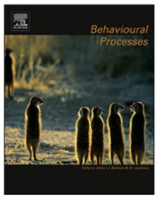
Behavioural Processes 160 (2019) 1–9

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Is play a behavior system, and, if so, what kind?

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ARTICLE INFO

Keywords:
Social play
Object play
Locomotor-rotational play
Behavior systems
Mechanisms
Functions
Evolutionary history

ABSTRACT

Given that many behavior patterns cluster together in sequences that are organized to solve specific problems (e.g., foraging), a fruitful perspective within which to study behaviors is as distinct 'behavior systems'. Unlike many behavior systems that are widespread (e.g., anti-predator behavior, foraging, reproduction), behavior that can be relegated as playful is diverse, involving behavior patterns that are typically present in other behavior systems, sporadic in its phylogenetic distribution and relatively rare, suggesting that play is not a distinct behavior system. Yet the most striking and complex forms of play have the organizational integrity that suggests that it is a behavior system. One model that we develop in this paper, involves three stages of evolutionary transition to account for how the former can evolve into the latter. First, play-like behavior emerges from the incomplete development of other, functional behavior systems in some lineages. Second, in some of those lineages, the behavior patterns typical of particular behavior systems (e.g., foraging) are reorganized, leading to the evolution of specific 'play behavior systems'. Third, some lineages that have independently evolved more than one such play behavior system, coalesce these into a 'super system', allowing some animals to combine behavior patterns from different behavior systems during play. Alternative models are considered, but irrespective of the model, the overall message from this paper is that the conceptual framework of the behavior system approach can provide some new insights into the organization and diversity of play present in the animal kingdom.

1. Introduction

A common framework for investigating and understanding how animals construct coherent functional sequences of movements has been to view behavior patterns as atomized components that can be combined and recombined in multiple ways to serve particular task demands (e.g., Flash and Hochner, 2005; Kolb and Whishaw, 2015; Skinner, 1938). An alternative has been to view behavior patterns, not as discrete components, but as constituents of 'behavior systems', defined as structurally and/or functionally coherent packages of causally related and hierarchically coordinated behavior patterns, the expression, organization and coordination of which may be controlled by highly specific environmental stimuli, sensorimotor processes and motivational mechanisms (Baerends, 1976; Tinbergen, 1951). Several lines of research support the explanatory and predictive value of the behavior systems conceptualization of behavioral organization. For example, rats deprived of food or water, were presented with a rolling ball bearing, which predicted either food or water. When the ball bearing predicted food, it was treated as a prey object. This was not the case when it predicted water. That is, a moving stimulus activated predatory behavior in hungry rats, but not in thirsty rats (Timberlake, 1983). Using the same test paradigm with several species of rodents showed that the ability of the ball bearing to activate functional sequences of predatory behavior differed with the degree of carnivory among the species (Timberlake and Washburne, 1989). Such findings suggest that particular stimuli do not simply elicit particular behavioral actions, but rather, depending on the context, the stimuli activate particular types of functionally coherent sequences of behavior: in this case, those related to predation.

In some cases, such behavioral findings are confirmed by physiological analyses. For example, as the imminence of a threat by a ground predator increases, chickens progress through a sequence of anti-predator behavior. The same sequence of behaviors can be activated in the same order of appearance by electrically stimulating particular brain circuits, independently of the presence of a predator (von Holst, 1973). That is, the sequence of actions is bound together in a connected system – a behavior system - in this case, geared for anti-predator defense. In other cases, what may be activated are coherent sequences of mating, aggression, nest building and so on (e.g., Adams, 1980; Kortland, 1955; Pfaff, 1999).

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https://doi.org/10.1016/j.beproc.2018.12.011
Received 14 August 2018; Received in revised form 10 December 2018; Accepted 13 December 2018
Available online 14 January 2019

There are different research traditions in studying behavior from a behavior systems perspective; some have focused on the functional connections between the behavior patterns involved (Timberlake, 1994, 2001), some on the causal relationships among the constituent components (Hogan, 1988, 2001), and some on the underlying neural mechanisms (Panksepp, 1998; Teitelbaum, 1982). But irrespective of these differences in research traditions, there is a common underlying framework: "That behavior is organized in functional motivational systems lies at the core of the set of ideas constituting the behavior systems perspective" (Burghardt and Bowers, 2017, p.3 42).

In the present paper, we examine whether the available evidence supports conceiving of play behavior as a 'play behavior system.' Considering that play activity contains behavior patterns that appear to be similar to those observed in other functional behavioral contexts, such as predation, fighting, and sex (e.g., Heymer, 1977; Meyer-Holzapfel, 1956; Millar, 1981), play could be considered a simulation of these behavior systems (Pellis and Burghardt, 2017). However, as stated by Burghardt (2006, p. 182): "…whether play…is a separate instinct (or behavior system) or is derived from other systems (such as predatory or fighting), is still an open issue in many species." Despite decades of research, too little is known about the connections between the various forms of play and the differences across the diverse lineages of animals that play (Burghardt, 2005) to evaluate the question at hand from the perspective of any one of the different behavior systems frameworks. Consequently, we pursue a more limited goal, that of whether a generic concept drawn from the behavior systems perspective – that is, that there are few independent behavior patterns and few stand-alone actions (Bowers, 2017) - can be used to answer some of the many puzzles associated with this enigmatic behavior.

