# How Play Makes for a More Adaptable Brain

## A Comparative and Neural Perspective

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Studies of rats and some primates show that rough-and-tumble play among juveniles improves social competence, cognition, and emotional regulation later in life. Most critically, such play makes animals better able to respond to unexpected situations. But not all animals engage in play, and not all animals that play appear to gain these benefits. Using a model developed by Burghardt (2005), the authors argue that there are enabling conditions—such as how behavior systems develop and the presence of surplus resources—that make play-like behavior possible. Once such behavior emerges, other enabling conditions help transform it into more exaggerated patterns of play that can be co-opted for various functions. For species living in complex social systems with an extended juvenility, play has become a tool to refine the control that the prefrontal cortex has over other neural circuits. Such control permits these animals to have more nuanced responses to a variety of situations. In short, the juvenile experience of play refines the brain to be more adaptable later in life. **Key words:** comparative studies; developmental benefits of play; play and adaptability; play in the animal kingdom

## Introduction

There is growing experimental evidence that play in rats, especially social play, serves an important developmental role. It helps refine social skills (Byrd and Briner 1999; van den Berg et al. 1999), improve the regulation of emotions (da Silva et al. 1996; von Frijtag et al. 2002), and enhance executive functions (Baarendse et al. 2013) by modifying the neural mechanisms that underlie them (Bell, Pellis, and Kolb 2010; Himmler, Pellis, and Kolb 2013). Data on several primate species (e.g., Kalcher-Sommersguter et al. 2011; Kempes et al. 2008), including humans (Lindsey and Colwell 2013; Pellegrini 1995), are consistent with these findings. In essence, the experience of play in the juvenile period pro-

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vides a context within which young animals can experience loss of control and deal with unpredictable events (Pellis, Pellis, and Foroud 2005), but do so in a rewarding setting (Panksepp 1998; Vanderschuren 2010). This appears to enable animals to train to deal with the unexpected vicissitudes of life (Pellis, Pellis, and Reinhart 2010; Špinka, Newberry, and Bekoff 2001). But before we explore how such play-induced brain changes can help make animals better at dealing with the life's uncertainties, we need to answer a more fundamental question.

We should be bear in mind that the animal kingdom consists of about thirty phyla that represent major groupings based on the unique features of each phylum's body plan. Consider the difference in body organization between an insect like an ant and a vertebrate like a dog. The division of body parts, the number and placement of the legs, the location and organization of the nervous and circulatory systems all differ in fundamental ways (Tudge 2002). An exhaustive review of the literature has shown that play occurs in only five of the thirty phyla (Burghardt 2005). For example, play appears in many species in the phylum Chordata, which includes people, dogs, and ravens and some species of the phylum Arthropoda, which contains insects (like ants), crustaceans (like shrimp), and arachnids (like spiders). We dot not find play, however, in the phylum Echinodermata, which contains starfish and sea urchins, or the phylum Annelida, which includes earthworms and leeches. Indeed, even in the phyla containing species that play, not all the species in those phyla play. For instance, researchers report that in Chordata only some in the subphylum Vertebrata (those creatures with a vertebral column like humans and fish) play, and among these vertebrates, play seems fairly common in many lineages of mammals, less common but present in some lineages of birds, but rare among other groups like amphibians, reptiles, or fish. In this context, we are left to wonder why play, which seems important to training some animals to be more adaptable and resilient, is so rare in the animal kingdom?

This rarity, rather than impeding our understanding of the origins and functions of play, may actually prove useful to it. Consider rough-and-tumble play (or play fighting) alone. When we examine it within a particular group of animals, such as the rodents, we find it absent in some species and present in others, and where present, it can range from simple to complex (Pellis and Iwaniuk 2004). In play's simplest form, one animal attacks another, who does not respond (Wilson 1973). Added complexity arises when the defender flees from the attacking partner (Pellis and Pasztor 1999). Still greater complexity comes with the defender holding its ground as it wards off the attack, but this too can vary in complexity, as some species are more likely to adopt defensive actions that promote close-quarter wrestling (Pellis, Pellis, and Dewsbury1989). On top of these gradations in complexity, there are also differences in frequency across species: even those having the most complex patterns do not necessarily use them with the same frequency (Pellis and Pellis 1998a). How does all this diversity map onto the functions of play?

