively in the paper on interspecific play by Brooks and Burghardt (2023, this special issue).

Through careful application of the five criteria described above, the breadth of play has expanded to include lizards, turtles, ray-finned and cartilaginous fishes, cephalopods, crustaceans, insects, and other groups (e.g., Burghardt 2005, 2014, Burghardt et al., 2014; Dapporto et al., 2006; Dinets, 2015, 2023, this special issue; Galpayage Dona et al., 2022). The widespread phylogenetic distribution of play strongly suggests that play is a heterogeneous phenomenon that has repeatedly evolved in the animal kingdom. Furthermore, in such groups, as well as in mammals and birds, the types of play (locomotor/rotational, object/predatory, and social) are unevenly distributed, and subdivisions abound. Although effective working criteria for identifying play are now available, lack of play in a species may be harder to establish,

especially in species that are little studied, that have insufficient observations to document the absence of play, or where play is simply assumed to be impossible. While the lack of evidence cannot be assumed to be evidence of absence, within taxa comparisons observed under comparable conditions, support the view that play is not universally present and, even when present, varies in its complexity and in the time devoted to playing (Lewis, 2000; Pellis and Pellis, 2009).

Advances in identifying play raise the critical issue of why play has emerged in some lineages and taxa within them and (apparently) not others or to different extents and complexities. What are the life-cycle, ecological, developmental, social, anatomical, neural, and physiological factors that underlie the emergence of play behavior or its precursors? Although a number of putative factors have been identified, the relative importance of these factors or how they can be evaluated and tested is greatly understudied. While a number of factors such as diet, illness, stress, behavioral flexibility, and learning to adapt to changing conditions have been advanced as influencing play behavior, whether these factors also figured into the evolution of play from a non-playful state is unknown, and scenarios are speculative even when plausible given current knowledge.

Burghardt (2005) proposed a hierarchical organization of three kinds of processes underlying the evolution of play. *Primary process play* includes those playful activities that, without necessarily producing any specific fitness benefits, can provide sufficient behavioral variability on which natural selection can work. These include threshold lowering, intention movements, low-level motivational conflicts, excess metabolic energy, and coping responses to both novel stimuli or the lack of stimulation (boredom). In *secondary process play*, play facilitates and optimizes the normal ontogeny of physiological, behavioral, and psychological

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activities and helps and maintains them. Play can be further transformed into *tertiary process play* by providing players with the ability to develop broader, richer, and more flexible skill sets that enable them to go beyond what is necessary for basic survival, provide capacities to cope with unexpected situations and changing physical and social settings, including innovative and creative problem solving (Spinka et al., 2001; Bateson and Martin, 2013; Burghardt, 2015). Therefore, this last step in these hierarchical transformations enables more sophisticated forms of play and creates scaffolds for acquiring new social competencies (Burghardt, 2005; Bateson, 1976; Palagi, 2018). Play fighting between peers is important in facilitating the development of social skills in juveniles that promote their integration into the social world. For example, in wild spotted hyenas (*Crocuta crocuta*), play fighting is a tool to enter the clan and help adults familiarize themselves with immature individuals with whom they will need to interact in the future (Drea et al., 1996; Nolfo et al., 2021). Play fighting experience in juvenile rats and hamsters leads to the development of adults who are better able to read and respond to social cues in both playful and other social contexts (Van den Berg et al., 1999; Burleson et al., 2016; Schneider et al., 2016; Stark and Pellis, 2020, 2021; Cooper et al., 2023, this special issue; Pellis et al., 2023, this special issue). The benefits gained from social play by immature animals may extend to broader social and non-social behavior in other rodents (Marks et al., 2017) and some primates as well (Heintz et al., 2017). Question 3 expands on the functions of play.

Advancing research on play may depend on having appropriate and sufficient representative taxa in a taxonomic group. The early studies of Pellis and Iwaniuk (1999a,b, 2000a,b) on adult play in primates and juvenile social play in rodents provided initial comparative insights more than 20 years ago. Indeed, the above-described three-stage evolutionary model developed by Burghardt (2005) has been very useful in accounting for the

variation present in the occurrence and complexity of play fighting in murid rodents (Pellis and Pellis, 2009). While recent developments have led to the pattern of phylogenetic change and some of the likely processes involved to be further elaborated in primates (e.g., O'Meara et al. 2015, Pellis, Pellis and Ham, 2023; Palagi, 2023), comparable studies in other taxonomic groups are still deficient. Only by identifying transitions from non-play to play and transitions in the complexity of play across diverse taxa will we make progress in answering this initial topic. Another key need is to gather data on the absence of play and the distribution of types of play in comparative analyses. Formal modeling has shown that play can arise without adaptive benefits in some situations (Auerbach et al., 2015), and that different development trajectories can underlie simple versus more complex play (Smaldino, et al., 2019). Studies on invertebrates or ectothermic vertebrates where play is rare in most taxa might provide essential insights.

2. Neural mechanisms

- Is there a singular neural mechanism involved in all cases of play or play type?

- Have different mechanisms converged to produce behavior patterns with similar properties?

In one sense, the first question has already been answered in the negative, for we already know that play is a heterogeneous category that seems to have evolved independently several times and that, moreover, the nervous systems of vertebrates and invertebrates are organized differently. We also know that some animal groups show all three major categories of play while others have only one or two of the three major play types (Burghardt, 2005; Graham and Burghardt, 2010). The developmental trajectories of the three main play types, when they occur in the same species, also may be rather different (Barrett and Bateson, 1978; Gomendio, 1988, Caro, 1995). Nonetheless, as most play examples and studies emphasize social play, the study of the circuitry of social play in vertebrates, especially among mammals, is of crucial importance.

Are there commonalities across all species (e.g., rodents, canids, cetaceans, bears, and primates) in rough-and-tumble play, or play fighting, and these commonalities may extend to include birds and perhaps other vertebrates?

The most intensively studied species with regard to the neural underpinnings of *social play* is the laboratory rat (Achterberg and Vanderschuren, 2023, this special issue; Cooper et al., 2023, this special issue; Pellis et al., 2023, this special issue; see Figure 1 for a sequence of play fighting in juvenile deer mice, a closely related species that exhibits similar play behavior). We emphasize *social* because it may not be the case that the same neural circuits are involved in other forms of play (e.g., locomotor, object). Nevertheless, it may be possible to draw telling connections across species. Some of the brain regions involved in rat social play (Siviy, 2016; Vanderschuren et al., 2016) are larger in primate species that exhibit more social play (Graham, 2011). For example, the striatum is involved in the play of rats (Pellis et al., 1993; Van Kerkhof et al., 2013), and this structure is volumetrically larger in species of primates that engage in more social play (Graham, 2011).

Figure 1 here

In contrast, no significant correlations have been found between increased amounts of non-social play and any neural system (Lewis, 2000; Lewis and Barton, 2004, 2006; Graham, 2011). This does not mean that the brain regions implicated in the execution of social play, such as the cortex, amygdala, hypothalamus, and striatum, are not involved in non-social play; it may simply be that social play is more cognitively and motorically demanding, and so requires more neural processing capacity (Lewis and Barton, 2006). Thus, with the currently available evidence, it cannot be determined whether there is a unitary 'play circuit', as proposed by Panksepp (1998), or if, as seems more likely to us, there exist distinct but overlapping circuits for each type of

play. Indeed, even after many studies over many decades, the 'social play circuit' characterized

for rats (e.g., the extensive neuronal activation analysis by Van Kerkhof et al., 2014) still needs

closer scrutiny, including with the increasingly sophisticated methods of rapidly advancing

neuroscience.

Various systems, from the hindbrain to the forebrain, are involved in the production and

regulation of social play in rats (Figure 2; Siviy, 2016; Vanderschuren et al., 2016; VanRyzin et

al., 2020; Achterberg and Vanderschuren, 2023, this special issue). An important division that

has been recently revealed is that there is a sub-circuit that regulates the motivation to play—

quite simply, how desirous an animal is to engage in play—and another that regulates the

pleasure gained from performing playful actions (Vanderschuren et al., 2016). That is, using

methods that directly tax the pleasurable versus the incentive motivational properties of play

(i.e., place conditioning and operant conditioning), it has been shown that the motivational, but

not the pleasurable aspects of social play behavior in rats depend on dopamine neurotransmission

(Achterberg et al., 2016; Vanderschuren et al., 2016). Conversely, stimulation of mu-opioid

receptors within the nucleus accumbens has been implicated in the pleasure that rats derive from

social play behavior (Trezza et al., 2011a). Opioid neurotransmission is also involved in the

motivation for social play behavior (Achterberg et al., 2019), but the exact neural locus remains

to be elucidated (Achterberg and Vanderschuren, 2023, this special issue).

Figure 2 here

While manipulating these neural circuits can predictably alter the frequency and content of

social play in rats, these same circuits are also involved in motivating and rewarding other

behaviors (e.g., eating, sex, and taking psychoactive drugs). Therefore, it cannot be claimed that

the neural circuit characterized for play in rats is a 'play circuit,' but rather, it may be a general

motivational/reward circuit (Berridge and Kringelbach, 2013) that for species that play is co-opted to regulate playful activity in addition to more primary pleasurable behaviors. There are as yet no studies that have identified specific neural networks solely utilized for play, much less circuits that are unique for any particular kind of play, although the neuronal activation study by Van Kerkhof et al. (2014) may be a useful first step.