2. What defines play and what do animals do when playing?

Burghardt (2005) combined the various features that have been used in previous attempts to characterize play (e.g., Bekoff and Byers, 1981; Fagen, 1981) into a definition of play involving five criteria, so that for a given behavioral sequence to be classified as play, it must satisfy all five criteria. The criteria are: (1) that the behavior is incompletely functional in the context expressed, (2) that it is voluntary or rewarding, (3) that it is, in some ways, modified developmentally or structurally compared with when it is used in its normal, functional context, (4) that it is performed repeatedly, but not necessarily in an invariant form, and (5) that it is initiated in healthy, relatively unstressed animals in a relaxed context. Central to these criteria is that they characterize play by when and how behavior patterns are performed.

Three major forms of play are generally recognized (Burghardt, 1998, 2005): (1) Locomotor play: involves a lone animal engaging in runs, jumps, kicks, whole body rotations, body shakes and sharp turns - behavior patterns that are often associated with anti-predator behavior (e.g., Byers, 1984; Martin and Bateson, 1985; Wilson and Kleiman, 1974); (2) object play: involves a lone animal engaging in carrying, flinging, ripping or otherwise manipulating an inanimate object - behavior patterns that are often associated with predation and foraging (e.g., Gamble and Cristol, 2002; Negro et al., 1996; O'Hara and Auersperg, 2017; Pellis, 1981a); and (3) social play: involves two or more conspecifics wrestling, chasing or otherwise contacting one another - behavior patterns often associated with allogrooming, mating, conspecific aggression and maternal care (e.g., Aldis, 1975; Lancaster, 1971; Pellis and Pellis, 2017a). There are some compelling cases of animals combining two or more of these forms of play. For example, during object play, animals may use a variety of locomotor movements (Burghardt et al., 2016), and during social play, animals may compete for an object (Shimada, 2012) or incorporate locomotor-rotational movements (Donaldson et al., 2002). In some primate species, object-assisted eye-covering play contains behavior patterns typically found in all three types of play, and might have cognitive implications for pretense (Palagi, 2018; Russon and Vasey, 2012).

Combining different types of play, as illustrated by the above examples, is consistent with a commonly held view of play, which is that during play animals mix together behavior patterns from a number of different behavior systems (Heymer, 1977; Meyer-Holzapfel, 1956; Millar, 1981). While in some species a few of the behavior patterns used may be unique to play (see Petrů et al., 2009), most are not (Burghardt, 2005; Fagen, 1981). Co-opting behavior patterns from diverse behavior systems would require the ability to disconnect specific behavior patterns from the coherent sequences of behavior patterns embedded in conspecific aggression, predation, mating and so on. Thus, engaging in play would not have the functional coherence typically associated with behavior systems (Bower, 2017). Rather, play may be more consistent with atomistic views of behavior (see above), whereby animals are able to combine and recombine a variety of independent behavior patterns. The fragmentary way that some aspects of behavior emerge during the development of play (Graham and Burghardt, 2010) may be consistent with this view.

3. Is play an illusory behavioral category created by immaturity?

Play is most often associated with juvenile animals (Bekoff and Byers, 1981), a period defined as occurring between weaning and sexual maturity (Pagel and Harvey, 1993). During the juvenile period, many behavior systems that are essential in infancy gradually disappear and many that are useful in adulthood gradually emerge (Coppinger and Smith, 1989). It is in this transitional age that those sequences of behavior most likely to be labeled play occur (Fagen, 1981). In species that can play in multiple ways, the different types of play wax and wane at different ages, and phases of their maturation may overlap (e.g., Barrett and Bateson, 1978; Gomendio, 1988; Pellis, 1981a).

At some stages of the development of behavior systems, the constituent motor patterns may not only emerge in a piecemeal manner, but also compared to their adult form, they may be incomplete, modified and/or misdirected (e.g., Eilam and Golani, 1988; Golani and Fentress, 1985; Groothuis, 1993; Vestergaard et al., 1990). In addition, with multiple systems overlapping in their development, behavior patterns from more than one system can occur concurrently. For example, righting from supine to prone on the ground involves several, independent behavior systems that depend on different sensory triggers, such as vestibular and several forms of tactile input (Magnus, 1926). During development, there is a serial order in the emergence of these righting behavior systems, but there is also overlap. For instance, when body tactile righting first emerges in infant rats, two distinct forms overlap in their development. When the rats are turned over onto their backs, tactile stimulation on the upper body triggers righting movements by the forelimbs and tactile stimulation of the hindquarters triggers righting movements by the hind limbs. As both are triggered simultaneously, the combined movements by the fore and hind limbs may interfere with one another delaying successful righting (Pellis et al., 1991). In the fully mature state, the forequarter righting system is dominant over the hindquarter righting system, so that the latter is only triggered if the former is prevented (Magnus, 1926). Based on these developmental considerations, immaturity may account for both the modified execution of particular actions and the mixing of behavior patterns from multiple behavior systems in what may be labeled as play. Indeed, the modified performance of behavior patterns evident in play may simply reflect immaturity of an animal's sensorimotor system (Fentress, 1983).