As a useful organizing principle, we recognize that not everything we call play has a function and that even those forms of play that are functional have many different functions. Before delving much further into this issue, we should make clear what we mean by function in a biological sense. When we consider a trait—whether a behavioral trait like play or an anatomical trait like the horns of a goat—in terms of the functions it serves, we look primarily at how the trait contributes to an animal's survival and reproduction. In an evolutionary sense, we call traits functional if they increase the "fitness" of the possessor, such as giving the animal a reproductive advantage over its competitors. That trait may do so indirectly, by enabling the possessor to survive longer and thus enjoy more opportunities to breed, or it may do so directly, by making the possessor, for example, better at winning mates or rearing young. However, when we use the word "function" in more colloquial parlance, we tend to mean something different. For example, when we eat that extra slice of Thanksgiving pumpkin pie, we do so because it is delicious, not because we are hungry. So eating functions to increase our pleasure. In the context of play, we may say animal A performs X during play because the animal finds it pleasurable to do so, meaning that the function of the behavior is to induce pleasure. We resolve these divergent usages of the term "function" by recognizing that we do pleasurable things because for our ancestors pleasurable activities generally increased their fitness (eating and having sex come to mind). Pleasure seems to induce us to do things, like play that increase our fitness.

While most functional accounts of play focus on the way play in juveniles produces better functioning adults (Baldwin 1986; Fagen 1981), this emphasis on the young neglects the considerable play in which adults engage (Cohen 2006). Yet in some lineages of animals that play, such as the order of primates (to which we, chimpanzees, and rhesus monkeys belong), adults continue to play in 50 percent or more of species (Pellis and Iwaniuk 1999, 2000a). Some comparative evidence shows that when adults play, the play can have several immediate functions, such as regulating intragroup and intergroup tensions (Palagi 2011) and enabling them to navigate dominance relationships (Pellis 2002). Thus, some functions of play offer immediate, rather than delayed, benefits.

When researchers focus on delayed functions, the difficulties increase, as it becomes more problematic to decide which adult skills to compare with the purported gains made from juvenile play. Indeed, associations that seem promising in one species evaporate when researchers study another species, leading some to a dismal view of play as having minimal or modest benefits at best (Martin and Caro 1985). For example, a recent paper on play and development in free-living marmots has shown a convincing correlation between juvenile play and a later capacity to gain dominance (Blumstein et al. 2013), and work on free-living bears has found that cubs that play more are also more likely to survive to weaning (Fagen and Fagen 2004). But detailed studies of free-living meerkats (an African species of social mongoose) that specifically tested these functions, among others, found no support for them (Sharpe 2005a, b, c; Sharpe and Cherry 2003). The paucity of evidence and the conflicting support provided for the different functions of play add to the problems raised by the absence of play in much of the animal kingdom and to the variation in the complexity of play seen in the species that engage in it (Burghardt 2005; Pellis and Pellis 2009).

The comparative evidence clearly shows that play is not a unitary trait, neither does it have a clear and singular function. Talking about play in this way seems to lead to pointless arguments about the supposed benefits of play (Fagen 1981; Martin and Caro 1985). In our view, the best way to address the conceptual and empirical difficulties created by the absence of play in so many branches of the animal kingdom (and by the diversity in the patterns of play among those species that do play) and to pinpoint the illusive functions of play is to examine the variability in the structure and function of play in a historical context. This perspective recognizes that, within lineages, patterns considered as play may have undergone unique transformations, with different functions becoming possible with different kinds of transformations (Burghardt 2005; Pellis and Pellis 2009). For example, the play of cats has a stronger link to the underlying motivations associated with predation (Hall 1998) than does the play of dogs, in which stronger social influences pervade (Biben 1982).

## The Origins and Multiple Transformations of Play

Compare two juvenile chimpanzees engaged in play fighting and two immature cockroaches tussling for no apparent reason. Most readers would have little difficulty labeling the behavior of the chimpanzees as play, but they would most likely label that of the cockroaches as some form of immature aggression (Fagen 1981). With examples like these in mind, Burghardt (1984, 1988) has deliberately focused on the borderlines of play, those cases with elements of behavior that, observed in a mammal, would be called play, but observed in non-mammals, would probably not be called that. This focus on borderline cases led to two major breakthroughs (Burghardt 2005). First, Burghardt developed a comprehensive definition of play as behavior that meets five criteria. These are: (1) the behavior should not be completely functional in the context in which it occurs, (2) it should be voluntary, (3) it should be modified in some way compared to its normal occurrence in a functional context, (4) it should be performed repeatedly but not necessarily invariantly, and (5) it should appear in healthy, unstressed animals. In applying these criteria, researchers have shown that not only does some behavior in mammals—such as dogs and monkeys—qualify as play, but that some behavior in animals as diverse as turtles, wasps, and octopus also does so (e.g., Dapporto, Turillazzi, and Palagi 2006; Kramer and Burghardt 1998; Kuba et al. 2006). Indeed, as we already noted, the rigorous application of these criteria has led to identifying play in a wide range of animals from several phyla. However, this still leaves play unidentified in most phyla and, again, as we noted, not all lineages of species within phyla in which play occurs exhibit behavior that can be considered play.