Currently, the most parsimonious hypothesis proposed on the neural circuitry of play is that the different lineages that have evolved play (Burghardt, 2005) have done so by tapping into the same motivational/reward circuitry that is present for sustaining other, more immediately necessary activities (e.g., feeding). Dedicated circuits that exploit this general circuit for play rather than for feeding could then evolve later. The application of overlapping appetitive behavior circuits described by Craig (1918) a century ago is now receiving increased attention in neuroscience and may be particularly applicable to play. Given that some species lineages have evolved one type of play to the exclusion of another (e.g., social play but not object play) and for those that engage in multiple forms of play, some are more dominant than others (e.g., locomotor is more frequent than social), it is likely that the general system has been tapped into separately by neural circuits that are specifically engaged when playing in a particular mode. However, some species seem to be able to fluidly combine different types of play (e.g., Shimada, 2012; Burghardt et al., 2016; Palagi, 2018; Palagi and Bergman, 2021), suggesting that the specific neural circuits have become connected in a network. Indeed, the evolution of play proceeding from single forms to multiple and then multiple forms that can merge together may require a series of changes in the neural systems involved (Pellis et al., 2019).

Given the progress made in identifying the neural circuits that are important for social play in rats (Achterberg and Vanderschuren, 2023, this special issue; VanRyzin et al., 2020), it should

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be possible to determine whether these same circuits are also the ones that regulate locomotor play and object play, or are different circuits involved, even if some overlap is present? Addressing these questions requires a combination of behavioral methods and sophisticated neuroscience approaches. In the last two decades, techniques have been developed by which precisely identified populations of neurons (i.e., those with a certain cytoarchitecture, projection target, or those activated after certain behaviors or events occur) can be labeled, stimulated, or inactivated, such as Daun02 inactivation, optogenetics, and chemogenetics (Cruz et al., 2013; Deisseroth, 2015; Roth, 2016). Combination of these techniques with methods that can directly study the pleasurable aspects of play (Trezza et al., 2011b), its incentive motivational properties (Achterberg et al., 2016), or its behavioral microstructure (Pellis et al., 2022) will help dissect the neural pathways through which social play behavior in rats comes about. Moreover, we need to study in more detail which sensory information (olfactory, visual, tactile or auditory) rats require to interpret the behavior of conspecifics as 'playful' (Thor and Holloway, 1982; Siviy and Panksepp, 1987; Pellis et al., 1996; Burke et al., 2018; Whishaw et al., 2021); most likely this will comprise a combination of signals of different sensory modalities. A next step should then be to assess whether these same neural mechanisms underlie social play behavior in other species and other types of playful behavior as well.

3. **Adaptive benefits of play**

- What is adaptive about play?

- Under what conditions, if any, does play benefit juvenile and/or adult behavior?

- What are the factors underlying the loss of play in some species within a lineage?

- What insights do such findings provide?

While many potential functions of play have been suggested over the decades, the old idea that play is for the practice of instincts (e.g., Groos, 1898) has been supplanted by more broad claims that through play, animals can assess their performance in relation to those of others (Thompson, 1998), prepare themselves for unpredictable events and changing environments (Spinka, et al., 2001), or acquire information about their worlds (Schank, et al., 2023, this special issue). Play might also enhance subtle social, physical, and physiological traits, alleviate stress and boredom, and have many functions or even none at all other than short-term respite and experiencing positive states, allowing for more efficient deployment of non-play behavior in later contexts. Play is clearly multilayered and a rich and deep well to explore.

Consistent with the hypothesis that the origins of play may not depend on fitness benefits to be maintained are findings on individual and breed differences in playfulness. Social play in rats exhibits a high degree of intra-strain individual variation (e.g., Achterberg et al., 2023; Ham and Pellis, 2023; Melotti et al., 214; Lampe et al., 2019.), providing the opportunity for differences in the frequency and preferred styles of expression to evolve across strains (Himmler et al., 2016). However, although such inter-strain variation depends on differences in the underlying neural mechanisms (Siviy, 2020), differences in play can arise from selection of non-play traits (Reinhart et al., 2004), as is also the case for the variation in the play of breeds of dogs (Burghardt et al., 2016; Coppinger et al., 1987). This suggests that there is inherent variation in the degree of playfulness both within and between breeds. Although, some of this variation may arise from environmental and epigenetic influences (e.g., Arnold and Siviy, 2002; Parent and Meaney, 2008), studies of locomotor play in mice shows that some of the variation in play arises from genetic variation (Whitehead et al., 2023; Walker and Byers, 1991). Interestingly, selected lines of mice bred for differences in locomotor activity did not reflect those differences in their

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degree of locomotor play as juveniles, indicating that the traits selected for do not necessarily have a direct relationship with playfulness (Whitehead et al., 2023). A similar conclusion is plausible for differences in the social play of differentially selected lines of rats (Reinhart et al., 2004, 2006). These findings suggest that there is likely considerable intra- and interspecific variation in play that can vary dramatically from population to population and season to season (e.g., Baldwin and Baldwin, 1973; Berger, 1980; Pellis, 1981; Barrett et al., 1992), which is not visible to natural selection (Pellis and Iwaniuk, 2004; Pellis, Pellis and Ham, 2023), as long as any derived functional benefits are maintained by threshold levels of the key experiences (Pellis, Pellis, Ham et al., 2023, this special issue). If conditions lead to those experiences falling below that threshold, then natural selection likely acts to eliminate that type of play (Pellis and Iwaniuk, 1999b). However, the implication is that not all the variation in play present across lineages (Burghardt, 2005) is adaptive, strongly pointing to the importance of studying the origins and history of play in different lineages (see question 3 below).

Because play behaviors, especially in immature animals, may not immediately contribute to the organism's survival in the ethological context expressed (Burghardt, 2005), they can be costly. The costs can simply be opportunity costs involved in reduced time spent in fitness-enhancing behaviors like foraging or real costs such as increased risk of predation or injury. Costly behaviors cannot increase by natural selection unless they also convey benefits in the organism's reproductive lifespan that can offset the costs, which for the play of immature animals are typically viewed as delayed benefits (Fagen, 1981; Baldwin, 1986), although even for immature animals short-term benefits, including pleasurable feelings, may also accrue, along with improved physical and social skills. Smaldino et al. (2019) recently explored this idea with a mathematical model and discussed how multiple factors relating to an organism's life history,

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including the time course of play investment, can contribute to the adaptive nature of different types of play. Uncovering exactly how such cost-benefit tradeoffs unfold in the life courses of different species that play is a major question for play research. But play also has immediate benefits, such as gaining general muscular and perceptual exercise, coordination skills, and emotional well-being, that are often ignored but need to be considered. In a recent paper, Francesconi et al. (2024) examined social behavior based on the proximity to and distance from the health check in a group of young heifers and steers. The authors found that, compared to a control period, social play was inhibited on the day after the check, and it peaked on the following day, thus suggesting that social play can be a strategy animals adopt to cope with stressful situations. Indeed, the immediate benefits of play are mostly expressed in adults (e.g., Pellis, 2002; Palagi, 2011, 2023, this special issue; Nahallage et al., 2016).

Regarding the question of play's adaptive value, formal modeling suggests that simple play may occur and even evolve without any direct benefit being present, either immediate or delayed, as long as simple play behaviors involve minimal costs or risks (Auerbach et al., 2015; Malpress and Špinka, 2023). Additionally, given the multiple transitions from lack of play to play in different taxa and to different degrees of complexity in play once it evolves (Burghardt, 2005; Pellis and Pellis, 2009), the current functions of play should be distinguished from the processes underlying the origins of play (Pellis et al., 2015). Play, as is true of many traits, may have originated as a byproduct of selection on other traits that are linked genetically to those underlying the identifying criteria for play via pleiotropy or coevolution (Gould 1991; Jiang and Zhang, 2023).

It may be instructive to consider another phenomenon, contrafreeloading, first documented in the comparative psychology literature 50 years ago (Jenssen, 1963; Osborne, 1977). It turns

out that contrary to standard behaviorist reinforcement theory, numerous species have been

documented preferring to 'work' for food rather than obtaining it 'free.' This clearly confounded

researchers, and consequently has not been highly visible in traditional learning courses. While

the connection with play was not explicitly made by the early researchers, Smith et al. (2021) did

so in their documentation of contrafreeloading in parrots. Issues of escaping boredom and

unstimulating environments, also associated with play (Burghardt, 1984), can thus be involved

rather than behavior only being shaped by explicit adaptive processes traditionally conceived.

The autoshaping phenomenon (also referred to as sign-tracking), where animals seem to 'teach'

themselves the means to obtain reinforcers in situations similar to classical (Pavlovian)

conditioning, may also be instructive. This was first clearly documented in pigeon key pecking

responses to visual stimuli (Brown and Jenkins, 1968) but has been documented in many species

and contexts. Such phenomena may encourage behavioral variability that can converge on

adaptive consequences.