From this developmental perspective, play may not be a distinct form of behavior at all, but rather, what appears as 'play' may be a byproduct of the maturation of behavior systems and their possible interactions. Indeed, with regard to play fighting, one of the most commonly studied forms of play (Pellis and Pellis, 1998), several authors have argued that play fighting is simply the immature expression of aggression (e.g., Cervantes et al., 2007; Hurst et al., 1996; Lazar and

Fig. 1. Photographs depict the three phases of pounding in an adult long-tailed macaque as it attempts to crack open a nut. In the first frame (left), the monkey positions its hand on the ground before lifting its arm prior to the strike (upswing). Then, in the second frame (middle), the monkey repositions its hand and body immediately prior to the strike (adjustment) and in the final frame (right), it strikes the nut onto the ground (downswing). In both adults and juveniles, the same basic organization is also involved when pounding stones. (Photographs are extracted from a video sequence). (Reprinted from Pelletier, 2017).

Beckhorn, 1974; Taylor, 1980). However, for some species, the developmental sequence does not fit this hypothesis of 'play as immaturity'.

In some mammalian species with litters of multiple young, the newborns may actively engage in aggression to access preferred nipples (Skok and Škorjanc, 2014). That is, aggression precedes the onset of play, which in all such species becomes most prevalent around weaning. In some cases, the stakes can be very high indeed. In spotted hyenas, the mother digs a den in which she deposits the newborns, with the young being able to move to the entrance to access her nipples. However, the mother is too large to get into the den. The young agonistically compete for priority access to the available nipples, and the fighting can be fatal (Frank et al., 1991; Smale et al., 1995). Thus, for this species, not only does serious fighting precede the onset of playful fighting, but also the serious fighting is sufficiently well developed on first appearance as to be wielded as a lethal weapon (Drea et al., 1996). In such a case, claiming that playful fighting represents an immature phase of the development of aggression makes little sense.

Also counter to the 'play as immaturity' hypothesis is that, in many species, play fighting can continue in adulthood (Pellis and Iwaniuk, 2000), and, when it does, while there may be some age differences in performance, the play fighting is recognizably play (e.g., Bauer and Smuts, 2007; Ciani et al., 2012; Cordoni, 2009; Palagi, 2006; Pellis and Pellis, 1992). However, for some behavior systems in some species, insufficient activation of the behavior system in adults can lead to incomplete or misdirected behavioral sequences (Kortland, 1955). For example, as the mating season approaches, geese may exhibit incomplete sequences of courtship, but even though early in the season courtship does not lead to mating, the constituent behavior patterns are executed in their fully competent adult form (Pellis, 1982). Comparisons of how the same behavior patterns are executed by juveniles and by adults during play are needed to determine whether there is a playful form of execution.

In some species of monkeys, such as Japanese macaques, both juveniles and adults engage in extensive play with objects, especially stones. To highlight a few of the behavior patterns involved, these stones can be carried, gathered into piles, shaken, pounded onto substrates, struck and rubbed together (Huffman, 1984; Leca et al., 2007; Nahallage and Huffman, 2007a). A detailed evaluation of such stone-directed play behavior in long-tailed macaques indicates that all of the 36 behavior patterns involved belong to the foraging behavior system. Moreover, a comparison across three species of macaques revealed differing numbers of stone play behavior patterns, with the differences matching species differences in the complexity of their foraging behavior (Pelletier et al., 2017). Among some predatory animals, play with objects or prey is associated with the activation of a foraging behavior system, such as when they are hungry and food is not available or when food (prey) is available, but the animals are inhibited from killing and eating the prey (Biben, 1979; Hall, 1998; Pellis, 1991; Pellis et al., 1988). Such misdirected behavior patterns associated with predation may be mistakenly characterized as play. However, unlike the case for immature animals, given the sensorimotor competence of adults, their misdirected play should not exhibit the inefficient execution of the behavior patterns that comprise some of the key criteria in Burghardt's definition of play.

Long-tailed macaques use a pounding action to strike hard-shelled nuts onto the ground, which, with sufficient repetition, can lead to the shell cracking. The monkey is then able to extract the nut and eat it. Similar pounding is used with comparable sized stones during object play. Both juveniles and adults pound stones, but only adult males are able to crack the nuts successfully. If juvenile-typical play involves executing actions in an immature manner, then the kinematics of stone pounding should differ from that seen in the adults. Similarly, if stone handling is misdirected foraging behavior in adults, then pounding stones should be structurally similar to pounding nuts. Sequences of pounding nuts in which the flesh of the nut was extracted and eaten by adults were compared to sequences when adults pounded comparable sized stones. Unlike the nuts that are eaten, the stones that are pounded are neither eaten nor chewed. Sequences of stone pounding by juvenile monkeys were also analyzed and compared to both the stone pounding and the nut pounding by the adults (Pelletier, 2017).

The pounding performed by adults and by juveniles of stones and nuts have the same, basic, three-part sequence. From a seated position, the monkey raises the stone (upswing), and modifies its body and hand position to orient the object toward the location of the strike (adjustment). Finally, there is the pounding action itself, in which the monkey strikes the object on the ground (downswing) (Fig. 1). Measuring a variety of parameters of the actions associated with each phase reveals that adults pounding a food item (i.e., nut) differ significantly on most parameters compared to when the pounding involves a non-food item (i.e., stone). This suggests that motorically competent animals modify their movements when using the same pounding action during play relative to how the same actions are executed during foraging. Moreover, stone pounding by juveniles - who are unable to crack nuts - resembles adult stone pounding (Table 1), suggesting that the play mode of executing actions in juveniles is not simply a byproduct of immaturity (Fentress, 1983), but rather, is a pattern of execution unique to play. There are some differences between adults and juveniles, indicating that the juveniles are in the process of improving their sensorimotor skills, but immaturity does not account for the commonalities in the pounding of stones by juveniles and adults. The playful execution of these behavior patterns is play-typical, not a byproduct of immaturity.

