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Play Behavior

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Introduction

The occurrence and value of play in humans, especially as it relates to developmental processes, has been intensively studied (Smith 2010). In contrast, the study of play in nonhumans has had a more checkered history, really only getting serious attention from the 1970s onwards (Burghardt 2005). Moreover, this research has tended to fall into two broad camps with little or no overlap: experimental studies, mainly on rats, have focused on the neurobehavioral mechanisms involved in producing play (e.g., Siviy 2016), and observational studies, on a broader diversity of species, of captive, semi-captive, and free-living animals have focused on the functions of play that may have been important for its evolution (e.g., Martin and Caro 1985).

Recently, both these strands of research have gained sufficient maturity that major works have appeared integrating these divergent fields while also attempting to unify studies of human and nonhuman animals (e.g., Burghardt 2005; Pellegrini 2011; Pellis and Pellis 2009). Recent special issues of journals devoted to play illustrate the progress that can be achieved when

researchers from multiple disciplines talk to one another (e.g., *American Journal of Play*, 7(1), 2014; *Animal Behavior & Cognition*, 1(2), 2014; *Adaptive Behaviour*, 23(6), 2015; *Behaviour*, 153(6/7), 2016; *Current Biology*, 25(1), 2014). Indeed, there are glimmers of a comprehensive model gradually taking shape. Still, for all the progress that is evident in comparative analyses of play, it is important to take stock as to what we know or think we know, identify the key intractable issues, and characterize the questions and methods most likely to be fruitful in the coming decades.

Defining Play

The first big problem to resolve is that of defining the phenomenon in question. There have been many attempts at defining play (Fagen 1981). These have, to varying degrees, included such distinguishing features as play being autotelic (i.e., done for its own sake), voluntary, and as having no immediate function. As much of the content of play is derived from behavior seen in other functional contexts such as sex, aggression, predation, and antipredator behavior, it is these characteristics that emphasize how the behavior is performed and the context in which it is performed that are critical for distinguishing play from its nonplayful counterparts (Heymer 1977). These characteristics make actions that are performed during play playful rather than serious,

but the application of such criteria tends to be subjective.

The subjectivity inherent in identifying play has led to disputes over what is and is not play. For example, even though the competitive interactions of immature cockroaches appears to be autotelic, with the behavior patterns typical of serious fighting being performed in a way that does not lead to the outcomes typical of aggression, the behavior is not deemed to be play (Fagen 1981). Similar interactions with these properties, involving two puppies or two kittens, would near universally be labeled as play. Indeed, even the mainstay of neurobehavioral research on play, the laboratory rat, had its juvenile play-like social behavior labeled immature aggression by some researchers, until the neurobiological evidence became overwhelming that play involves different behavior and engages distinct, neural mechanisms compared to aggression (Pellis and Pellis 2009). The more animals are like us, the more likely is their autotelic behavior to be labeled as play.

Burghardt (2005) developed a definition of play involving five criteria to lessen the impact of such subjective judgments. To qualify as play, the behavior in question has to (1) be incompletely functional in the context expressed, (2) be voluntary or rewarding, (3) be, in some ways, modified developmentally or structurally compared with when it is used in its normal, functional context, (4) be performed repeatedly, but not necessarily in an invariant form, and (5) be initiated by healthy, relatively unstressed animals in a relaxed context. Two things distinguish this criteria-based definition from earlier definitions. First, it includes all the major criteria that were grouped together in different ways in previous definitions, and it requires that all need to be met before the conclusion is drawn that the behavior in question qualifies as play. This greatly reduces the importance of the observer's "gut feeling" when making this decision. Second, the criteria can be met to varying degrees: one species may just minimally make the grade, whereas another may greatly exceed that minimum. This latter issue is particularly important to diminish our mammal-centric biases. Indeed, using these criteria, behavioral sequences from a wide range of nonmammalian species,

including nonvertebrate ones, have been categorized as play (Burghardt 2005; Pellis et al. 2014).

Another important contribution of this multi-criteria definition is that it has provided a way to distinguish, objectively, play from other behaviors that have often been confounded with play, such as stereotypies and exploration (Burghardt 2005; Pellis and Burghardt 2017). The advent of this definition, however, has not completely solved the problem of unambiguously distinguishing play. Two of the criteria are particularly problematic. While traditionally neglected as a subject of study, play in some species continues into adulthood and adults can use play in a variety of contexts that confer immediate benefits to the players (Palagi 2011). These immediate functions can make applying criterion #2 that "play behavior is incompletely functional in the context expressed," difficult to apply.