An important question that then emerges is what, if any, functional benefits can arise from

play. Furthermore, can such benefits be transformed into more complex patterns of play

(Burghardt, 2005; Smaldino et al., 2019)? That is, what aspects of play provide feedback to the

player such that fitness is enhanced and thus further promotes the evolutionary transformation of

those components (including secondary to tertiary play processes; see Schank et al., 2023, this

issue for a theoretical framework and model higher-level play processes could evolve to acquire

information)?

The history of studying the adaptive benefits of play has been a vexed one. Dozens of

putative and intuitively plausible functions have been proposed (Fagen 1981; Baldwin 1986), but

most of these have proven difficult to validate empirically, as shown in a devastating critique of

early claims (Martin and Caro, 1985) and the much later critiques of pretend play in children (Lillard et al., 2013). For example, it has long been postulated that play by juveniles trains them in the use of species-typical behavior that will be used more effectively later in life (often summarized as the 'instinct-practice hypothesis'; Groos, 1898). Consider, then, the case of 'play fighting,' a frequently observed form of play in the social domain, which, as the name implies, resembles serious fighting (Aldis, 1975; Fagen, 1981). An obvious prediction of Groos' hypothesis is that play fighting as juveniles helps the animals to become better fighters in adulthood, improving their ability to defeat opponents and gain dominance (Symons, 1978; Smith, 1982). Yet, evidence for this theoretically challenging hypothesis is mixed: some studies find the predicted positive relationship (marmots, Blumstein et al., 2013; American mink, Ahloy et al., 2017), while others do not (meerkats, Sharpe, 2005). Other observations emphasize the correlation between juvenile play and the adult serious behaviors it supposedly mimics. For example, Javan slow lorises (*Nycticebus javanicus*) use venom during their competitive interactions, and in adult-juvenile play, which is very frequent, the juvenile play patterns show striking similarities with the venom postures adopted by adults during real competitive interactions. Considering the importance of venom in this highly territorial species, the authors argued that "venomous" playful interactions prepare juveniles for future real venomous encounters (Barrett et al., 2021). But this approach takes us only so far, as in other cases, it is not the most difficult to execute actions that are performed during play. For example, in many ungulates with horns and antlers, it is the delivery of head strikes that is the most dangerous and difficult to execute during serious fighting (Geist, 1966, 1978), but such actions are rarely reported during play fighting (Byers, 1984; Miller and Byers, 1998).

This is not only a problem with fitness benefits of social play. Experiments testing the claim that object play facilitates predation, as in cats, have also had negative results (Martin and Caro, 1985), as have attempts to test this hypothesis more recently in mink (Dawson et al., 2022). The problem is twofold. First, not all species play similarly with the same level of complexity. For example, unlike cats, mink show little interest in static objects as used in this study (Schank, pers. obs.). Second, play is likely multifunctional, so not all species will exhibit all functional outcomes. Hence, the choice of species and type of play engaged in can have a major impact on the conclusions drawn from any given study.

Intensive studies of play fighting, albeit primarily in rats, suggest that it is not simply that engaging in play improves species-typical motor actions as Groos expected, but rather, such play enhances socio-cognitive skills, which produce more adaptable animals across a variety of domains. Play fighting includes competitive interactions that involve the same form of advantage characteristic of serious fighting (e.g., the same bodily targets are bitten) in some species (Aldis, 1975), but not in all. In some species, play fighting can involve competition for targets typical of more serious fighting (Aldis, 1975) but also of predation, sex, or other affiliative activities, such as grooming (Pellis and Pellis, 2017, 2018; Pellis et al., 2023 this special issue). Hence, what is generally referred to as 'play fighting' is also a heterogeneous category, and irrespective of the type of adult behavior being simulated, can vary markedly in complexity. The simplest form differs only marginally from the adult behavior being simulated, whereas the most complex can have elements that are not only greatly modified but may also contain elements that are unique to the playful context (Pellis and Pellis, 2009; Palagi, 2018). Irrespective of the type of behavior recruited, all play fighting involves competition (see Fig. 1 in question 2), but competition is attenuated to some degree by cooperation, resulting in reciprocation and role reversals that are

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not seen in serious fighting (Pellis and Pellis, 2017; Maglieri et al., 2020; Bagnato et al., 2023).

Moreover, while some degree of reciprocity is necessary to sustain play fights, how cooperation is embedded into competitive play fights varies across species (Pellis and Pellis, 2016a). With such diversity, it is little wonder that a unitary function is unlikely to be revealed in all species studied (Burghardt and Pellis, 2019; Pellis and Burghardt, 2017). Given the progress afforded by detailed studies of rats and some other rodents, they provide good models with which to explore the mechanisms by which play can lead to beneficial outcomes (for recent reviews in this special issue, see Cooper et al., 2023; Nunes et al., 2023; Pellis et al., 2023).

As noted in the Neural mechanisms section, play fighting in rats involves the activation of widespread neural circuits throughout the brain (Siviy, 2016; Vanderschuren et al., 2016). However, rats that have been decorticated at birth play just as frequently and with the same level of complexity as intact siblings, both as juveniles and as adults (Pellis and Pellis, 2009). That is, the development of social play does not require the most recently evolved part of the brain, the cortex (Himmler et al., 2016). However, while the play of juvenile rats that have been decorticated at birth superficially resembles that of intact rats, they fail to modify their playful actions when playing with a novel partner or if the partner makes an unexpected movement. These contextual adjustments involve neural circuits in the prefrontal cortex (PFC; Pellis and Pellis, 2016b), the area of the cortex associated with executive functions, such as impulse control and behavioral inhibition, short-term memory, attention and decision-making (Miller and Cohen, 2001; Dalley et al., 2004; Robbins and Arnsten, 2009; Floresco, 2013). Indeed, pharmacological inactivation of the rat PFC (that temporally takes this brain region offline and can so distinguish between development versus execution of a certain behavior, being relatively unconfounded by functional compensation by other brain circuits) has been shown to profoundly reduce social

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play behavior in rats (van Kerkhof et al., 2013). Moreover, the experience of play and other

social behavior in juvenile rats and some other rodents in the juvenile period changes the

physiology and anatomy of the neurons in the PFC, and these changes are associated with

improved sociocognitive behavior (Lukkes et al., 2009; Bell et al., 2010; Himmler et al., 2013;

Baarendse et al., 2013; Pellis et al., 2014; Vanderschuren and Trezza, 2014; Burleson et al.,

2016; Schneider et al., 2016; Marks et al., 2017; Stark and Pellis, 2020, 2021; Bijlsma et al.,

2022; Bijlsma et al., 2023; Stark et al., 2023; Ham et al., 2024). Important evidence to support

this idea has come from studies in which young rats have been denied social play by socially

isolating them during the period in development when they would normally show most social

play (see Vanderschuren and Trezza, 2014; Pellis et al., 2023 this special issue). Deprivation of

social play behavior rendered these rats especially impaired in novel, changeable, or challenging

situations. Thus, these animals showed inadequate responses to social conflict, greater difficulty

coping with sudden changes in task requirements, altered PFC physiology, and increased

vulnerability to substance abuse (Van den Berg et al., 1999; Von Frijtag et al., 2002; Lukkes et

al., 2009; Himmler et al., 2013; Baarendse et al.,2013; Baarendse et al., 2014; Vanderschuren

and Trezza, 2014; Whitaker et al., 2013; Lesscher et al., 2015).

The general conclusion that can be drawn from this research is that while the cortex may

not be necessary to develop play or execute the basic play repertoire (Pellis et al., 1992;

Panksepp et al., 1994), modifying that execution with context (Pellis et al., 2006; Bell et al.,

2009; Himmler et al., 2014) does require an intact PFC, and the experiences derived from play

modify the development of the PFC (Lukkes et al., 2009; Bell et al., 2010; Baarendse et al.,

2013; Bijlsma et al., 2022; 2023). Moreover, the changes in the PFC lead to animals that are

better able to adapt to a wide range of social and non-social contexts (Baarendse et al., 2013;

Bijlsma et al., 2022). That is, the experiences derived from play fighting trains the animal to be better equipped to deal with the vicissitudes of life more generally (Špinka et al., 2001; Pellis et al., 2010). Simpler versions of social play that primarily involve locomotor play can improve motor performance but not sociocognitive processes (Nunes et al., 2004; Richter et al., 2016), although some evidence is also emerging about the effect of social play on animal personality (Hurst-Hopf et al., 2023). The key feature of complex social play that seems crucial to gaining socio-cognitive benefits is having to negotiate reciprocity and so ensure appropriate levels of role reversals during play fighting (Schneider et al., 2016; Pellis et al., 2017; Stark et al., 2021; Ham et al., 2024). In this way, only species with the capacity to engage in complex play fighting requiring reciprocal exchanges are likely to gain these benefits from playing. This starts to make sense of the variability across species, both in their complexity and the benefits they may gain from playing. The fact that even the same type of play may have varying functions or no clear value across different species and contexts certainly complicates our search but also suggests that play is capable of priming far more behavioral and evolutionary change than even the most avid promoters of play appreciated. Indeed, behavioral play complexity may lead to mental rehearsal, imaginative, and pretend play (Gleason and White, 2023, this special issue).