That play is not simply an immature version of a developing behavior system such as aggression, is further supported by findings showing that the opportunity to engage in play fighting is highly rewarding. Young rats will learn to take the correct turn in a T-maze so as to gain access to a peer (Humphreys and Einon, 1981) and will move to an enclosure, in a conditioned place preference task, in which the animal has had experience in playing with a partner (Trezza et al., 2009). In both of these cases, if the target partner is rendered less playful by the administration of a drug, the effect on the choice of arm or enclosure to enter is muted. This suggests that playing is more rewarding than simply seeking non-playful social contact. This last point is further emphasized by studies with juvenile chimpanzees (Mason et al., 1963).

Table 1
Various behavioral parameters involved in pounding a nut or a stone by Long-tailed macaques are shown. Two pairs of groups are compared. First, similarities and differences in nut and stone pounding are shown for adult males, and second, similarities and differences in stone pounding are shown for adult males and juveniles.

Behavioral elements	Adults (nut pounding (NP) versus stone pounding (SP))	Stone play (adults (A) versus juveniles (J))
Speed of upswing	Measure: **NP** > **SP*** Variability: **NP** < **SP****	Measure: **A** = **J**[a] Variability: **A** > **J**[b]
Speed of downswing	Measure: **NP** > **SP** Variability: **NP** < **SP**	Measure: **A** = **J** Variability: **A** > **J**
Object height above ground	Measure: **NP** > **SP** Variability: **NP** < **SP**	Measure: **A** = **J** Variability: **A** = **J**
Hand-to-head distance at apex of upswing	Measure: **NP** < **SP** Variability: **NP** < **SP**	Measure: **A** > **J** Variability: **A** = **J**
Torso orientation towards location of object strike	Measure: **NP** = **SP** Variability: **NP** = **SP**	Measure: **A** > **J** Variability: **A** < **J**
Gaze directed at location of strike area	Measure: **NP** > **SP** Variability: **NP** < **SP**	Measure: **A** = **J** Variability: **A** = **J**

[a] The mean difference in the actual measure between the two groups are compared.

[b] The variance in the performance is compared between the two groups.

The animals were trained to press levers to access either preferred food or a social partner and for the latter, the access could be limited to touching and being in close proximity or to permit full playful engagement. Engagement in play was chosen more often than simple social contact, and the opportunity to play could also trump access to food, even when the animals were hungry. These studies, along with a host of others involving manipulation of the brain reward mechanisms, strongly support the view that animals not only find play rewarding, but will, in some circumstances, trade off opportunities for other motivationally salient activities, such as feeding, to engage in play (Vandershuren, 2010).

Given that immaturity cannot by itself explain what animals do during play and that play has a strong rewarding value for many animals, the conclusion that play constitutes its own behavior system (e.g., Panksepp, 1998; Panksepp and Biven, 2012; Siviy and Panksepp, 2011) begins to look compelling. However, there are some limitations to this view. First, the play, in all the examples discussed thus far, is what most people think of as play – calves frolicking, kittens wrestling and dogs engaging in a tug-of-war over a stick. These forms of play not only meet Burghardt's five criteria, but also do so by a wide margin. What about species that do not play or ones that play but only barely meet the five criteria? Second, if play can be conceived as a behavior system, what kind of system would it be? It could be a 'super-play system' - one that can co-opt and mix behavior patterns from many other behavior systems. However, given that there are only a few documented cases of such mixing, it is also possible that there are multiple, independent 'play behavior systems', with only some species having the capacity to combine some of these systems.

4. Placing play in its phylogenetic context

Of the 30 or so phyla in the animal kingdom, only three have so far been shown to contain species that play (i.e., meet the five criteria), and within those phyla, not all lineages therein have playful species (Burghardt, 2005). Even in the most playful phylum, Chordata, play is not universal. First, it has only been reported in the subphylum, Vertebrata, and, within that subphylum, it is sporadic across most classes, only being prevalent in birds and especially in mammals. And even within mammals, there are orders that do not play. Further, within some playful orders, there are species that do not play. Since 2005, although the application of the five criteria-based definition of play has added more species from diverse taxa to the playful side of the ledger, the general picture has not changed (Pellis and Burghardt, 2017; Pellis et al., 2015).

Closer inspection of the type of play exhibited shows that 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 (Fagen, 1981). However, a comparative analysis of social play and locomotor play in murid rodents reveals a negative correlation (Pellis and Iwaniuk, 2004), so that an increase in the complexity of one type of play is accompanied by a decrease in the complexity of the other. Further, even within a species, these forms of play can vary independently of one another across different, genetically selected strains (Schneider et al., 2016). Finally, studies 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; Melotti et al., 2014).

These phylogenetic considerations suggest that play evolved multiple times in the animal kingdom, with different types of play evolving independently of one another, although a few species that have more than one type of play in their repertoire show evidence that they can mix those types in novel ways (e.g., Burghardt et al., 2016; Shimada, 2012). It is in the context of this patchy distribution of play and its various forms, that the questions related as to whether play constitutes a behavior system needs to be considered. For example, what the phylogeny shows is that mixing behavior patterns from multiple behavior systems is not a universal defining feature of play, and indeed, may be the exception (Pellis and Pellis, 2017b) rather than the rule (Norscia and Palagi, 2016). This would suggest that there are least two levels in the evolution of a 'play behavior system'. First, following the evolution of some type of play in a lineage, the behavior patterns associated with that play are gradually transformed into an organization that has the functional coherence typical of behavior systems. Second, some lineages with more than one type of play are able to evolve mechanisms that can combine those different types of play into a super-play behavior system.