Similarly, in some situations, play has been shown to reduce stress. Thus, while severe stress may dampen play, mild to moderate levels of stress may actually facilitate its occurrence (Pellis and Burghardt 2017), making criterion #5, "that play is initiated in healthy, relatively unstressed animals in a relaxed context," difficult to apply in some cases. These limitations are not insurmountable, but to reduce the subjectivity involved in determining how much stress is too much or how small the immediate function needs to be requires more detailed knowledge of the specific case in question. The five criteria are thus a good starting point, but should be applied with the recognition that, to be effective, further research on the behavior and species under investigation may be required to make an objective decision on some of the criteria. Nonetheless, armed with a workable definition, one that can transcend the typically narrow, comparative confines of mammals and a few birds, examination of some of the deeper progress that has been made in the study of play is possible.

The Many Forms of Play

While in humans play can take many varied forms (Smith 2010), in nonhuman animals three major

forms of play are generally recognized (Burghardt 2005). These are locomotor play, involving a lone animal engaging in running, jumping, kicking, and making turns; object play, involving a lone animal engaging in carrying, flinging, ripping, or otherwise manipulating an inanimate object; and social play, involving two or more conspecifics wrestling, chasing, or otherwise manipulating one another. While most cases reported of all these types of play meet the five criteria (Burghardt 2005), there are unresolved issues about the relationship among the types of behaviors encompassed by each kind of play.

When engaged in object play, animals may include a variety of locomotor movements, and social play may involve competition for an object or incorporate locomotor-rotational movements (Burghardt 2005). Consequently, these three types of play may be intermingled in a variety of ways. A further complication is that, often, labeling the three types of play is based on the target of the play (i.e., self, other, object) and not on the actual content of the actions performed, which may be quite varied. For example, the locomotor play of many prey species, such as ungulates, involves the playful execution of the runs, jumps, turns, and other protean movements that are otherwise seen, functionally, in antipredator behavior, whereas, in some species, some of the locomotor behavior may be not only unrelated to antipredator behavior, but are also unique to play, such as the pirouettes done by chimpanzees (Nishida and Inaba 2009). Labeling both as locomotor play may confound behavioral processes that are very different. Conversely, cats may playfully direct predatory behavior patterns to either inanimate objects or to conspecifics. The problem in this case is that even though the same behavior patterns may be used, the differences in target would lead to the behavioral sequences being categorized as different kinds of play. It is not self-evident as to why the behavioral patterns performed have a lower priority in categorizing play than does the target to which they are directed.

Social play can also be diverse in content. Social interactions involving behavior patterns typical of nurturing young (play mothering),

courtship and copulation (sex play), or conspecific aggression (play fighting), have all been categorized as social play (Burghardt 2005; Fagen 1981; Pellis and Pellis 2009). Indeed, even “play fighting” may be an amalgam of behavioral sequences that can involve competitive interactions of diverse origins: the animals may compete for contact with body targets typical of aggression, courtship, greeting, or grooming (Pellis and Pellis 2009).

All this diversity in the content of play raises important questions about both the neurobehavioral mechanisms that produce play and the possible functions that play may serve. One approach has been to view play as being encompassed by a unitary motivational system, whereby behavioral elements from different functional systems can be intermixed (Heymer 1977). Such a view is supported by some studies, convincingly showing that two or more types of play are intermingled, such as object and social play in Japanese macaques (e.g., Shimada 2012). However, contrary to this perspective are accumulating data that suggest that different types of play have different origins and involve different neurobehavioral systems.

First, at a broad phylogenetic level, the three different types of play may appear independently of one another across different lineages (Burghardt 2005). That is, object play can evolve in a lineage independently of either social or locomotor play, and so on. For example, object play is either absent or rudimentary among rodents, whereas locomotor play and social play are quite prevalent. However, even in cases in which locomotor play and the social play are both present and appear to be performed in an intermixed manner, they may not be causally linked. Indeed, when comparing across species, there is a negative correlation between social play and locomotor play – an increase in the complexity of one type of play is accompanied by a decrease in the complexity of the other (Pellis and Pellis 2009). Such a relationship extends to the subspecies level, with some strains of rats having more locomotor play and some more social play (Schneider et al. 2016). Thus, at a phylogenetic level, different types of play can not only have independent

origins, but also follow independent evolutionary changes.

Second, in species which have multiple types of play, different types of play wax and wane at different ages (Burghardt 2005; Pellis and Pellis 2009). That is, the different types of play appear developmentally dissociated. Third, studies of individual differences within species have shown that individuals that exhibit more of one type of play are not more likely to exhibit more of the other types of play (Ahloy Dallaire and Mason 2016; Lampe et al. 2017). Being more playful does not make an individual equally more playful in all ways.

Given that data on phylogenetic trends, developmental changes and individual differences show that different forms of play are independent, how can the cases in which animals seem to intermix behavior patterns from different functional systems be explained? There is an important methodological issue that needs to be resolved before any deeper biological understanding can be gained.