Species having to solve more unpredictable problems, especially social ones, should be more likely to evolve the complex play fighting needed to promote the refinement of socio-cognitive skills. The available data on primates tend to be consistent with this hypothesis. Species with more complex and unstable social relationships tend to engage in play behaviors as juveniles that exaggerate the experiences that seem important for refining socio-cognitive skills (Pellis et al., 2014; Palagi, 2018). Is the Syrian hamster an exception? Syrian hamsters live solitarily as adults, apparently only interacting affiliatively during sex or when rearing infants

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(Rowell, 1961; Nowak, 1991). Social interactions in this species have been shown to be mediated by the mesolimbic system (Cross, et al., 2024) So why should their play fighting be as complex as that of rats (Pellis and Pellis, 2009), and why should their play be able to similarly modify the PFC and improve socio-cognitive skills (Burleson et al., 2016; Cooper, et al., 2023, this special issue)? Relationship instability may actually be a factor, as adults do not have frequent interactions with the same partners and thus need to reestablish them. Perhaps the need to perform adequately in a largely solitary social system with limited, but critically important, social dominance and competition makes this more important for both sexes (Whitten et al., 2023; Kyle et al., 2019). Bears, who also are highly playful when young, but lead rather solitary adult lives outside mother-cub relationships, represent a similar situation (e.g., Burghardt and Burghardt, 1972; Fagen and Fagen, 2004, 2009). The social complexity of the lives of more 'solitary' animals is often underestimated (Leyhausen, 1965).

An especially challenging aspect for the study of the adaptiveness of play is determining how the costs of play for juveniles are balanced by benefits achieved as adults, if the benefits of play are not immediate or important, but short-term, a topic from play's origins (Pellis et al., 2015). A recent agent-based model investigated this problem in the context of social groups in which adults could either pool resources, such as food, needed for reproduction or not do so. Schank et al. (2018) showed that agents that engaged in and experienced sufficient fair play as juveniles subsequently pooled resources and fairly divided them as adults, thus enjoying higher average fecundity due to reducing resource inequality. An interesting aspect of this model is that it introduced mortality costs into juvenile social play. As noted earlier, play can result in injury or increased predation, this model allowed the introduction of different rates of juvenile play mortality on the evolution of fair play. Even when juvenile mortality costs were as high as 10%,

social play that is fair could evolve under some biologically plausible conditions (Schank et al., 2018). This demonstrates that it should be feasible to develop evolutionary models that allow us to calculate the cost-benefit tradeoffs across developmental stages and thereby test precise evolutionary predictions. Evolutionary models show that the benefits of risk-pooling depend heavily on both the intra-individual variation in risk and the inter-individual correlation in risk (Winterhalder, 1986; Jones and Ready, 2022), making it difficult to draw overly general conclusions from this model; future research on the evolution of social play can meaningfully engage with this literature to make predictions about inter-species variation in the presence of social play that involves minimizing fitness variation.

While the model by Schank et al. (2018) demonstrated that fair play can withstand moderate juvenile mortality, many theoretical questions are left unaddressed. Fair play is vulnerable to cheating. Could fair play evolve despite cheating? Could fair play evolve if some cooperators learned to retaliate against defectors even at substantial cost to themselves? Alternatively, excessive cheating could lead to them being ostracized by the group (e.g., Wilmer, 1991; Suomi, 2005) limiting further opportunities to play and so reducing the benefits to be gained from playing. In the public goods game framework used by Schank et al. (2018), agents contributed all of their resources. Within this framework, could smaller contributions to a common pool of resources support the evolution of fairness? If these questions can be answered affirmatively, then we would then have the beginnings a broad theoretical foundation for the evolution of fair play and its functional role in adult fair behavior with deep implications for our conceptions of social behavior and social psychology.

Modeling approaches also provide a potential means by which to resolve seemingly anomalous cases like the Syrian hamster, which as an adult, is a solitary species, but is almost as

socially playful as rats when juveniles (Pellis and Pellis, 1988). Are there contexts in their life history when behaving fairly has a fitness return? Given the patchy distribution of this species in a war-ravaged zone, it is unlikely that field studies in the foreseeable future will reveal what such fitness opportunities may be (although related, equally solitary species may be available). Mathematical and computational models can help to better explore the plausibility of candidate mechanisms and to identify more pointed targets for empirical validation of theoretical ideas (Haldane, 1964; Smaldino, 2017; 2023). Models can be extremely valuable in identifying complex evolutionary trajectories, which are often difficult to conceptualize in their absence. For example, consider more abstract models of the evolution of cooperation, which is central to the behavior of social animals. Models have shown how conditions that are initially unfavorable to cooperators can, in fact, lead to more cooperation in the long run if populations are even minimally structured and selfish groups are less sustainable than cooperative ones (Smaldino et al., 2013). Similarly, Akçay (2018) showed that when the prevalence of cooperation selects for the broadening of network ties, this can, in turn, destabilize that same cooperation. While there has been some modeling of the evolution of play (Auerbach et al., 2015; Cenni and Fawcett, 2018; Dugatkin and Bekoff, 2003; Durand and Schank, 2015; Grunloh and Mangel, 2015; Schank et al., 2018; Smaldino et al., 2019; Mallpress and Špinka, 2023; Schank et al., 2023, this special issue), more focus on play by modelers could lead to some productive breakthroughs.

Still, there are some suggestive cases that could be useful to point to an empirical way forward. Perhaps, more analogous to Syrian hamsters, which do not play in adulthood in laboratory conditions (Pellis and Iwaniuk, 2004), is the case for some bears. Immature bears engage in complex play fighting as juveniles (Burghardt and Burghardt, 1972; Henry and Herrero, 1974; Fagen and Fagen, 2004, 2009) but are quite solitary as adults. There are reports

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that, like many primates, including humans (Epps, 1974; Moore, 1985; Pellis and Iwaniuk, 1999a), during mating male and female bears spend time engaged in social play as a precursor to copulation (e.g., Wemmer and Murtaugh, 1981; Herrero and Hamer, 1977), again suggesting that the ability to engage in fair play can overcome mutual antagonism. Primates may be particularly useful for comparative studies as species vary in both the degree of reciprocation in the play fighting they engage in as juveniles (Palagi, 2018; Reinhart et al., 2010; Kraus et al., 2019) and in the retention of play fighting in adulthood (Palagi, 2023; see topic 6, Adult play below). Given that much more is known about the natural history of a wide range of primates than is the case for rodents, this mammalian lineage may be particularly amenable to the use of modern comparative statistical techniques to identify the factors that have promoted the evolution of complex patterns of play (O'Meara et al., 2015). This paper found hints, after controlling for phylogenetic relatedness, that traits such as diet, habitat, age of reproduction and weaning, and metabolic rate all may influence the presence of social or sexual play. Future studies with more power may reach more definitive conclusions.

4. The complexity of play

- Why is juvenile play more complex in some lineages and not others?

- What are the conditions that have promoted changes in juvenile play that have made it more complex?

- What conditions have enabled play to acquire novel functions (tertiary process play) in some lineages and not others?

Complex forms of social play appear in some lineages but not in others. To make the picture even more complicated, identifying species exhibiting play on a phylogenetic tree produces a patchy distribution, suggesting multiple gains and losses of play behavior. Why do

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we see such a puzzling distribution? Some potential answers have been identified. Both theoretical models and empirical data suggest that complex play behavior requires time to emerge during development and requires a certain degree of freedom to be expressed (Smaldino et al., 2019). The development of complex social play seems to correlate with an increased delay in the onset of sexual maturity, which translates into a prolongation of the juvenile stage (Pellis and Iwaniuk, 2000b). This is also true for several animal taxa in which play continues into adulthood (Fagen, 1981; Palagi, 2006, 2023; Ciani et al., 2012). Another potential factor is missing data: in understudied species, it is possible that lack of play represents too few observations to identify play, which actually may be present.

Diamond and Bond (2003) found that in birds (mainly parrots and corvids), complex social play, but not simpler forms of social play, show a linkage with long periods of development. Indeed, longer periods of juvenility are positively correlated with the complexity and prevalence of social play in both rodents and primates (Pellis and Iwaniuk, 2000b). Also, brain size is positively correlated with both complexity and frequency of social play in birds (Kaplan, 2020, 2023, this special issue) and at least three taxa of mammals (Iwaniuk et al., 2001; Lewis, 2000). Given that larger-brained species have longer periods of immaturity (Joffe, 1997), it is possible that lineages with larger brains increase the opportunity for play indirectly by increasing the juvenile period. Also, since more complex play patterns involve neural circuits in the expanded forebrains afforded by increased brain size (Pellis and Pellis, 2016b), the transition from simpler to more complex play may occur at particular branching points in the phylogeny of lineages. This suggests that these two types of playful strategies can be categorized as distinct at both functional and evolutionary levels.