Clearly, play seems relatively rare in the animal kingdom, and the fact that it appears among distantly related phyla implies that play must have arisen independently many times (Burghardt 2005). These comparative data confirmed a hypothesis that the conditions enabling play to arise are multiple and likely occur only in peculiar circumstances (Burghardt 1984, 1988). Moreover, in many cases, these enabling conditions create play that is barely recognizable as play; yet, in some lineages, the play is so spectacular and exaggerated that few observers, if any, would refuse to call it play. Indeed, to recognize the play of some turtles as being play, Burghardt had to speed up the film he watched. No such speeding up of the film is necessary to recognize the play of otters. Thus, first, we have to overcome our own prejudices and limitations as observers, but when we do we need, second, to recognize that not all the play we observe is the same. In short, some cases that fit Burghardt's criteria, just barely do so, whereas others do so completely.

These considerations led to Burghardt's second major insight. Play arises as a byproduct of enabling conditions, producing an incipient or play-like form of behavior that may be borderline in qualifying as play (primary-process play). But once such play is present, further conditions may exaggerate its frequency or its content making it more recognizably play (secondary-process play). Additional enabling factors may lead to even more exaggerated behavior unquestionably related to the play category (tertiary-process play). That is, in this historical perspective, the conditions for the origins of play can be characterized and distinguished from the conditions that may act to transform play further (figure 1). Moreover, even though in its origins, play may have arisen as a byproduct of propitious circumstances and so without any functional benefits, once such behavior existed, the various transformations that then accrued could have created the conditions for novel functions to arise (Burghardt 2005).

The broad comparative view of play, then, reveals a diverse range of phenomena encompassed within the label of play. Different lineages have evolved play-like behavior, and then some of those lineages have further transformed that behavior into patterns of play that serve particular functions. Importantly, this framework allows for those functions to be multiple and disparate, with some overlapping due to convergence and some differing due to divergence. Certainly, this framework can account for both the presence and absence of play in the animal kingdom and for the complex array of functions that it can support. Comparative research on variations in the social play of rodents provides examples of each of these kinds of transformations as envisioned by Burghardt's theoretical schema.

## The View from Rodents and Their Play Fighting

Rodentia is the largest order of the class Mammalia, consisting of about 40 percent of all mammal species. For example, there are about two thousand species of rodents, but less than three hundred species of primates. The rodents are divided into three major subgroups; the rat-like or mouse-like rodents (murid rodents) are the most abundant, comprising about 50 percent of all rodent species (e.g., rats, mice, gerbils, and hamsters). The other two groups consist of the squirrel-like and the guinea pig-like rodents (Nowak 1999). Detailed analysis of play fighting in murid rodents shows that play is not distributed in a uniform manner (Pellis and Pellis 1998a). In this group, such play can be absent, and, if present, can be simple, complex, or something in between. Given their differing patterns of relatedness to one another, the possible transformations in the content of play can be traced. To do so, we need a specialized approach from