Some reports of mixing are of the following form: a piglet in a crowded pen jumps forward and rotates in the air, striking another piglet on the flank, which leads to a brief tussle between them. Such a sequence has been interpreted as a bout of locomotor play merging into a bout of social play (e.g., Donaldson et al. 2002). That is, locomotor actions are intermixed with socially competitive actions. However, this interpretation may be premature. Consider a young gosling nibbling on grass in a pasture, walking with lowered head while doing so. Periodically, it raises its head and scans its surroundings, and if it has strayed too far from its parents, the gosling will orient and run towards a parent. During this run, the gosling may bump into a sibling, which leads to a brief tussle, before one or both run towards the parents again (Pellis and Pellis 2009). It would seem unlikely that, in such a case, the running and the social competition resulted from the same motivational substrate. Rather, the most parsimonious explanation would be that the social interaction was an incidental byproduct of one gosling accidentally bumping into another while running towards a parent. Similarly, in animals in close proximity,

it cannot be assumed that the running, jumping, and turning are motivated by the same processes that lead to playful competitive interactions when they make contact with a nearby conspecific. Simply scoring the locomotor movements and social actions independently of the context within which they arise can be misleading.

The latter point needs also to be considered when scoring behavior patterns associated with play and then concluding that because some of them occur in functional contexts associated with conspecific aggression and others with anti-predator behavior, sex, etc., that play involves mixing behavior from different functional contexts (Heymer 1977). For example, in grasshopper mice and ground squirrels, play fighting involves two types of competitive interactions – in the mice, they either compete to lick and groom their partner's shoulder area (as in precopulatory behavior) or to bite the nape of their neck (as in predatory behavior), and in ground squirrels, they either compete to mount one another (as in sex) or to bite their partner's shoulder (as in aggression). Individual play bouts last 2–3 s, but over a specific sample period, pairs can engage in dozens of playful interactions. Simply scoring the incidence of mounting, licking and grooming, and biting would suggest that these species mix elements from sexual and aggressive or from sexual and predatory behavior. However, detailed analysis of sequences shows that a play fight that began with a bite directed at the shoulder (squirrels) or to the nape (grasshopper mice) was not countered with counterattacks to lick/groom the shoulder or to mount. Rather, each sequence of attack and defense was appropriate for the target attacked, and only once that sequence was completed would a new sequence start that could involve an attack directed at the opposite target (Pellis and Pellis 2009). That is, at this finer grain time scale, sex and aggression or sex and predation were not mixed.

The conclusion to be drawn is that the apparent intermixing of behavioral elements from multiple functional behavioral systems may be an illusion, and that, in the moment-to-moment context of performing playful actions, behavioral elements

from different systems remain distinct. However, there are striking examples of mixing, such as the object-social play of Japanese macaques (Shimada 2012) that cannot be so dismissed. To reconcile such divergent findings, play must be considered with regard to phylogenetic history.

The Origins and Evolutionary Transformation of Play

Burghardt (2005) developed a model for the independent evolutionary origins and transformation of play across many different lineages of animals that may have important implications for our understanding of both the independence and the combining of types of play. The model asserts that, under certain conditions, such as readily available food, surplus energy, a relatively protected environment, prolonged juvenile development, and with sufficient neural resources to experience boredom, play-like behavior may emerge. This incipient or *primary process play* is the form of play that is most widespread in the animal kingdom, with locomotor, object, or social forms predominating in different lineages (Burghardt 2005). The behavior patterns performed in such play may not differ markedly from their appearance in functional contexts, but the usual functional consequences do not arise. It is possible that under particularly benevolent conditions, such play may be sustained even if it is neutral with regard to fitness benefits (Pellis et al. 2014). An avenue by which such primitive play may begin to gain a fitness advantage has been recently explored in a mathematical model. If the play, at least in its social guise, forces competitors to squander some of their developmental resources, then the cost of inducing that play can be an advantage to the initiator if its cost is smaller than that paid by the competitor (Auerbach et al. 2015).