Compared to chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) show some paedomorphic traits, especially in the ontogeny of playful activity, and have delayed development of social inhibition (Hare et al., 2012). A study focusing on the developmental trajectories of social play in chimpanzees and bonobos demonstrated that the simplest form of social play, involving locomotor-rotational movements, is negatively correlated with increasing age in both species. The most striking divergence in their developmental pathways is in play fighting, the most complex form of social play. While the frequency of play fighting involving more than two subjects (polyadic sessions) is negatively correlated with increasing age in chimpanzees, it did not correlate with increasing age in bonobos. Therefore, it seems that the divergence of complex play between the two *Pan* species can be detected well before individuals reach sexual maturity (Palagi and Cordoni, 2012).

In altricial species, as shown for many species of birds and mammals, the needs of offspring, such as food and protection from predators, are provided by parents, especially mothers in mammals, and this permits (but does not obligate) juveniles to spend a large amount of time in playing (Fagen, 1993). However, if the role of the parents is essential to foster the development of complex forms of play in offspring, overprotectiveness by parents can limit the playful experience of the infants (social canalization *sensu*; Berman, 1982). This is the case in species characterized by high levels of competition and despotism in social relationships (Palagi, 2018, 2023). In such species, mothers prevent their infants from engaging in social interactions with other group members, resulting in a contraction of the social networks that infants can navigate. Such contraction can limit the range and number of social stimuli needed to develop more complex forms of playful strategies (Ciani et al., 2012). In nonavian reptiles and other animals where offspring receive little or no parental care, opportunities for extended juvenile

play may be even more constrained, limiting the period when benefits of play can be obtained (Burghardt, 1984, 1988). The logic of this relationship between developmental period and the evolution of complex play has recently been demonstrated by mathematical modeling (Smaldino et al., 2019).

An additional key factor influencing the appearance of sophisticated forms of juvenile play in some lineages and not in others seems to be related to social complexity. Due to their frequently splitting and merging subgroups of variable composition, fission-fusion societies represent the most challenging type of social organization. This social flexibility requires a certain level of plasticity, which can be acquired through sophisticated forms of social play. Complex forms of social play have been reported in many mammal species showing these kinds of social organization, such as bottlenose dolphins (*Tursiops truncatus*, Mackey et al., 2014), spotted hyenas (*Crocuta crocuta*, Nolfo et al., 2021, 2022), African elephants (*Loxodonta africana*, Lee and Moss, 2014), black-handed spider monkey (*Ateles geoffroyi,* Pellis and Pellis, 1997), geladas (Gallo et al., 2021) chimpanzees (*Pan troglodytes*, Palagi, 2007), and bonobos (*Pan paniscus*, Palagi, 2006, 2008; Bertini et al., 2022). The number of potential players is also important in shaping the complexity of play. In those species living in small, familiar groups, infants have only their siblings (often only one, if any) with whom to play. This results in a contraction of potential social stimuli to which the young are exposed and limits the amplitude of the playful repertoire that can be developed.

The relationship of social complexity in the evolution of sophisticated forms of social play in juveniles also appears to be true for birds. This is well illustrated by two congeneric species of parrots from New Zealand. Compared to the kaka (*Nestor meridionalis*), juvenile keas (*N. notabilis*) show prolonged social relationships with adults with whom they continue to interact

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for long periods of time (Diamond et al., 2006). In kakas, juvenile social play is briefer, more

predictable, less variable in sequence, and involves fewer players, thus appearing more

homogeneous than the social play present in keas. However, the most striking difference

between the two species is in social object play, which is pervasive among keas but has not been

observed in kakas. The ability to mix two forms of play, such as object and social play, is

symptomatic of a higher level of behavioral plasticity in keas. The authors interpreted such

plasticity in the light of the species differences in both their ecology (i.e., keas need to engage in

more exploratory foraging) and their social environment (i.e., keas maintain more extensive

associations between juveniles and adults).

Another interesting dichotomy in the development of play complexity can be found in the

comparison between chimpanzees and bonobos in object and social play (Koops et al., 2015).

Wild immature chimpanzees seem to reach higher levels of complexity in object play compared

to immature bonobos, which, as mentioned above, appear to be more plastic in their social

playful interactions. When there is considerable variance in foraging success rates—that is, when

the likelihood of obtaining a valuable resource is relatively low due to the difficulty of gaining

it—an appropriate use of strategic tools seems to be necessary. Such "tools" can be based on

social strategies (e.g., cooperative behavior) and/or on the manipulative ability to modify the

physical environment to increase the probability of reaching otherwise unattainable food. In

these cases, object play is favored and becomes more complex during ontogeny. Koops et al.

(2015) provided evidence that the propensity of chimpanzees, compared to bonobos, to engage in

more complex forms of object play does not depend on differences in the ecological

opportunities available to each species. Moreover, a recent eye-tracking study showed that while

bonobos pay more attention to social cues, chimpanzees seem to be more attentive to target

objects, thus suggesting a trade-off between the motivation to manipulate objects and to pay attention to conspecifics (Kano et al., 2015). Interestingly, it is in chimpanzees, who emphasize object play and not in bonobos, that using sticks for termite mound fishing, using stones to crack nuts, or forming leaves into cups for water have been recorded.

In conclusion, it appears that the patchy phylogenetic distribution of play complexity in juveniles can be explained by a combination of several variables acting together in a synergistic (and selective) way to produce more competent adults. However, exactly how those variables each contribute to the development of play, especially how they interact with the neurophysiology, morphology, and socio-ecology of each species, is as yet unknown. Furthermore, if transitions occur where a behavior is being gained or lost, there may be a lag between the selection occurring at a given time and the adaptive function of a trait. Focused research in the field, zoos (Brando and Burghardt, 2019), and laboratories, along with formal modeling, are needed to characterize more fully the mechanisms and evolution of such behavior, including possible implications for our species.

5. Mechanisms underlying differences in play

- How do the socio-ecology, morphology, affective, motivational, and cognitive traits of a species contribute to differences in play?

- What are the roles of surplus time and energy, motivation, motor abilities, and behavioral repertoires?

These are large and complicated issues, and thus promise to be studied for many years given the great differences among the diverse species that play. But to begin, play seems to involve both a motivational component and a performance component, a point documented in the neural mechanisms section above and a distinction made earlier by Eibl-Eibesfeldt (e.g., 1982),

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where components of play performance derive from instinctive (behavior) systems (e.g., see Schank et al., 2023, this special issue). Motivational factors have been reviewed and applied to the ontogeny of play in dogs (Burghardt et al., 2016), but much more work needs to be done, as also noted in Pellis et al. (2019). Emotion and hedonic factors are also organismal processes affecting play (Burghardt, 2019), as well as the contrast between wanting and liking (e.g., Berridge, 2019; Berridge and Robinson, 2003; Berridge et al., 2009).

While play has now been documented in diverse lineages of invertebrates and vertebrates, it is undoubtedly most common in mammals and birds (Fagen, 1981; Burghardt, 2005; Kaplan, 2020). This suggests that there are aspects of the biology of these groups that make the expression and evolution of play more likely. A number of putative factors have been proposed, but their relative importance, if any, has not been rigorously established. Some of these factors derive from the Surplus Resource Theory (SRT) of play proposed to explain the origins and expression of play (Burghardt, 1988, 2005). This theory proposes that animals that have more time free from performing necessary activities such as foraging, predator avoidance, dominance and territorial defense, and reproductive activities should play more than others, including other members of the same species. Well-maintained captive animals generally play more than their wild counterparts. Animals whose juvenile period is spent under the care of parents who provide resources and protection live in a setting where play can be expressed at lower costs. In species whose natural behavioral repertoire allows them to perform more complex motor actions (e.g., use of forepaw digits in primates compared to lizards), individuals are more likely to show more novel and complex movements. Animals whose normal repertoire of movements, postures, facial expressions, and vocalizations are more varied are expected to deploy them in more non-stereotyped and varied ways. Obtaining quantitative measures of such repertoires should be

pursued, and some interesting avenues have been explored. For example, Changizi (2003) compared the relationship among encephalization index, number of muscle types, and behavioral repertoire size for a sample of about 40 species of eutherian mammals from 10 orders. He found that "the number of muscle types C increases as a function of the number of ethobehavior types" (p. 164) and also that "behavioral repertoire size appears to be significantly correlated with encephalization" (p. 166). Indeed, although not mentioning play, he claims to have demonstrated that "muscles are acting in a combinatorial, or language-like manner in the construction of ethobehaviors" (p. 164). These preliminary findings could provide quantitative empirical support for SRT and the greatly increased amount and complexity of play in endotherms. Application of these findings to the variation in the play across diverse species of mammals is timely.