5. An evolutionary transformation model

Burghardt (2005) developed a model for the independent evolutionary origins and transformation of play across different lineages of animals. This model asserts that, under certain conditions, such as readily available food, surplus energy, a relatively protected environment, prolonged juvenile period and with sufficient neural resources to experience boredom, playful 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 differ little, if at all, from how they appear in their normally occurring functional contexts, but the usual functional consequences of their performance do not arise. It is possible that, under particularly benevolent conditions, such play may be maintained in the population even if it is neutral with regard to fitness benefits (Auerbach et al., 2015).

If conditions are favorable and primary process play provides players with fitness-enhancing advantages by facilitating the performance of the behavior patterns derived from particular behavior systems, then the play is transformed into *secondary process* play. This transformation involves the features of play that are most crucial to those benefits being subjected to natural selection, so that the critical behavior patterns either increase in their frequency and/or are modified in their form to serve that function better. Such transformation not only involves the play becoming more distinctly playful, but also requires the evolution of novel, control mechanisms that are capable of modifying the expression of the behavior patterns from the behavior

system being simulated (Burghardt, 2005; Pellis et al., 2015).

Again, when ecological, developmental, life history and psychological factors permit, secondary process play may be further transformed into *tertiary process* play. Functionally, the benefits of tertiary process play may extend beyond feedback on the behavior system being simulated, so that the benefits gained from performing behavior patterns derived from a particular behavior system can lead to improved motor, social and cognitive skills that can be deployed in a variety of situations and across different behavior systems. To achieve such a functional transformation requires further modifications as to how behavior patterns are expressed during play and this requires the further evolution of novel control mechanisms that make the play even less like the behavior system being simulated (Burghardt, 2005; Pellis et al., 2015). A broad outline of such a transformational process has been characterized empirically for the social play present in the juveniles from sixteen species of murid (i.e., mouse-like) rodents (Pellis and Iwaniuk, 2004; Pellis and Pellis, 1998, 2009; Pellis et al., 2014).

In murid rodents, social play in the form of play fighting primarily involves attack and defense of body targets otherwise contacted during adult precopulatory behavior, and, across species, this competition can differ markedly in its complexity (Pellis and Pellis, 2009). In the simplest forms of such play, one animal may attack the play target of its partner and the partner either does not defend itself, or if it does defend itself, limits that defense to evading contact, thus withdrawing from the attacker (equivalent to primary process play). At a more complex level, not only does defense occur relatively frequently, but in this case, many instances of defense involve the use of tactics that promote the occurrence of playful wrestling (equivalent to secondary process play). Even greater levels of complexity are achieved by the participants increasing the frequency of launching counterattacks and adopting maneuvers that facilitate role reversals between the partners, so leading to prolonged and repetitive play fighting (equivalent to tertiary process play). An example of this highly complex form of play fighting is shown in Fig. 2 for a pair of juvenile rats (for diagrams illustrating the simpler versions of such play, see Pellis and Pellis, 2009).

From a mechanistic perspective, changes in the complexity of the form of play in murid rodents appear to be accompanied by changes in the neural mechanisms that regulate play (Pellis and Iwaniuk, 2004). The decreasing resemblance between what is performed during play and during adult sexual behavior with increasing complexity of play is likely underpinned by changes in such neural control mechanisms. The subcortical brain changes associated with changes in complexity remain to be characterized (Pellis and Iwaniuk, 2004; Siviy, 2016), but what has become clear is that the most complex forms of play engage cortical brain mechanisms (Pellis and Pellis, 2016). From a functional perspective, there is little evidence for the fitness enhancing effects of the simplest forms of play. The most complex forms of play affect not only adult sexual performance, but also cognitive skills useful in non-social and social contexts.

Studies with rats have been particularly useful in showing empirically these diverse effects of play experience. Compared to adult rats that have been deprived of experiencing juvenile-typical experience of play with peers, ones having had such play experience exhibit improved sexual performance (Moore, 1985), are better able to navigate mazes successfully (Einon et al., 1981), have greater impulse control (Baarendse et al., 2013), better social memory (Schneider et al., 2016) and have greater ability to coordinate their movements with a social partner (Pellis et al., 1999). The transformative nature of play across lineages and the unique phylogenetic histories of different lineages suggest a model for the origin of ‘play behavior systems’.

As in the murid rodent model showing the transformation of social play from primary to tertiary process play (Pellis and Pellis, 2009) other forms of play may exhibit similar patterns of transformation within lineages. Unfortunately, neither object nor locomotor play has had comparable detailed studies within specific lineages. Nonetheless, comparisons across wider swathes of species from different lineages suggest similar patterns. For example, as noted earlier, locomotor play frequently involves behavior patterns otherwise seen in anti-predator behavior. Within-lineage comparisons show that the complexity with which these behavior patterns can be executed and combined can vary (Pellis and Iwaniuk, 2004). However, in some species, locomotor play can involve behavior patterns that are not present in anti-predator behavior, such as running or climbing with the eyes closed, as is done by some monkeys and apes (Kavanagh, 1978; Palagi, 2018; Russon and Vasey, 2012), or the playful pirouettes of chimpanzees (Nishida and Inaba, 2009). These latter examples seem consistent with the behavior being tertiary process play in which the actions have become divorced from the underlying functional system from which they may have originally been derived.