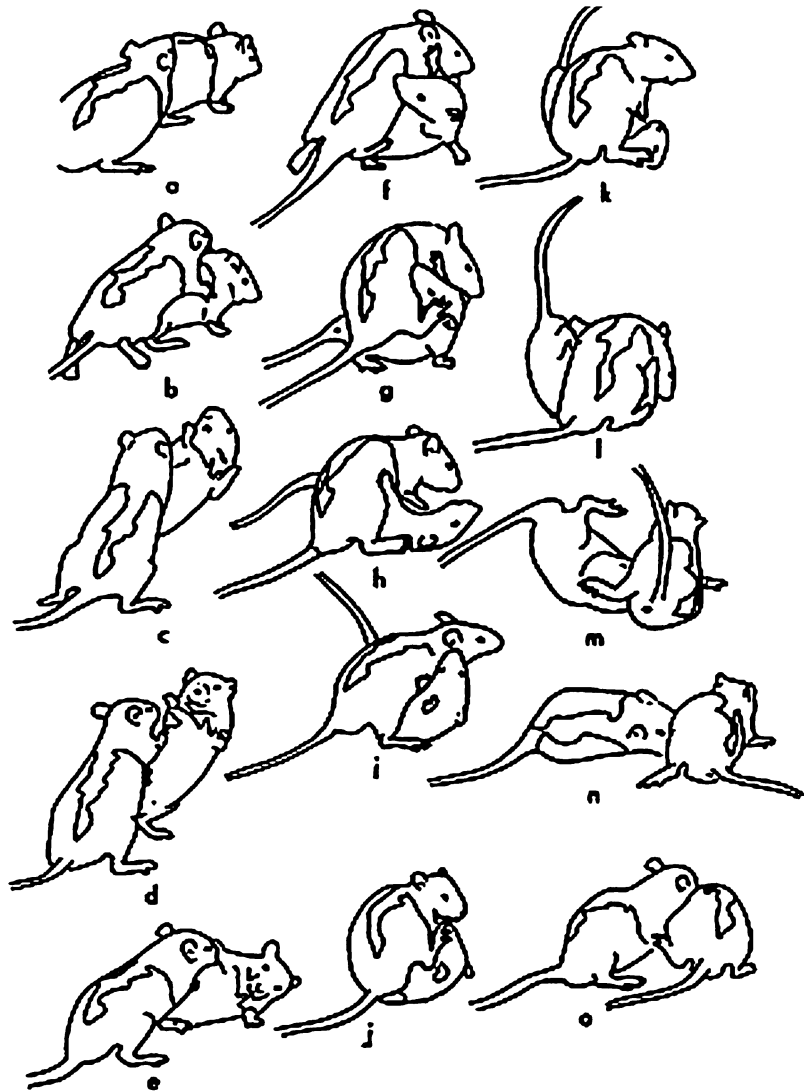
As noted in the transformational model, if conditions are favorable and primary process play provides players with a fitness enhancing advantage, then the features of the play that are most crucial to that advantage may be subjected to natural selection, so that the critical behavior

patterns are either increased in their frequency and/or modified in their form to serve that function better (Burghardt 2005; Pellis et al. 2014). In this way, the play can become even more playful as it is transformed into *secondary process play* and, more strikingly so, as it is further transformed into *tertiary process play*. It should be noted that, in a species with only primary process play, the five criteria in Burghardt's definition of play may only be met to a minimal degree, whereas in a species with secondary or tertiary play, many of the criteria may be fulfilled by a wide margin. This variation, in turn, may account for the marked variation in the complexity of play characterized when researchers contrast cases across a wide comparative range of lineages (Burghardt 2005; Fagen 1981; Pellis and Pellis 2009). The relative fitness gain characterized in the primary process play modeled by Auerbach et al. (2015) also suggests one of the necessary conditions that lead to further transformations of play.

Again, models suggest that once a potential benefit emerges that enhances fitness, play can quickly spread in a population (Durand and Schank 2015). With regard to social play, if playing provides fitness enhancement to one partner at the expense of another, one can imagine a situation arising in which there is a fitness advantage for mechanisms to evolve in competitors to offset that advantage. That is, a kind of arms race develops, with a momentary advantage gained by partners initiating play being neutralized by new actions by the recipients, leading to ever greater levels of complexity in the play performed (Pellis and Pellis 2016). The broad outline of such a transformational process has been characterized for the play of murid (i.e., mouse-like) rodents (Pellis and Pellis 2009; Pellis et al. 2014).

In murid rodents, social play in the form of play fighting involves attack and defense of body targets otherwise contacted during adult pre-copulatory behavior, and across species, this competition can differ markedly in its complexity. At the simplest levels, there are species that do not engage in any such play and some that attack but do not defend. At a more complex level, defense occurs, but that defense involves evading contact, not wrestling. The addition of tactics that promote

Play Behavior, Fig. 1 A sequence of play fighting is shown for a pair of juvenile rats. The rat on the left approaches another rat from the rear (a) and pounces towards its partner's nape (b). Before contact is made, the defender rotates around its longitudinal axis (c) to face its attacker (d), but the attacker continues to move forward pushing the defender onto its side (e). The defender then rolls over onto its back as its attacker stands over it, restraining the defender's movements while continuing to reach for its nape (f–h). The supine defender launches a counterattack to its partner's nape (i), which is blocked (j, k). With continued squirming by the supine partner, the rat on top (l) is pushed off by the supine defender (m). The original defender then stands up (n) and lunges towards its partner's nape (o). The sequence involves repeated attack and defense of the nape and role reversals to which partner attacks and which defends (Reprinted from Pellis and Pellis (1987) with permission)



the occurrence of playful wrestling makes play even more complex. Finally, high frequencies of counterattack lead to even more complex play fighting, as partners can reverse roles over the course of the encounter. For example, in Fig. 1, play fighting in a pair of juvenile rats is shown, in which attack, defense, and counterattack lead to a protracted interaction involving close-quarter bodily contact.