Animals capable of more vigorous and sustained behavior, most notably in endothermic mammals and birds, are, arguably, more likely to engage in play sufficiently frequently for benefits to accrue. Animals with greater cognitive ability may be more likely to have play reinforced either ontogenetically or phylogenetically. For example, if a novel solution to a task arises through play, a more cognitively adept species may be more likely to incorporate it into its repertoire and deploy it functionally. There are other possibilities, and domestication may provide one avenue of understanding since many domesticated species seem more playful than their ancestral stock. Retention of juvenile characters into maturity (i.e., paedomorphism) may be involved in this (e.g., Dugatkin and Trut, 2017). More research involving species in which adults, as well as juveniles, play versus those in which play is largely restricted to juveniles would be useful here.

Experiments, both laboratory and natural, exist in which food availability, exposure to predators and stressors (social and physical), and other related manipulations have been

performed. Many of the resultant findings support the general role of the factors listed above. However, their relative importance within and across taxonomic groups is unknown. Until their relative importance is determined, we will not have a predictive science of play. This is where the role of modeling play, and testing the effects of different factors in both isolation and combination would be helpful. A study by Cully et al. (2015) showed how "play-like" behavior in a six-legged robot could prepare the robot for movement when one or more of its legs was "unexpectedly" damaged, providing an in-principle demonstration of the uncertainty hypothesis. However, models of both must be complemented by empirical data. The collection of such data and organizing it into useful databases should be pursued. In all of these approaches, however, it must be recognized that what holds for one type of play—e.g., locomotor, social, object or pretend, vocal—may not hold for the others.

As already noted in the section on Neural mechanisms, we do not know whether the brain mechanisms involved in social play are also involved in non-social forms of play. So, even in well-studied groups such as mammals (Siviy, 2016; Vanderschuren et al., 2016), whether different types of play involve common or heterogeneous mechanisms remains unresolved. There are plausible models, with supporting empirical evidence that suggest that different types of play have independent origins, and if multiple types of play are sufficiently evolved, they can be combined into novel forms of play (Pellis et al., 2019). If so, this would predict that independent, mutually exclusive types of play should be the ancestral state and combined forms of play, the derived state. A recent phylogenetic analysis of the distribution of different types of play fighting in primates is consistent with this prediction (Pellis, Pellis, and Ham, 2023). Alternatively, there are theoretical frameworks being developed that also make a plausible case for common origins of play types across a wide swathe of the animal kingdom (Lewis, 2023).

Given that these different perspectives can explain subsets of play phenomena, suggests that we have some way to go in understanding the mechanisms that underlie play and how these mechanisms have evolved. Consequently, the mechanisms underlying differences in play may pose the most challenging problems to resolve in the coming decades. Resolution will require both greater comparative breadth in our knowledge of the distribution of play and greater depth of knowledge of the psychological and neural mechanisms in as many different species as possible.

6. Adult play

- Why do some, but not all, species keep playing as adults?

- What are the conditions that have promoted play to persist into adulthood in some lineages and not others?

- What are the conditions that have promoted adults from some lineages to use play to navigate social relationships in fitness-enhancing ways?

Play is often primarily an immature affair. It may begin to be expressed shortly after birth or hatching, reaching its peak in juvenility and declining with sexual maturity (Panksepp, 1981; Fagen, 1993). However, this decline is sometimes forestalled, with play invading the adult stage. In social species, mothers and other adults can play with infants and juveniles, which are often initiated by these immature animals and can be influenced by unbalanced demographic factors, as when a social group has few immature animals, limiting the opportunity to play with other peers (Pellis and Iwaniuk, 2000a; Palagi, 2006). A more intriguing and biologically important question is understanding cases where adults select *other adults* as play partners (Palagi, 2011; Pellis, 2002).

The occurrence of social play in adults strongly reinforces the hypothesis that this costly activity (in terms of time and energy) must have some immediate benefits since adults, unlike juveniles, have already acquired through ontogeny the necessary competence to deal with physical and social environments (Palagi, 2006; Palagi et al., 2016; Palagi and Paoli, 2007). During the pre-feeding time, a period during which a strong conflict of interest arises, adult bonobos engage in social play more than a control period (a time window far from food distribution) to dissipate anxiety. Later, when food arrived, those individuals who played together were more likely to peacefully share their food (Palagi et al., 2006). Adult-adult play behaviors can be found in many different contexts, but what they seem to have in common is that play is used to create familiarity between subjects, negotiate social relationships, and lower social tension (Palagi, 2023, in this special issue). In adults, play can also be highly rewarding. In bonobos, when engaging in play fighting, adult females laugh during each others' physical solicitation (Palagi, 2008; Palagi et al., 2022). In captive geladas, females exhibit unique behaviors in their use of social play. They engage in play with both other adult females and immature individuals, suggesting their strong inclination for such interactions. This behavioral pattern is typical of species that possess more relaxed and fluid social relationships, as opposed to rigid and domineering ones. This interpretation is further upheld by the positive correlation observed between play and friendly behaviors like grooming and support during conflicts within each age group (adult females and immature individuals). This evidence, combined with the absence of a link between aggressive encounters and social play, indicates that female geladas employ play to assess social dynamics and enhance their social bonds (Mancini and Palagi, 2009).

In solitary species, adult-adult play can be used as a courtship strategy to ensure a basic level of affiliation between males and females. Several nocturnal prosimian species adopt playful contacts as an ice-breaker mechanism to favor sexual interactions (see the genera *Mirza*, *Daubentonia*, *Lepilemur*, and *Perodicticus;* Norscia and Palagi, 2016). In solitary living species that form hierarchical dominance relationships and where territories overlap, play between adults (including males) can be used to increase or maintain their tolerance of one another (wild brown bears, *Ursus arctos*, Clapham and Kitchin, 2016; polar bears, *Ursus maritimus*, Latour ,1981). Among sifaka (*Propithecus verreauxi*) at the beginning of the mating season, adult males belonging to different groups may engage in play fighting to reduce the social tension arising from their unfamiliarity with one another (Antonacci et al., 2010).

Interestingly, the necessity to develop and maintain social bonds appears to be the main force for the evolution of adult play in some species of birds as well. This is well exemplified in the clade of large-bodied parrots from New Zealand mentioned earlier. Keas (*Nestor notabilis*) live in complex social groups, and the young have prolonged post-fledging associations with other juveniles and with adults. In this species, social play is distributed across and between all age-classes, with adult males and females exhibiting a distinctive form of social play ('toss' play; Diamond and Bond, 1999). This adult-typical form of play may have an important role in courtship and pair formation (Diamond and Bond, 2003). Neither adult-juvenile or adult-adult play is present in the closely related kakapo (*Strigops habroptilus*) or kaka (*Nestor meridionalis*), which lack sustained social relationships once the young fledge.

What all these examples indicate is that adult-adult social play is present in species that need to deal with high levels of unpredictability in their social relationships and interactions (Nolfo et al., 2021). Play can overcome such uncertainty and, in some cases, help foster more

stable and persistent relationships. An example comes from social carnivores. The African painted wild dogs (*Lycaon pictus*) engage in social play to synchronize the pack activity just before hunting. In this species, play seems to serve as a sort of recruitment to motivate each other to actively cooperate and reach a common goal (van Lawick and Goodall, 1970).

Comparisons among species with similar social systems but differing degrees of dominance asymmetries have supported this general conclusion. In more egalitarian and tolerant species, power is uniformly distributed, and the asymmetries in most relationships are weaker (Flack and de Waal, 2004). In contrast, in more despotic species, power is disproportionately held by a few dominant individuals. In despotic species, most interactions among group members involve formal displays, limiting the need and opportunity for other, more ambiguous forms of social interaction such as play. In egalitarian species, social relationships are not crystallized or fixed according to hierarchy or nepotism and so require constant re-evaluation and updating. Formal displays are less useful in such species to negotiate subtle changes in social relationships, and it is in such species that adult-adult play is more prevalent. Empirically based comparative studies in different genera have consistently shown that play is more frequent and freely expressed in egalitarian than in despotic species (Palagi, 2006, 2008; Ciani et al., 2012; Cordoni et al., 2018).

In bonobo societies, adult females negotiate and maintain their relationships both through alliances and peaceful contacts. In chimpanzees, there are also coalitions, alliances, and some forms of conflict management but, in contrast with bonobos, these activities are limited to males (Palagi and Demuru, 2017). Moreover, hierarchical dynamics are not as rigidly codified in bonobos, and regular social assessment seems to be the key factor in sustaining these more relaxed relationships. Adult-adult play in the two species shows striking differences, with adult bonobos engaging in higher levels of social play compared to chimpanzees. In bonobos, most

adult play is initiated and maintained by the females, and it is common to observe two unrelated

females playing together with their babies. A pair of adult females playing with one another and

their young can subsequently attract other adult females, leading to polyadic interactions among

the adults (Palagi, 2008). Since bonobos live in a female-bonded society, it is not surprising that

female relationships are mediated by play, a versatile activity that creates the conditions to

increase social knowledge and trust among partners, increasing opportunities for cooperation to

achieve social benefits (e.g., female feeding priority over males).