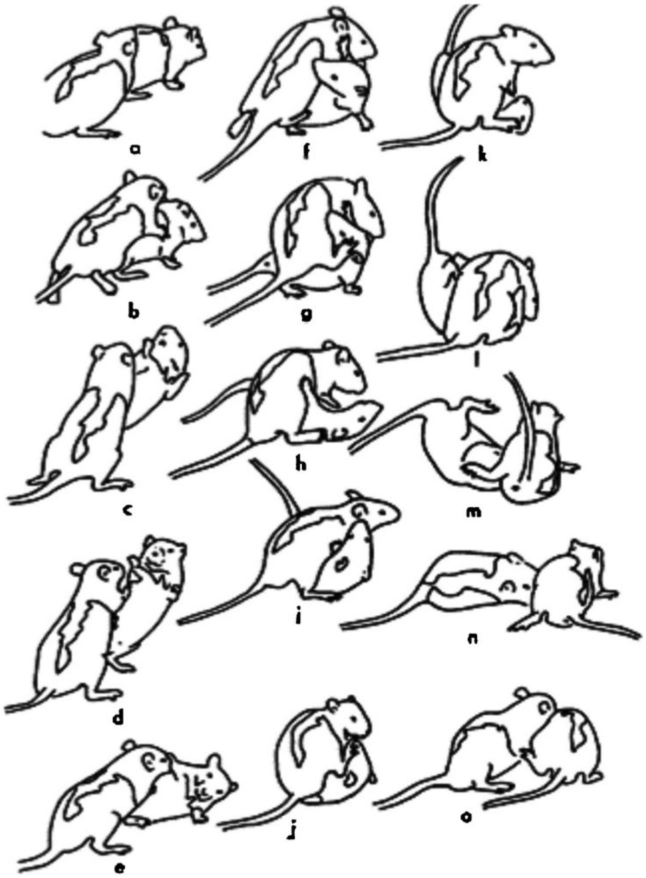

Fig. 2. A sequence of play fighting is shown for a pair of juvenile rats. The rat on the left approaches the second rat (a), and then pounces on it, from the rear (b). However, before contact can be made, the defender rotates around its longitudinal axis (c) to face its attacker (d). By moving forward, the attacker pushes the defender onto its side (e). The defender then rolls over onto its back as the attacker continues to reach for its nape (f–h). Once in the supine position, the defender launches an attack on its partner's nape (i), but fails due to its partner's use of its hind foot (j, k). Eventually, the rat on top (l) is pushed off by the supine animal (m), which then regains its' footing (n). The original defender then lunges towards its partner's nape (o). The whole sequence involves repeated attack and defense of the nape and frequent role reversals between the partners with regard to which one attacks and which one defends. (Reprinted from Pellis and Pellis, 1987, with permission.)

Similarly, object play, which is exhibited widely across lineages of animals (Burghardt, 2005), can vary markedly in the frequency and complexity of its expression (Fagen, 1981). In most cases, such play appears to involve manipulative behavior patterns typical of foraging and predation, but this can range from using unitary patterns infrequently to using complex sequences of many behavior patterns often (e.g., Gamble and Cristol, 2002; Negro et al., 1996; O'Hara and

Auersperg, 2017; Pellis, 1981a). Again, where comparisons are available in a more closely related lineage of species, a similar pattern is revealed (e.g., Nahallage and Huffman, 2008, 2012; Pelletier et al., 2017; Torigoe, 1987). Strikingly, some forms of object play can involve elements that go beyond foraging behavior patterns, such as when dolphins blow bubbles (Hill et al., 2017), or when bonobos don plants, straw or blankets as 'hats' (Palagi, 2018). Again, such examples seem consistent with the behavior being tertiary process play in which the actions have become divorced from the underlying functional system from which they may originally have been derived.

6. A path from the many to the one

When the maturation of a particular behavior system in a lineage occurs in a manner that meets the minimum requirements of Burghardt's five criteria, that lineage may be considered to exhibit play. But such primary process play is barely distinguishable from the behavior system from which its behavior patterns are derived. However, for secondary and tertiary process play to evolve, novel functional and causal processes are involved. In order for such play to exhibit the coherence typically associated with behavior systems (Hogan, 2001; Timberlake, 2001), novel mechanisms are needed, mechanisms that can lead to behavioral and contextual dissociation from the behavior system from which the behavior patterns used during play are derived.

Such dissociation can be illustrated by object and predatory play. As already noted, for some species, play with objects or prey corresponds to the daily cycle of foraging, in that it is most frequent when the animals are most likely to eat, with the play representing misdirected foraging behavior (e.g., Hall and Bradshaw, 1998; Pellis, 1981a, 1991). Similarly, when a predator is confronted by a prey that is large or otherwise threatening, the inhibition of predatory attack can lead to the vacillation in contact and withdrawal typically seen in play (Biben, 1979; Hall, 1998; Pellis et al., 1988). However, in other species, object play does not cycle with the daily foraging or eating pattern (e.g., Ahloy Dallaire and Mason, 2016) and may include behavior patterns that are not limited to foraging/predatory behavior (e.g., Giljov et al., 2017). That is, in the latter cases, object play does not simply reflect activation of the foraging and feeding behavior systems.