From a mechanistic perspective, the greater complexity in the form of the play is accompanied by changes in the neural mechanisms that regulate play (Pellis and Pellis 2009). In the case of murid

rodents, these changes in neural organization gradually lead to more and more differentiation from the sexual behavior being performed during play. Other than the precocial expression of emerging behavior patterns, there is little evidence that the simplest forms of play require novel mechanisms to sustain it. In contrast, more complex forms of play require changes to the regulatory mechanisms that produce sex-related behavior. The most complex forms require novel involvement of cortical systems (Pellis and Pellis 2016). From a functional perspective, there is little evidence for the fitness enhancing effects of the

simplest forms of play, but more complex ones appear to have detectable effects on the development of sexual performance and for the most complex ones, additional benefits for the development of more general cognitive and social skills (Pellis et al. 2014).

The transformation of play across lineages and the unique attributes afforded by different lineages begins to provide a solution to the conundrum of different forms of play having originated independently, but clearly, in some species, intermixed in novel ways. First, a lineage must have evolved more than one type of play to afford the opportunity of intermixing behavior from different types of play (Burghardt 2005). Second, the lineage in question must have the resources to combine these different elements effectively when the opportunity presents itself. For example, as noted above, the two most common and elaborate forms of play in rodents – social and locomotor play – are negatively correlated (Pellis and Pellis 2009). That is, increased complexity in one is coupled with a decreased complexity in the other, suggesting that there may be limited neural resources available to allow for the expansion of both types of play. It may, therefore, not be surprising to discover that some of the most convincing cases of intermixing are to be found in primates (e.g., Shimada 2012) – a lineage with a larger brain to body ratio than that in rodents (Eisenberg 1981).

As noted above, while insufficiently fine-scale temporal and contextual analyses may account for many of the presumed reports of intermixing during play, some cases may be true reflections of the composite play possible in some species (Palagi and Norscia 2016). The above transformational model offers a means by which to account for the species differences that may underlie some of this variation in being able to intermix behavioral elements from the different functional systems being mimicked during play. At least one of the crucial resources needed to make the transition from maintaining independent play systems to novel combinations of such systems is to have a sufficiently large brain. A potential way that such neural resources could make the difference is

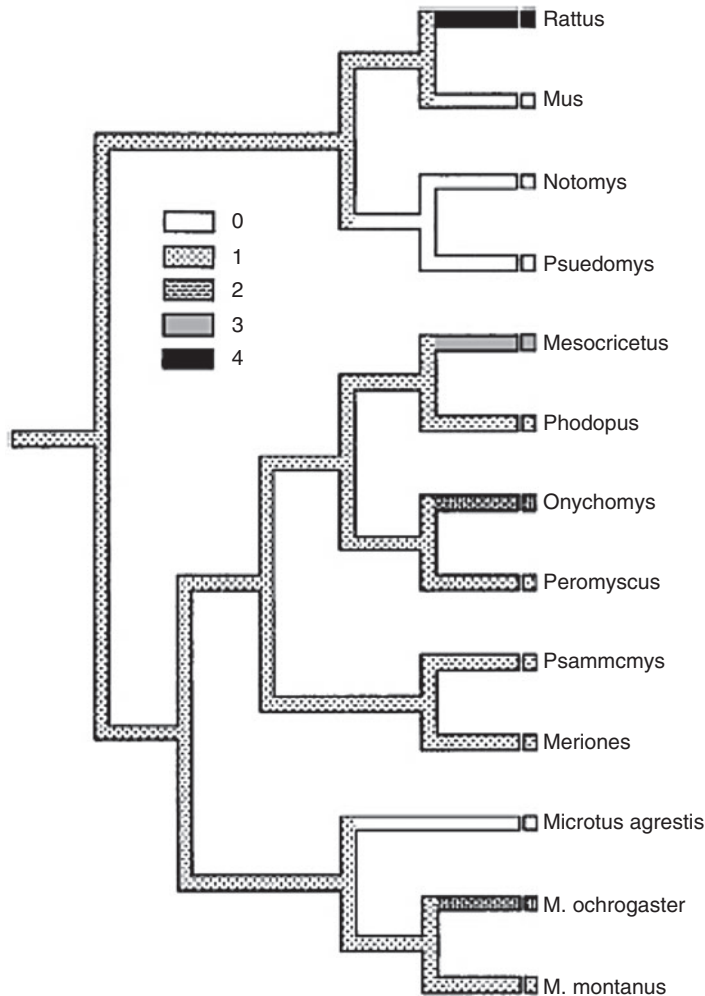
reflected in the brain-level changes needed to make social play more complex (Pellis and Pellis 2016).