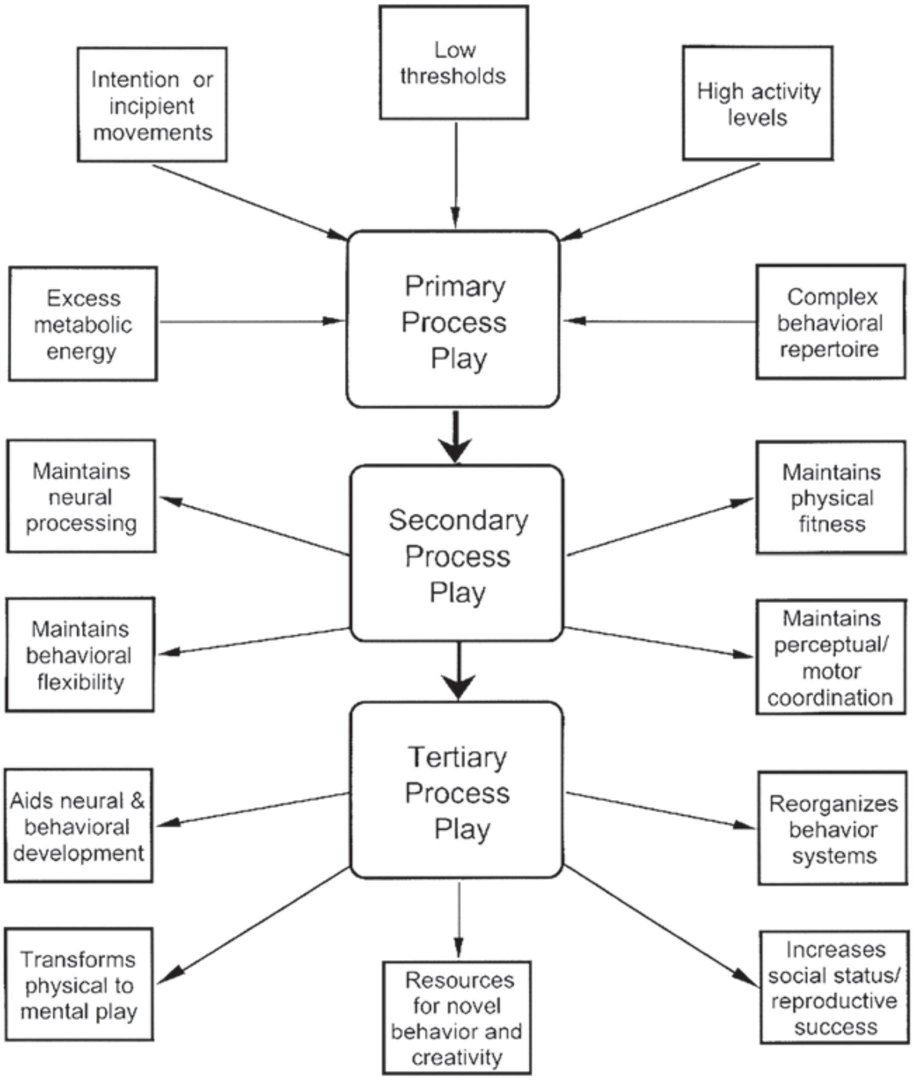

Figure 1. Sequential transformations of play over evolutionary time and their enabling factors (Burghardt 2005, reprinted with permission)

comparative biology, and this needs some explanation.

Species can be placed on a tree diagram (i.e., a cladogram) that shows the pattern of relatedness among the set of species. Importantly, cladograms do not claim ancestor-descendent relationships among the species, rather, all the species appear on the terminal branches with species linked to one another at nodes, which represent bifurcation points at which presumed ancestors have diverged into the daughter species (Hennig 1966). Placing the murid species on a cladogram, the degree of complexity of the play fighting performed can be mapped. In doing so, using the assumption of parsimony so that the tree shows the fewest transitions possible, the pattern of transformation in the lineage and branches of the lineage can be determined (figure 2).

The cladogram shows two important patterns. First, the most likely ancestral state suggests the animals have moderate levels of complexity in their play (dark stippling). Second, the terminal branches show that extant species have either exaggerated that complexity (black for most complex, grey for next most complex) or reduced it (light stippling for simplified play, white for play being absent or near absent). Consistent with Burghardt's framework, the cladogram of the rodents shows that play changes in form over evolutionary time with different lineages transforming play in different ways. The elimination of play shown in some lineages also proves telling. While the costs—small, moderate, or large—of playing have been debated (Martin and Caro 1985), specific cases have emerged that suggest play can be costly, indeed. For example, in free-living chimpanzees in West Africa, play fighting appears as a means of transmitting lethal infectious diseases, which, in some years, may lead to a major culling of juveniles (Kuehl et al. 2008). Again, whether the costs sustained are small or large may depend on whether a particular lineage has co-opted play for some critical fitness-enhancing function. Sustaining larger costs suggests larger counterbalancing benefits for play to be maintained in the population. The rodent cladogram indicates that if the benefits are insufficient, play will be eliminated.