The examples discussed above suggest the following model. For all three types of play, it seems likely that different lineages have transformed play from primary through secondary to tertiary processes. Therefore, it would seem that multiple behavior systems (e.g., foraging, aggression, sex, anti-predator behavior) have evolved independently into different, specific play behavior systems. Again, that for some lineages this occurred for one behavior system, but not others, attests to their independent evolution (Burghardt, 2005). Thus, as a first step, there may be multiple play behavior systems that have evolved from their parent behavior systems (e.g., the anti-predator behavior system spawning the locomotor play behavior system). Then, for some species that have evolved more than one form of tertiary process play, if they have the necessary neural, cognitive and ecological resources available, novel mechanisms may have evolved to combine different types of play into truly mixed patterns (Pellis and Pellis, 2017b). That is, multiple play behavior systems are combined into a super-play behavior system (Fig. 3).

7. Testing the theory and future directions for studying play

An alternative way to view the sporadic emergence of play in the animal kingdom is to treat it like migration, which also appears to be idiosyncratic and sporadic in its distribution, but actually relies on common functional and causal processes (Dingle, 2006). In this way, it is more like universal behavior systems such as feeding or fighting: that is, the structural components are the same and the functional associations of those components are similar. This is unlike our 'many to one' hypothesis in which we posit different causal processes leading to convergence of similar outcomes. Rather, this alternative would posit parallel evolution in which different lineages use the same core, causal processes to produce comparable outcomes repeatedly. There are precedents for such parallel evolution. For example, sea slugs appear to use the same conserved neural circuits to evolve, repeatedly, similar behavior patterns across diverse species within the lineage (Katz, 2011). Similar parallel evolution may occur across diverse lineages. For example, domestication involves similar causal mechanisms to produce a comparable suite of behavioral, neural and physiological traits across diverse lineages (Wilkins et al., 2014). Just like there is a 'domestication syndrome' or a 'migration syndrome', there could be a 'play syndrome'. Such a syndrome would make all play behavior systems one system, but one that may have different behavioral manifestations, depending on the idiosyncrasies of particular lineages.

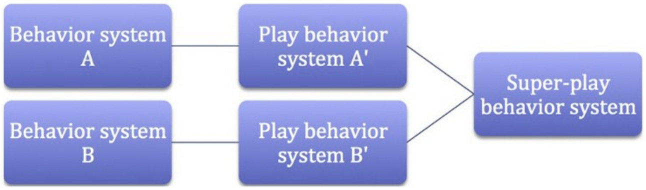

Fig. 3. A two-step transformation model, showing that, initially, distinct play behavior systems evolve from the behavior systems from which their behavior patterns are derived, but then, as the play is transformed, further emancipating the play behavior systems from their parent behavior systems, they can converge into a more unitary behavior system. The sequence of changes is from left to right.

Finding commonalities in the neural circuits that are unique to play and then determining how these co-vary across members of a closely related clade that differ in their playfulness would be an important step in identifying such common mechanisms. For example, in rats, there are strain differences in the frequency of initiating play fighting and in the likelihood of using different types of behavior patterns for playful defense (Himmler et al., 2014). For some strains, reduced playfulness is associated with altered activity of the mesolimbic dopamine system (Siviy et al., 2011). This is consistent with the finding that the motivation to engage in play depends on this dopaminergic system. Conversely, the rewards gained from playing depend on the brain reward mechanisms that involve endogenous opioids (Vanderschuren et al., 2016). Information on how these mechanisms naturally vary across species could be of value in determining how much particular species play and how they play. There are limitations in our current knowledge that need to be remedied to be able to use a neurobiological approach.

The first limitation is that most of our knowledge about the neural controls over play is based on the laboratory rat (Siviy and Panksepp, 2011; Vandershuren et al., 2016). What has been shown is that the neural circuit involved spans areas in the forebrain, midbrain and hindbrain (Siviy, 2016). Some comparative studies with primates suggest that a similar network may be involved in this clade (Graham, 2011), but this remains to be empirically tested. The consistency between rats and primates leads to the second limitation; that, in both cases, this network has been established for animals engaging in play fighting. Unfortunately, comparable studies have not been done with any species from any lineage engaging in locomotor or object play, so we do not know if the same circuit is involved across different forms of play and if so, if there are unique causal connections among the components of this circuit for different types of play. The third limitation is that components of this circuit are used across a range of behaviors and not just play. For example, parts of the prefrontal cortex (PFC) are activated during social play (Gordon et al., 2002; Hehar et al., 2016) and damage to areas of the PFC modifies how they play socially and affects the attractiveness of such damaged rats as play partners (Bell et al., 2009; Pellis et al., 2006). But the PFC regulates socio-cognitive skills that influence many aspects of social behavior, not just play (Pellis and Pellis, 2016). Similarly, even if the circuits involved in motivating and

rewarding play fighting in rats (Vandershuren et al., 2016) were found to have a similar role in object and locomotor play, this would not necessarily mean that there is a common play circuit as these neural systems are utilized in all motivated behaviors (Berridge and Kringelbach, 2013). There is much comparative work to be done both across species and across types of play before neurobiology can help resolve the question of what kind of behavior system(s) may constitute play. On a more positive note, the details emerging from studies on rats (Siviy, 2016; Vandershuren et al., 2016) are providing a framework for comparative studies on social play in other species (e.g., Burleson et al., 2016; Graham, 2011) and on other forms of play (Riters et al., 2018).