The Playful Brain

In rats, play has been shown to engage a complex neural circuit of interconnected systems (Siviy 2016). Thus, there are hindbrain systems that generate the appropriate behavior patterns, midbrain systems that motivate and reward the execution of play, lower forebrain systems that regulate the emotions involved and upper forebrain systems that modulate the actions performed to ensure that they are contextually appropriate.

Intriguingly, rats that have had their cortex removed at birth exhibit normal levels of play in the juvenile period, with similar frequencies of attack, defense and counterattack, and exhibit similar levels of reciprocation in their play (Pellis and Pellis 2016). That is, neural circuits below the level of the cortex are sufficient to motivate and execute play and provide the reward necessary to sustain it. This is consistent with the likelihood that the changes needed to transform primary process play into secondary process play in rodents have involved alterations to subcortical circuits (Pellis and Pellis 2009). While not needed to produce or maintain play, cortical circuits, especially those of the prefrontal cortex, are critically involved in modifying the play executed to adapt it, contextually, to both the identity and the actions of the partner (Pellis and Pellis 2016). That is, transforming play from secondary process play to tertiary process play requires higher levels of neural control over the mechanisms regulating it, to make play more complex and adaptable to novel contexts.

Viewed from the knowledge gained thus far about the neural mechanisms involved in producing, maintaining and adaptively modifying social play in rats, a possible way for more complex play to evolve is for there to be more neural resources engaged, especially by adding more control from neural circuits higher up in the neural hierarchy. Comparatively, even among murid rodents, only



Play Behavior, Fig. 2 The evolution of complexity in play fighting is shown for several species of murid rodents. The species are mapped onto a cladogram, a tree-like diagram that shows the pattern of relatedness among the species, with those sharing a closer node being more closely related than to those from nodes further away. For example, *Rattus* and *Mus* are more closely related to one another than to *Notomys*, but they are both more closely related to *Notomys* than they are to *Mesocricetus*. The insert represents play complexity with the score of 0 indicating little or no play and a score of 4 indicating very complex play. The base of the tree shows that the ancestral state was one of moderate complexity. The species on the terminal branches independently either increased or

decreased the complexity of their play. Note that for most species, only the genus is shown, as only one species is represented for that genus. In the case of voles (*Microtus*), more than one species of the same genus are shown (*M. agrestis* = European vole; *M. ochrogaster* = prairie vole; *M. montanus* = montane vole). For the other genera, *Rattus* represents the Norway rat, *Mus* the house mouse, *Notomys* and *Psuedomys* represent two species of hopping mice, *Mesocricetus* represents the Syrian golden hamster, *Phodopus* the Djungarian hamster, *Onychomys* the Northern grasshopper mouse, *Peromyscus* the deer mouse, *Meriones* the Mongolian gerbil and *Psammomys* the fat sand jird (Reprinted from Whishaw et al. (2001) with permission)

some species have achieved the levels of complexity in social play present in rats, and these have emerged seemingly independently (Fig. 2). These findings lead to two considerations.

First, while some species of rodents do not play at all and many of those that do have relatively simple forms (Pellis and Pellis 2009), in some other lineages, especially primates, there is not a

Play Behavior, Table 1 The complexity and evolutionary transformations across different types of play can be mapped in a two-dimensional space, accommodating a wide range of species

Type/complexity ^a	Absent	Primary process	Secondary process	Tertiary process
Object		SH, NR, HM, MG		
Locomotor	SH ^b		MG	NR, HM
Social		HM	MG	SH, NR

^aPlay can be either absent, or, if present, can be of varying degrees of complexity using the framework from Burghardt (2005)

^bAbbreviations represent different species of murid rodents: *SH* Syrian golden hamster, *NR* Norway rat, *HM* house mouse, *MG* Mongolian gerbil. For sources on the primary data on the play of these species, see Pellis and Pellis (2009)

single species of which we are aware that does not play, with that play probably being at least as complex as that present in rats (Fagen 1981; Palagi and Norscia 2016). That is, lineages with more neural capacity available may be more likely to spawn species with complex play (Pellis and Pellis 2009). Second, the sporadic nature of evolving more complex patterns of play in rodents (Fig. 2) suggests that factors other than increased brain size, such as favorable energy budgets and social systems, may be needed to promote the further evolution of playful complexity (Burghardt 2005). These considerations have a direct impact on why some species may be able to intermix different behavioral elements in their play.