Broadening the comparative framework to include the other major subdivisions of rodents (Pellis and Iwaniuk 2004) and embedding rodents with the other orders of mammals (Burghardt 2005) suggests that the ancestral group giving rise to the rodents either did not play or had a very rudimentary pattern of play. Using this pattern as a starting point to consider the variation across extant species of rodents, a rough framework can be developed for the kinds of play envisaged in Burghardt's primary, secondary, and tertiary processes. However, we must keep a caveat in mind: such a framing of extant species does not represent the true pattern of evolutionary change, since, as shown in figure 2, there have been losses as well as gains. Nonetheless, the play in the extant species can be ordered in a manner that conceptually illustrates the kind of grades of organization and transformation envisaged by Burghardt's model (figure 1).

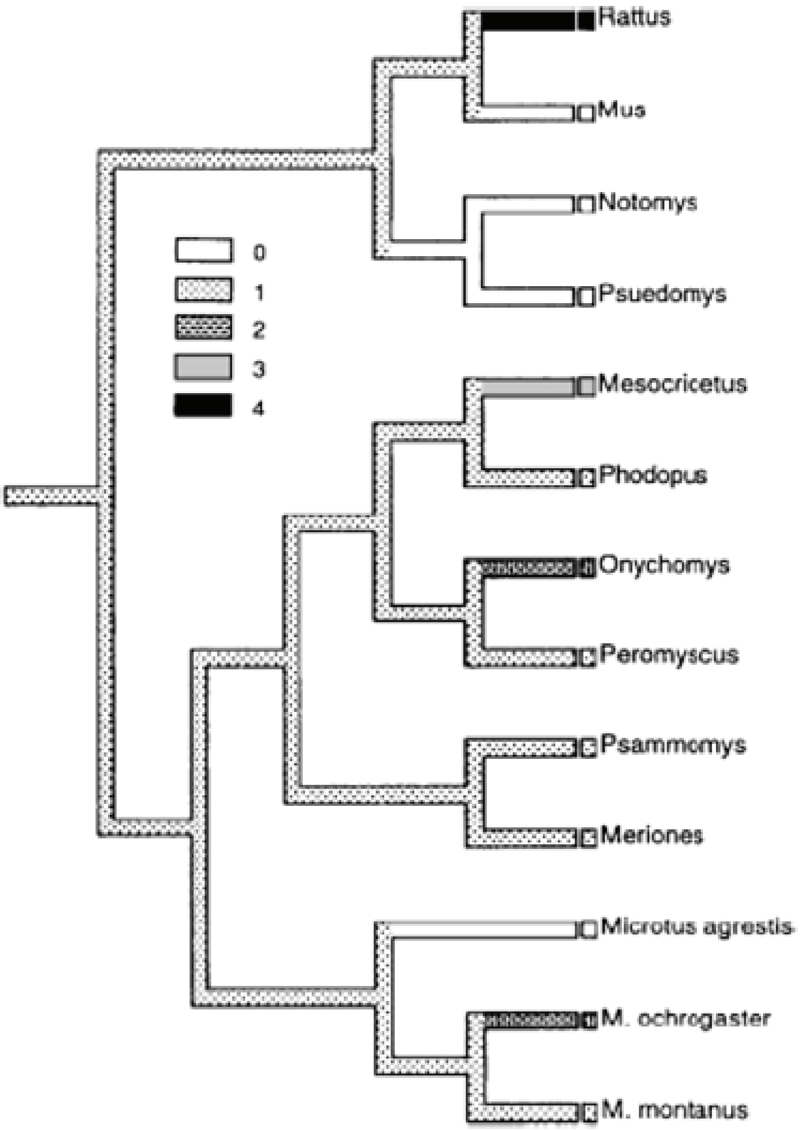

Figure 2. Complexity of play fighting and its evolution for murid rodents (Whishaw et al. 2001, reprinted with permission)

Among murid rodents, play fighting primarily involves the simulation of precopulatory behavior, in which partners compete for access to the body targets that are contacted during adult sexual encounters. For example, rats compete to contact and nuzzle the nape of the neck, and Djungarian hamsters compete to lick and nuzzle the partner's mouth, whereas during serious aggression, these species attempt to bite each other on the rump and lower flanks (Pellis 1993). Despite these similarities, there are species differences in the degree of similarity of the playful version of this behavior to the adult, functional version (Pellis and Pellis 1998a). Importantly for the evolution of play, the developing behavioral system changes in a piecemeal manner, which, without regulatory control, can be expressed precociously. Add to this an environment offering protection against predators and abundant resources provided by parents, and the likelihood of precociously performed behavior increases—and may do so to the level in which it begins to meet the criteria for it to be labeled as play (Burghardt 2005). Therefore, for some rodents, when the behavior closely resembles the expression of precocial sexual behavior, we may think of it as play-like behavior, or incipient play (figure 3). Such an origin would be consistent with Burghardt's primary process play. Once the presence of this fragmented, immature behavior becomes a reliable part of the experiential world in which the animal develops, it can substitute for maturational processes that are otherwise insensitive to experience. This second stage may not involve any modifications to the content of the immature behavior expressed, but simply by its increased frequency of performance, such behavior in the juvenile stage could nonetheless provide essential, experiential feedback for wiring the brain, and so, at least functionally, may be thought of as rudimentary play fighting rather than simply as immature behavior (figure 3). This, then, reflects a transformation that would make the play more like Burghardt's secondary-process play.