The behavioral detail available in how animals play across a wide range of species is also deficient. For example, what is meant by play involving the mixing of behavior patterns from different behavior systems (e.g., Meyer-Holzapfel, 1956) is ambiguous. When animals use behavior patterns simultaneously, as when two Japanese monkeys compete for access to a stick (Shimada, 2012), the mixing is evident. Often, however, mixing is assumed when there is a looser temporal association, such as when a piglet jumps and rotates in the air, and, as it does so, crashes into another piglet, which then leads to a brief play fight (Donaldson et al., 2002). Alternative explanations, such as incidental contact leading to an activation of a different sequence of behavior, are usually not considered (Pellis and Pellis, 2017b). Some detailed studies of play fighting illustrate the problem. Play fighting involves animals competing for some advantage over one another (Aldis, 1975), with the advantage sought being the same as that from a particular behavior system being simulated. For example, rats compete for nuzzling another's nape (as in sex) (see Fig. 2), and Australian magpies peck the side of their partner's head (as in aggression) (Pellis, 1981b). The play fighting of some species can involve competing for more than one advantage (Pellis and Pellis, 2017a), and these species give us the opportunity to test whether behaviors derived from different behavior systems are mixed during playful sequences.

For example, ground squirrels engage in competitive playful interactions in which they attempt either to bite each other on the shoulders (as in aggression) or mount one another (as in sex) (Nunes et al., 1999; Pasztor et al., 2001); grasshopper mice either compete to bite each other on the nape of the neck (as in predation) or lick, groom and nuzzle the sides of their partner's shoulders (as in precopulatory behavior) (Pellis et al., 2000); and gray mouse lemurs compete to bite each other on the face (as in aggression), groom each others' faces and upper bodies (as in social affiliation) or mount one another (as in sex) (Pellis and Pellis, 2018). Detailed temporal and kinematic analyses of play fighting sequences in all these species show that there is no mixing within a sequence – a play fight starts and ends with attack and defense related to only one type of advantage. Once such a play fight is terminated, another involving competition for another advantage may commence. Thus, on a broad time scale over the entire duration of a play session or over successive sessions, play fighting involves behavior patterns from multiple behavior systems, but in the moment-to-moment moves and countermoves when engaged in a particular play fight, the animals do not mix behavior patterns from different behavior systems (Pellis and Pellis, 2017a).

Of course, the sequential pattern of an aggressive play fight being followed by a sexual play fight may still reflect a common play behavior system. Indeed, our hypothesized model (Fig. 3) provides a means for this level of mixing. The constituent play behavior systems (aggression and sex) may retain sufficient coherence within each system to maintain functional cohesion of the behavior patterns involved, so that aggressive and sex behavior patterns are not interspersed. Nevertheless, at the super-play behavior system level, the interspersed sequences of aggressive and sexual play may form part of a seamless session of play. Perhaps as dynamic imaging techniques become available that can track brain circuit activity in freely behaving animals (Bermudez-Contreras et al., 2018), objective evidence may be obtained to determine if the participants perceive the overall interaction, one involving sequentially occurring aggressive and sexual play, as one continuous bout of play or as discrete encounters. In addition, more detailed studies are needed of species that engage in multiple forms of play to provide a comparative data set on the various ways in which behavior patterns or sequences of behavior patterns derived from different behavior systems can be juxtaposed.

8. Conclusion

Many instances of what qualifies as being labeled play has the functional coherence in the organization of how its constituent behavior patterns are ordered to make it look like a behavior system as defined by Burghardt and Bowers, (2017). However, given that most of the behavior patterns used in play are co-opted from other behavior systems (e.g., anti-predator behavior, conspecific aggression, sex, foraging), how play originated and how it has achieved the coherence of a behavior system is unresolved. Also, since there are multiple forms of play (e.g., social, object, locomotor) that in many lineages have evolved independently (Burghardt, 2005), it is unclear how, in some species, these may coalesce so that they are integrated together in coherent sequences of behavior. Finally, no existing theory provides an explanation for how novel behavior patterns - those that are not part of the repertoire of any of the behavior systems simulated during play (e.g., Palagi, 2018; Petrů et al., 2009) - arise and become incorporated in the play of some species. The evolutionary-based hypothesis suggested in this paper provides an attempt to answer these questions and does so in a manner that can integrate the vast species differences that exist in the presence and content of play across the animal kingdom. Even though the 'many to one' hypothesis is coherent and can account for that variation, so may an alternative 'play syndrome' hypothesis. Empirical limitations in our knowledge about play do not yet permit the construction of formal competing models of the components of how a play behavior system may be organized. Nonetheless, by thinking about play from a behavior systems perspective at least two viable hypotheses emerged, hypotheses that may be useful in directing further empirical research.

Acknowledgments

We thank Robert Bowers for inviting our contribution and we dedicate our paper to William Timberlake, who provided so many useful developments to behavior systems thinking. We also thank the editor and the reviewers for their thoughtful comments. Much of the work on which we base our framework was supported by grants from the Natural Sciences and Engineering Research Council of Canada (grant numbers: 2015-06034 and 2018-03706) to JBL and SMP.

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