The differences in social style and play across species of macaques (*Macaca* sp.) show a

similar pattern. Tonkean macaques (*Macaca tonkeana*) and Japanese macaques (*M. fuscata*) are

two species at the opposite extremes in the social tolerance gradient of the genus proposed by

Thierry et al. (2000). Play in the tolerant Tonkean macaque, compared to that in the more

despotic Japanese macaque, is more cooperative among juveniles (Reinhart et al., 2010) and is

performed more among adults, and at both ages, they do not show any preference for play

partners based on age, sex or dominance (Ciani et al., 2012; Reinhart et al., 2010). Also,

grooming, the most important social glue in primates, is extremely limited in *M. fuscata* but very

common in Tonkean macaques where, and in some cases, it can lead to play fighting (Ciani et

al., 2012).

Do primates learn how to play from their social environments, or are the differences in

their play behavior (and related social organization) genetic? One way to disentangle genetic

predispositions from learned modes of dealing with different social partners is to perform cross-

fostering experiments. For example, de Waal and Johanowicz (1993) sought to ascertain the role

of social experience in determining the levels of reconciliation in macaques. The two species

used were the more tolerant Stumptail macaque (*Macaca arctoides*), a species showing high

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levels of conciliatory contacts, and the more despotic rhesus macaque (*M. mulatta*), a species

that rarely engages in reconciliation. Rhesus macaque infants raised by stumptail macaque

mothers showed a threefold increase in reconciliation behavior compared to rhesus infants raised

by rhesus mothers. Therefore, the social style of a despotic species *can* be modified through

interaction with a species characterized by a more tolerant dominance style. Experiments are

needed to see if a similar result would be obtained for adult social play if Japanese macaque

infants were raised by Tonkean macaques. Data supporting the hypothesis that social

environment influences the development and maintainance of play propensity comes from our

own species. Social play seems to have an important cultural role in egalitarian and tolerant

human societies, in which the presence of free play, including humor, pervades many social

activities and regulates disputes promoting intra-group cooperation (Fry, 2014; Gray, 2014).

    The "self-domestication process", in which domestication-like changes are present in wild

animals due to natural selection acting to reduce aggressive tendencies (Hare et al., 2012), could

play a role in the retention of juvenile traits into adulthood. Such a mechanism could be an

important factor producing species differences in tolerance between bonobos and chimpanzees,

and among different species of macaques. Recently, Raviv et al. (2023) suggested that elephants

may express some features associated with self-domestication (e.g., low levels of aggression,

high propensity to prosociality, extended juvenile period). In particular, elephants show a high

tendency for playfulness. The authors reinforced their proposal about the self-domestication

process in elephants by demonstrating that genes previously associated with domestication have

been positively selected in these species. Although the self-domestication process is highly

difficult to demonstrate, a similar process could have played a role in human evolution (Henrich,

2016) and may be partly responsible for why humans exhibit such a wide range of play behavior

into adulthood. However, the hypothesis of self-domestication is not sufficient to explain why in highly hierarchical and despotic species, adult play can also be present (e.g., *Crocuta crocuta*, Nolfo et al., 2021, 2022). Whatever the mechanisms involved, adult-adult play seems to evolve when species are exposed to high levels of social unpredictability and face the need to continuously renegotiate and ascertain their social relationships (Palagi, 2023, this special issue).

7. Creativity, culture, ritualized behavior, and play

- Has behavioral play evolution also facilitated mental rehearsal, planning, imagination, pretense, and even cultural evolution?

- What is the relation between play and ritual?

- Play has been proposed as an initial driver of ritualized behavior and communication in animals through a process of ontogenetic ritualization as well as natural and sexual selection.

- Can such processes be modeled and tested?

Play may be not only a product of evolutionary processes but also a driver of behavioral and psychological change, influencing evolution at both the biological (neural, genetic, epigenetic) and cultural levels (as well as their interaction; Jablonka and Lamb, 2005; Richerson, and Boyd, 2005). Play can drive behavioral and psychological change through two routes. First, play can be the vehicle for creating new behaviors that have novel and adaptive functions. That is, play can promote, facilitate, and even produce new behavior (tertiary process play). Animals, including human children, may engage in variable and flexible play behavior that consequently solves problems. Playful learning involves children using interactive items to gain knowledge. By playing with objects of different forms, children can explore the shapes of objects both visually and via touch. Such multimodal active exploration and free use of the object can lead to

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playful embodied learning (Lillard, 2005). Studies on early childhood programs across seven countries indicate that cognitive development is promoted through playful learning, including a diverse range of manipulated objects (Montie et al., 2006). In non-human primates, a classic example is a study by Schiller (1957), where chimpanzees playfully put sticks together and later deployed this innovation in problem-solving. It is, perhaps, not a giant step from remembering such playfully obtained abilities as joining sticks together to experiment with behavioral possibilities mentally without performing all the operations physically. If this is the case, play may be a major source and propeller of cognitive evolution.

Play may thus be a key aspect of innovation and creativity, and a number of examples have been reported (Bateson and Martin, 2013; Burghardt, 2015; Kuczaj, 2017). The use of stones to engage in drawing-like activities observed in some individuals of a gelada colony is an illustrative example of how an innovative behavior can emerge (Pallante et al., 2023). Thus, innovation is not only for what is called "Big C" creativity, which changes society or some aspect thereof (i.e., in science or art), but also includes the more modest process of discovery in individuals during their normal ontogeny. "Little c" and "mini c" creativity may mark developmental and educational attainments, formal and informal, throughout life. The link to major culture-wide creative artistic and scientific achievements, and their social underpinnings, may be on a continuum with these more modest play induced phenomena. Additionally, novel behavior can itself create novel situations and thus lead to cascading culture-wide effects.

The second route is when such novel behaviors become widely adopted, more stereotyped, conventional, and routine, and may no longer be recognized as play or fulfill the criteria necessary to characterize them as play (Burghardt, 2005). In this way, play could be the basis for innate patterns becoming incorporated into instinctive behavior systems (Burghardt and Bowers,

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2017) underlying species-typical behavior. This is a variant of the *Baldwin effect* (Baldwin 1896) which was long ago advanced as an alternative to the Lamarckian 'lapsed intelligence' view supported by Romanes (1883). Under changing conditions, an animal may have the capacity to respond adaptively (e.g., via learning, habituation), a process labeled innate or congenital plasticity. The inherited (genetic) underpinnings of the behavioral change, which initially needed experiential input, could, over generations, accumulate directional changes that facilitate increasingly rapid acquisition of the adaptive behavior to the point where the behavior no longer needed learning (or related processes) for it to be induced when needed. Thus, the behavior could be triggered without the previously needed environmental input. A variant of this process is *ontogenetic ritualization*, whereby play produces novel behavioral variants that then become incorporated into an individual's—or, more importantly, a group's—behavioral repertoire, and acquire novel functions. This idea was initially proposed by Thorpe (1966), advocated with examples in chimpanzee communication by Tomasello et al. (1997), and perhaps most clearly documented in the long-term studies of stone play by Huffman and colleagues in Japanese macaques (Huffman et al., 2016; Leca, 2023, this special issue) and geladas (Cangiano and Palagi, 2020). If stone clacking becomes widespread, highly stereotyped, and used in a functional, social context, it may represent an ongoing process of play to ritual. Clearly, play may have a role in both instigating novel behavior to changing conditions and the development of widespread stereotyped rituals, both cultural and instinctive.

The noted play scholar Huizinga (1955) claimed that play was at the root of almost all human cultural attainments, including rituals and, more recently, video games (Nguyen and Bavelier, 2023, this special issue). This idea has been revisited in recent years (see Burghardt, 2018b, 2020). How might this process work out in animal play?

One illustrative example is the facial expression called Relaxed Open Mouth (ROM), one of the most effective ways to express the motivation and invitation to play, which is widespread among playful social mammals. ROM is considered a ritualized pattern derived from the typical biting action (van Hooff and Preuschoft, 2003). According to the signal ritualization process (*sensu* Tinbergen, 1951, 1952), ROM can derive from a separation of the different motor components forming the action of biting with a total inhibition of the biting act. In this way, the action is initiated but not concluded. This ritualized version of biting, completely lacking any harmful intent, informs the receiver of the benign attitude of the sender (Palagi, 2008). The operational demonstration of the presence of ROM as a playful signal in a given species requires that the mouth opening is temporally disassociated from agonistic biting (dogs, *Canis familiaris*, Maglieri et al., 2022; ringtailed lemurs, *Lemur catta*, Palagi et al., 2014; South American sea lions, *Otaria flavescens*, Llamazares-Martín et al., 2017, *Suricata suricatta*, Palagi et al., 2019). The ROM is clearly a part of the species' evolved behavioral repertoire, but it may have evolved through ethological ritualization involving a Baldwin Effect-like mechanism.