A further transformation can arise by modifying the content of the juvenile version of adult sexual encounters. For example, if the majority of the beneficial experiences derived from play fighting occurs when the animals are wrestling one another, then increasing the frequency of the tactics of attack and defense that increase the frequency of wrestling would be advantageous, and, in the absence of countervailing costs, would be selected for, and the organization of the play would, over generations, change to that we see in the adult sexual encounters. Once modifications have been made to the organization of play fighting itself, not only would this behavior facilitate the development of sex, but it also would become an essential component of the normal developmental experience. Thus, with this third step, the playful interactions become both quantitatively and qualitatively different from sexual interactions and the label of rudimentary play seems insufficient and would be better labeled true play fighting (figure 3).

| Behavior and context | Consequences and functions | Classification |
|---|---|---|
| Components of sexual behavior, especially precopulatory elements. These are expressed in a precocious manner during the juvenile period. | None | *Incipient play*<br>(i.e., play-like behavior) |
| Under appropriate conditions, precocious sexual behavior becomes a frequent and expected component of the juvenile period. However, at this stage, the juvenile interactions differ little from adult sexual interactions. | Precopulatory behavior becomes necessary for the maturation of normal, adult sexual performance. | *Rudimentary play fighting* |
| Some components of precopulatory sexual behavior are elaborated during the juvenile period, making the interactions more clearly different from adult sexual behavior | These elaborations ensure that the necessary sexual skills are acquired during the juvenile period. | *True play fighting* |
| Under some conditions, this sexually derived pattern of play fighting is modified to a more exaggerated degree and co-opted into use in novel domains of juvenile and adult life | These patterns of interactions now serve nonsexual as well as sexual functions. | *Emancipated play fighting* |

Figure 3. Hypothetical stages in the transformation of immature sexual behavior into play fighting in murid rodents (adapted from Pellis 1993, reprinted with permission)

This transformation is more consistent with Burghardt's tertiary-process play.

Note that in the model, what has transpired is that, through successive changes, precocial sexual behavior has been transformed into playful behavior, functioning to promote the development of sexual skills. In rats, the organization of play fighting is more greatly modified than in any other murid rodents so far studied (Pellis and Pellis 1998a), which suggests another layer of transformation. Juvenile play in rats has been further modified, so that it not only facilitates the development of sexual behavior but also the promotion of social competence beyond the sexual domain. Even more strikingly, play fighting itself is retained into adulthood as a tool for social assessment and manipulation (Pellis and Pellis 2011). Because of the novel organizational changes as well as its expansion beyond its original function in sexual development, this form of play fighting requires a different label, emancipated play fighting (figure 3). It may be merely semantic whether such a transformation corresponds to an advanced tertiary-process play or represents an addition to Burghardt's original formulation, quaternary-process play. What is important is that new transformations are laid over past transformations with new functional opportunities emerging as further transformations are made.

The evidence supporting these various transformations in the play of rodents have been detailed elsewhere (Pellis and Pellis 2009); the key message to take from this brief review is that, when viewed comparatively, play has multiple levels of organization and potential functional uses. Thus, it is naïve to expect that all animals that play will play similarly or gain the same benefits. That being the case, we can go back to, and modify, our opening question: why is it that all animals do not play to accrue the kinds of benefits shown for rats?

To understand some of these transformations, it is first necessary to have an idea of how the vertebrate brain is organized. The brain divides into two major components: the cerebral cortices and the remainder (Kolb and Whishaw 2009). When we open the skull of a mammal, the largest and most obvious structure we see is the cortex, composed of two hemispheres that cover most of the rest of the brain. The subcortical structures lie beneath the cortical hemispheres. These different layers have complex patterns of interconnection with the different networks that modify each other's function.