Lineages such as primates, which have, as a group, above average brain size (Eisenberg 1981), have the neural capacity to produce moderate to highly complex play of more than one kind. All species observed have been reported to exhibit complex social play (Fagen 1981; Palagi and Norscia 2016). In addition, some species are noted for their complex locomotor play (e.g., Nishida and Inaba 2009), and others for their complex object play (e.g., Nahallage et al. 2016). Thus, species with the neural resources to evolve complex play of different types, under the right conditions, may also have the incentive, and the requisite level of neural control over play, to be able to intermix behavioral elements from different types of play into novel combinations. If this model is correct, then the intermixing of behavioral elements in play is not as previously thought, a key characteristic of play (Heymer 1977), but rather, is an evolved feature that arises

in the play of particular lineages. At present, there are some major holes in our knowledge that do not make a full evaluation of this model, or any alternative models, possible.

The biggest problem is that the only species for which knowledge of the neural circuitry involved in play is reasonably well developed is for the laboratory rat. In rats, while some play involves locomotor play, the vast majority involves social play, in the form of play fighting (Pellis and Pellis 2009). Consequently, discussions focused on the ‘mammalian play circuit’ (Siviy 2016) are really about the social play circuit of rats. Knowledge of the neural underpinnings of locomotor play and object play is exceedingly sparse. What does seem likely is that all forms of play are likely to tap into the brain’s reward mechanisms, but such a connection is true for most motivated behavior (Berridge and Kringelbach 2013), and so, in itself, is not especially revealing about how different forms of play connect to one another at a neural level. Moreover, as a comparative overview of play reveals, what is labeled as play may have many different grades of complexity (Burghardt 2005; Pellis et al. 2014).

Therefore, if species as model systems are to be selected, they need to be selected within a matrix that compares species with only one type of play and those with multiple types of play in their repertoire on one axis, and the degree of transformation (primary process play, secondary process play, tertiary process play) on the other (Table 1). For example, of the four species of murid rodents entered in Table 1 for illustrative purposes, all have, at best, primary process play for object play, but a more diverse distribution for the other

two types of play. One has very complex social play (e.g., Syrian golden hamsters) and one has very complex locomotor play (e.g., house mice), and another has social play and locomotor play that are both of moderate complexity. Only in rats does locomotor play involve hops, jumps, rotations, and runs that match that of house mice in complexity (tertiary process play) and have prolonged wrestling in their social play (see Fig. 1) that matches Syrian golden hamsters in complexity (tertiary process play).

While it is unknown whether the neural components involved in social play in rats (Siviy 2016) are the same as those involved in locomotor and object play, there is some degree of confidence that at least the major components of the social play circuit characterized in rats may also be active in the social play of other lineages, such as primates (Graham 2017). For the other dimension, that of level of transformation, if the picture for social play derived from rodents is reflective of the processes involved in other lineages and other forms of play, then it would be predicted that as any type of play increases in complexity, the level of control by cortical circuits would also increase. Therefore, cases of true intermixing of types of play would be expected to be limited to those species that have achieved tertiary process play in two or more kinds of play. For example, in rats, in which both social and locomotor play are very complex (Table 1), hops and other locomotor movements seen in solitary locomotor play are incorporated into their social play, suggesting a degree of intermixing of different types of play that is not present when one or more of the types of play present are at a lower grade of organization (Pellis and Pellis 2009). Much comparative neuroscience remains to be done.

The Functions of Play

The comparative literature has traditionally been focused on identifying the functions of play (Martin and Caro 1985). Recent studies with free-living populations of several species have revealed that functionally beneficial outcomes of play are present in some species, but not all (Pellis

and Burghardt 2017). In part, these mixed results may arise because of the comparative diversity in both the kinds of play that predominate and the level of complexity that such play may have across the species used for such tests. For example, a common function proposed for play fighting is that it provides training for combat skills (e.g., Fagen 1981). However, play fighting involving competition for an advantageous position typical of sex, as seen in rats or squirrels, may be a poor avenue for training combat skills (Pellis and Pellis 2009).

Furthermore, for play fighting to remain playful, the partners need to curtail their combat to some degree to allow for whatever minimum level of reciprocity is required for the species in question and this may attenuate the fitness benefits derived from the practice afforded. The level of reciprocity varies with species, with age, sex, and dominance relationships, but play cannot be sustained if contests are completely one-sided – in situations in which one individual attempts to dominate the play completely, its partner will refrain from playing further with that individual. Adhering to a mutually agreed level of reciprocity is needed to make play fighting “fair” and so induce the players to keep playing together (Palagi et al. 2016). Different lineages have evolved different rules for ensuring reciprocal exchanges during play fighting. In some, the combat actions themselves are executed in a restrained manner, whereas in others, the restraint is interjected once a combat tactic is used to gain the upper hand. Unlike the former species, in the latter ones, the combat tactics are executed in a way that is seemingly identical to how they are used in serious fighting (Pellis and Pellis 2009). For such species, play fighting may provide an avenue for training combat skills.