Ontogenetic ritualization applies to the evolution of intentional communication, which is well represented by the bodily gestures present in great apes and humans (Demuru et al., 2015; Liebel and Call, 2012). Subjects can initiate their playful social contact by always performing the same behavioral pattern (e.g., pushing) prior to making contact. If the behavioral pattern becomes predictable, the potential receiver can anticipate the action by responding even when only the first movement of that action is performed (e.g., arm raising). If the initiator perceives the anticipation of the receiver, they will begin to emphasize the first motor action (e.g., arm raising) that is part of the complete playful motor sequence (e.g., pushing). There is, therefore, a disarticulation of the behavioral pattern to its more basic elements, which can then assume

specific signaling functions. A similar phenomenon has been recently demonstrated also in dogs. In a very recent dog breed, the Czechoslovakian wolfdog, the play bow communicates the motivation of the performer to renovate the playful interaction by probably underlining the benign intent of the signaler. Hence, the motor ritualization of an advantage position (the play bow position allows the animal to rapidly start a movement in any direction) becomes an invitation to restart a play session (Maglieri et al., 2023).

Mammal and bird mental capabilities have evolved rather quickly along with their enlarged nervous systems. The endothermy and increased metabolic rates found in these animals allow for much higher rates of behavioral actions of a vigorous and persistent nature. This would have increased the production of behavioral variants through play (and other systems) and provided opportunities for selection at genetic, ontogenetic, and cultural levels. Feedback possibilities per generation would be much higher, which could then "supercharge" further cognitive and neural evolution. For example, several corvids, as well as babblers, hornbills, and parrots, show playful behavior with objects in social contexts. Similarly, the caching of objects by ravens (*Corvus corax*) fulfills all criteria listed for play by Burghardt (2005). It has been recently demonstrated that ravens are able to evaluate the competitive abilities of others by using their skills in play caching (Bugnyar et al., 2007). Therefore, play produces not only cognitive benefits to the performers but also to the observers, who can use play as an indicator of the quality of competitors or the condition of offspring. This may represent an extension of the parental competence assessment role of play advanced by Chiszar (1985). More generally, play may be involved in the evolution of the capacity of individuals to assess both cooperative and competitive agents. For example, Schank et al. (2023, this special issue) developed an evolutionary agent-based model to determine under what conditions a tertiary process play

learning mechanism could evolve in cooperative or competitive contexts. They found that a play learning mechanism evolved in both cooperative and competitive social contexts because it facilitated the "synchronization" of social information.

The roles for play in explaining adaptive behavior, ritualization, and the origins of convention and communication are speculative and not precisely described. Formal modeling, particularly computational modeling that can account for both behavioral and situational heterogeneity, is likely to be important in refining these ideas.

Concluding Remarks

We have attempted to show that diverse types of play behavior have differing attributes, functions, causal mechanisms, experiential/emotional components, developmental trajectories, and evolutionary histories. But beyond this treatment of outstanding questions about play, we feel that the biobehavioral sciences are also ripe for a more expansive and integrated comprehensive understanding of play phenomena. Such an understanding from multiple approaches will facilitate the incorporation of play into a broadened understanding of both biological and cultural evolution, as play has both important genetic and neural substrates as well as developmental, learned, social, and, in some species, cultural components. Indeed, while Tinbergen (1963) noted that there are multiple ways to answer 'why animals perform a particular behavior,' he also stressed the importance of integration—organisms are whole systems, not disjointed fragments. As we review different avenues of research, it becomes apparent that they are inseparable in that each informs the others. A particularly glaring example is that as we have come to know more about how the brain regulates play, at least social play in some laboratory rodents (Siviy, 2016; Vanderschuren et al., 2016; Van Ryzin et al., 2020; Achterberg & Vanderschuren, 2023, in this special issue), this knowledge has led to experimental research into

how play experience in the juvenile period influences the development of brain mechanisms associated with executive function skills (Cooper et al., 2023; Pellis et al., 2023, both in this special issue, as well as Bijlsma et al., 2022; Bijlsma et al., 2023). That is, a deeper understanding of the mechanisms of play has led to a better understanding of some of its functions, and so opens up new ways to make sense of some of the comparative variation seen in many types of play (see Dinets, 2023; Kaplan, 2023, both in this special issue). We see the same trend for study the play of adults (Palagi, 2023, in this special issue).

Thus, while each question/topic identified in this paper will require further effort and the development of appropriate methods, answers to any one will help to shape and refine the questions in other domains. To do this, as we have shown, researchers should tackle these topics with both empirical and formal theoretical investigation. Our conclusion is that those who have characterized play as merely a set of frivolous behaviors are mistaken. Play is a valuable tool for studying neurobehavioral, developmental, and evolutionary phenomena (Leca, 2023, in this special issue; Palagi, Burghardt et al., 2016; Pellis, Pellis, Ham, et al., 2022).

Acknowledgments

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Figure legends

Figure 1. Play fighting in a pair of juvenile deermice (*Peromyscus maniculatus*) is

shown, illustrating aproach (a), attack of the nape (b), defense (c-e), and counterattack

(f, g) leading to a role reversal (h-j). Such sequences are also typically present, and

indeed more frequent, in rats (see Figure 2 in Pellis et al., 2023, this special issue, for a

comparable sequence in a pair of juvenile rats). As in rats, deermice compete to contact

the partner's nape which is nuzzled if contacted. The figure is reprinted with permission

from Pellis et al., 1989.

Figure 2. A schematic view of the rat brain is shown with the most anterior portion on the left and the hind brain on the right. Embedded are the areas of the brain that have been shown to be involved in regulating the play fighting. These include the amygdala (Amyg), bed nucleus of the stria terminalis (BNST), dorsal raphe nucleus (DRN), hippocampus (Hipp), hypothalamus (hypo), lateral habenula (LHb), lateral septum (LS), motor cortex (MC), nucleus accumbens (NAc), olfactory bulb (OB), periaqueductal gray (PAG), prefrontal cortex (PFC) and ventral tegmental area (VTA). Each contributes a different aspect of regulatory control and some of the connections among the different areas are beginning to be understood (dotted lines). The figure is reprinted with permission from VanRyzin et al., 2020.
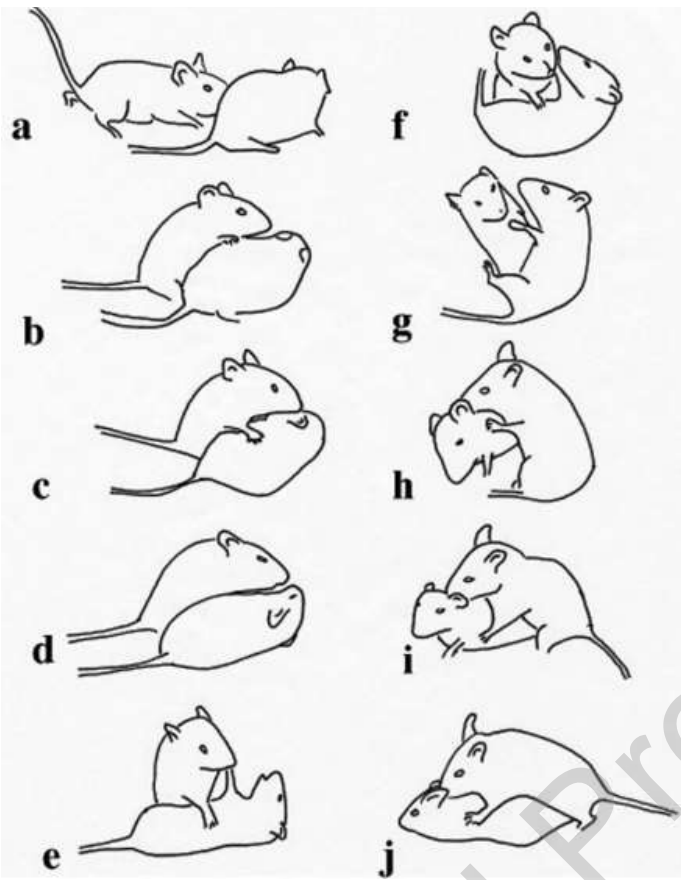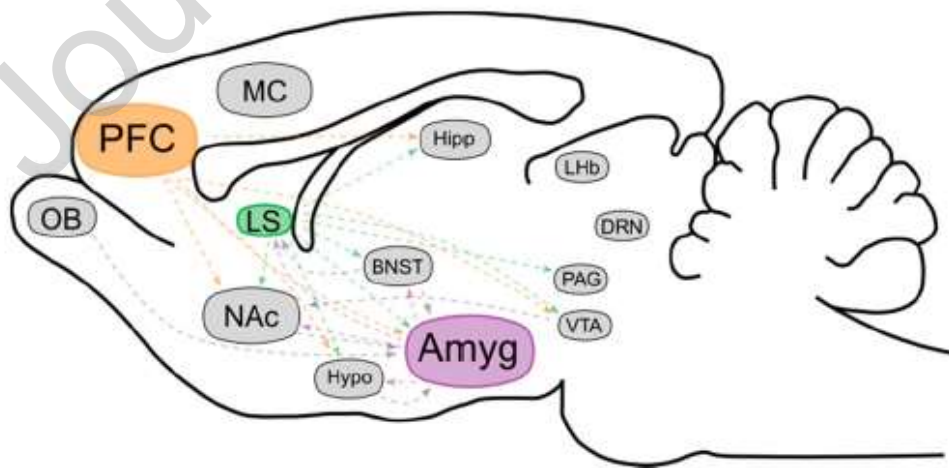
Figure 1.

Figure 2.