To explain why rats gain so much from playing as juveniles and other rodents do not, we need to keep several points in mind. First, the comparative evidence clearly shows that not all rodents play in a manner comparable to rats (Pellis and Pellis 1998a). Second, the organizational transformations present in rats that are not shared with other rodents involve novel regulatory controls originating in the cortex (Kamitakahara et al. 2007). Third, the higher-level cognitive benefits that accrue from playing in rats are not present in other rodents that play (Einon et al. 1981), and at least some of these cognitive benefits have been shown to involve changes in cortical function (Baarendse et al. 2013). That is, in rats play has been modified to provide a novel function—that of enhancing cortical regulation of emotional and cognitive processes—especially as they pertain to social behavior, and this has had the effect of modifying the cortical neural circuits important to such regulation (Bell et al. 2010; Himmler, Pellis, and Kolb 2013).

As we can see, the transformative approach to comparing play across species yields novel insights into play because it shows that not all species that play gain the same benefits from doing so. Moreover, the evolution of novel benefits require changing both how the play is organized to yield experiences that are important for shaping the development of the relevant brain mechanisms and the capacity of those brain mechanisms to be influenced by such experiences. Among close relatives of rats, play has been transformed in a way that has led to divergence in the form and function of play (see figure 2). However, we have already touched on the possibility that the higher-level transformations of play in rats have converged with organizational and functional properties similar to those we see in some primates. For example, the quaternary changes in the play of rats that influence the development of executive function are similar to those we see in humans and some other primates. Understanding that convergence can help frame the question about how the play-induced brain changes we see in any of these species may lead to improved adult social competency.

## Convergence in Play Fighting

Most of what we know about the impact of play fighting in primates on later social, emotional, and cognitive function comes from studies of Old World monkeys (Kempes et al. 2008) and apes (Kalcher-Sommersguter et al. 2011). In these groups of primates, play fighting appears primarily as a simulation of conspecific fighting—the same body targets are bitten and the same combat tactics are used (Aldis 1975; Owens 1975; Pellis and Pellis 1997; Reinhart et al. 2010; Symons 1978). For example, gorillas wrestle one another during both play fighting and serious fighting to gain access to the lateral edge of the shoulder, which is bitten if contacted (Schaller 1963). Even though the same target and tactics are used during both play fighting and serious fighting, applying the criteria for play established by Burghardt shows that play is not just an immature version of serious fighting. Thus, while the play fighting of rats has evolved from precocial sexual behavior and that of the rhesus monkey and gorillas from precocial agonistic behavior, depriving juvenile play experience in these species not only affects the development of their sexual and aggressive behaviors, but also has more wide-ranging effects on the development of social competency, emotional regulation, and cognitive performance (Pellis and Pellis 2009). Both rats and monkeys have modified their play fighting to exaggerate the experience of loss of control and unpredictability (Pellis, Pellis, and Foroud 2005; Petrù et al. 2008), and, indeed, it is unpredictability that provides the key experience.

In monkeys and apes, maternal interactions are critical to prepare the young animal for engaging in, and benefitting from, play with peers at a later age (Blum 2002; van Leeuwen, Mulenga, and Chidester 2014). These monkey studies show that even an inanimate surrogate mother is better than no mother at all, and, in this context, they found that a mobile, inanimate mother was better than a stationary one. The mobile mother moved up, down, and around the cage on an irregular schedule throughout the day. As crucially, the studies observed that the infants initiated more play with the mobile surrogate than with the stationary one and that they reacted to unexpected retreats and hits from the mobile surrogate. When these monkeys were weaned and introduced into peer groups, the monkeys that had been reared by mobile, surrogate mothers were more outgoing and more likely to approach other animals. They made fewer threats when they did so and paid more attention to novel social stimuli. Moreover, when they were young adults, they were also more likely to engage in successful copulations. Unlike those infants reared by the stationary surrogate mothers, those reared by the mobile surrogate mothers behaved more like the monkeys that had been reared by their natural mothers (Mason 1978).