These examples illustrate that species differences in how particular kinds of play are performed can greatly influence the development of particular skills. In the above case, a researcher selecting one species may find that there is a strong correlation between juvenile play fighting and adult fighting skills, whereas another researcher using a different species may find a weak or absent correlation. The situation becomes

even more complicated when both type of play and species differ. For example, during the juvenile period, the predominantly social play of rats is executed in such a manner that they experience many instances in which they lose and then regain control over their own bodies and over the movements of their partners (Pellis and Pellis 2009). The executive functions of the prefrontal cortex, such as those involving attention, short-term memory, emotional regulation, and decision making, are improved if rats engage in play with peers as juveniles (Pellis et al. 2014; Vanderschuren and Trezza 2014). That is, the play of rats has the effect of training them to be more resilient (Pellis and Pellis 2009). In contrast, in the house mouse, those individuals that play more appear to be less resilient as adults than those that play less (Richter et al. 2016). But there are two major differences to be considered: first, mice and rats may differ in the complexity of their neural control mechanisms, and second, in mice, unlike rats, the predominant form of play is locomotor play (Pellis and Pellis 2009). That is, the difference between the two species in the relationship between play and resiliency does not negate one another, as different forms of play may differ in their beneficial influences on development. Thus, while locomotor play may improve motor skills in some species, that species may not have the resources to improve executive functions with such play.

Another dimension to consider about the functions of play is whether the play has immediate or delayed benefits. In most examples for which benefits have been demonstrated, it has been for play in the juvenile period having beneficial consequences later in life, but in some cases, play appears to increase survival at that age in which it is performed (Pellis and Burghardt 2017). As already noted, the play of an adult with another adult likely only serves immediate benefits, not delayed ones (Palagi 2011; Pellis and Pellis 2009). It is this complex blend of the types of play present, the complexity of the play, the species involved, and the age of the players, which makes any test of a functional hypothesis likely to fail. Selecting the most appropriate species for the functional hypothesis to be tested may require consulting a matrix like that in Table 1, in which

species with particular types of play and play complexity can be identified. As for understanding the neurobehavioral mechanism of play, much more comparative work needs to be done before functions widely associated with play and those idiosyncratic to particular forms of play in particular species can be identified.

Conclusions

Even a casual reading of the above review will quickly reveal a major element that is missing in the story – most of the examples, and all those involving detailed analyses of behavioral content, neurobiology, and functional consequences involve mammals. What about all the other species and lineages that have been reported to meet the five point criteria in Burghardt's definition of play? Where do nonmammalian vertebrates fit in, much less the myriad invertebrates that play? We have deliberately focused our review on mammals to show that even within the taxon that has been most intensively studied with regard to play, there are some major gaps in our knowledge. By understanding the problems that need to be resolved so as to have a comprehensive theory of the mechanisms and functions of play in mammals, the difficulties in integrating a broader swathe of species from diverse lineages can be placed in context. Some studies of birds suggest that some of the same considerations outlined above also apply to this lineage. For example, increased brain size in birds increases the likelihood of play, but likely does so as it may in mammals, by lengthening the juvenile period and thus increasing the opportunity to play. Similarly, the complexity of social play can vary in birds in ways similar to that outlined above for mammals (Pellis and Pellis 2009). Further afield, only sporadic examples are available for reptiles, fish, and other non-mammalian/nonavian vertebrates (Burghardt 2005). The breadth of species becomes even more impoverished as examples are sought among invertebrates (Burghardt 2005; Pellis and Burghardt 2017). At present, the lack of breadth in the literature on the distribution of types and complexity of play makes the development of a

comprehensive theory that encompasses the whole animal kingdom highly elusive.

For example, in mammals, play is predominantly a phenomenon of the juvenile period (Fagen 1981), with some forms of play being retained in adults in some species (Palagi 2011; Nahallage et al. 2016). This requires an emphasis on the kinds of factors that have promoted play to emerge in the juvenile period of some species but not others (Burghardt 2005), and an understanding of the factors that have led to play in some of these species being retained in adulthood (Pellis and Pellis 2009). However, several species of cephalopods have been identified to engage in play with objects (Burghardt 2005), but all these octopuses are adults. To our knowledge, no one has reported play in the young of these species. This is perhaps understandable in that most of these species have planktonic young, thus being much smaller and of a different body shape to the adults, so likely do not have the neural wherewithal, the body morphology or the favorable ecological conditions that make play possible. Thus, in contrast to mammals, in cephalopods, play is a phenomenon of adulthood. Such contrasting aspects of behavioral phenomena that meet the conditions set by Burghardt's five criteria have to be taken seriously in developing general theories of play. Clearly, a first step in such an endeavor is to describe the types and complexity of play across a wider range of species from across many different taxa.

Cross-References

- ▶ Behavioral Variation
- ▶ Cladistic Analysis
- ▶ Heritability of Behavior
- ▶ Homoplasy
- ▶ Sociosexual Behavior

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