Play fighting in rats and monkeys provides a context for experiencing the unexpected—all the more so, since for play fighting to remain playful it has to follow a certain rule structure. Unlike in serious fighting, where winning is the sole object, in play fighting, the winning has to be attenuated so that some degree of reciprocity is possible (Pellis, Pellis, and Reinhart 2010). On the rare occasions that play fighting escalates to serious fighting in rats, one rat has used excessive force to restrain its partner (Pellis and Pellis 1998b). However, in the exuberance of play fighting, hits and bites may be delivered too firmly, and the partner may resist following the rules. The problem for the animal is to assess the situation and determine whether the excessive force was accidental or part of a concerted pattern and so decide how to react to the infraction. At the same time, as the animal loses control—often because of its own injection of reciprocity promoting movements that it performed (Pellis, Pellis, and Foroud 2005)—it has to recoup from the mishap but to do so without using excessive force. Not surprisingly, species such as rats and monkeys—species in which the organization of the play has been modified to exaggerate these experiences—develop in the absence of such play a compromised impulse control, emotional regulation, cognitive performance, and social competency.

## Play Fighting and the Development of Executive Function

Play fighting can be cognitively and emotionally challenging because it exaggerates the experience of loss of control, especially given the unpredictability that arises from having to use an implicit rule-structure (one that promotes reciprocity) to recover from instability in rapid sequences of behavior that may last only a few seconds. Yet these are precisely the experiences found frequently in the play fighting of many species. Moreover, growing evidence suggests that such experiences affect the development of the prefrontal cortex (at the anterior end of the cortex, abutting the front of the skull), the area of the cortex known for its role in executive function.

The term *executive function* here describes a collection of control processes necessary for the organization of complex—and often goal-oriented—sequences of movements in humans, monkeys, and rats. These include, but are not limited to, monitoring behavior, attention, resistance to interference, behavioral inhibition, planning, decision making, and task switching (*see* Dalley, Cardinal, and Robbins 2004 for a review) as well as impulse control (Baarendse et al. 2013).

Rats that have been reared in social isolation show many deficits linked to executive function. For example, they react with heightened anxiety to fearful situations (da Silva et al. 1996) and have an exaggerated stress response to such situations (von Frijtag et al. 2002); they overreact to benign social contact (Einon and Potegal 1991); they fail to behave submissively when confronted by a dominant rat, impulsively moving about and leaving a safe place (van den Berg et al., 1999); they have difficulty coordinating movements with a partner in both sexual and nonsexual contexts (Moore 1985; Pellis, Field, and Whishaw 1999); and they are less competent in solving cognitive tasks (Einon et al. 1981). However, before the link between play experience and executive function can be fully developed, we must consider an important caveat.

When we rear a young rat in social isolation, we deprive it of more than just the experience of playing with peers. The reasons to believe that a major contributor to the isolation-induced effects on such rats arise from the absence of play experience have been reviewed in detail elsewhere (Pellis and Pellis 2006). So here, we present only some of the key evidence. In the juvenile period (spanning from weaning at around twenty-three days after birth to when they sexually mature at around sixty days of age), rats devote about one hour of every twenty-four–hour cycle to play. Giving an isolated rat the opportunity to interact with a peer for one hour per day over the juvenile period proves sufficient to offset the many negative effects of isolation on behavior and cognition. However, giving the isolated juvenile an hour per day exposure to an adult does not (Einon and Morgan 1977; Einon, Morgan, and Kibbler 1978). Whether paired with a juvenile peer or an adult, the juvenile rat will socialize by sniffing, grooming, huddling, and, generally, coordinating its movements with its partner, but if paired with a peer, the socializing also includes playing together. Thus, at least to some extent, socializing that includes play appears to be important in relation to the deficits that arise from being reared in isolation during the juvenile period (e.g., Arakawa 2007a, 2007b).

Using the paradigm of housing juveniles either with adults or with other juveniles to avoid the rats being reared in complete isolation, researchers found that the opportunity to engage in social play with one other peer is sufficient to modify the rats' dendritic arbor (think of branches of a tree) of the neurons of the medial prefrontal cortex (mPFC) and that being reared with multiple social partners, whether or not they provide play experiences, is sufficient to modify the dendritic arbor of the neurons of the orbital frontal cortex (OFC) (Bell, Pellis, and Kolb 2010). Moreover, such studies show that for the mPFC, the play-induced neuronal changes result in increased dendritic plasticity when exposed to other experiences later in life (Himmler, Pellis, and Kolb 2013). Selective lesions of the mPFC and the OFC in rats that have been reared socially as juveniles reveal somewhat different roles for these circuits. With damage to the OFC, rats fail to modulate their social interactions with different partners—that is, they interact similarly with dominant and subordinate partners (Pellis et al. 2006). With damage to the mPFC, rats can modulate their play with partner identity, but appear to have difficulty in coordinating complex movements with their partners (Bell et al. 2009; Himmler et al., 2014). Therefore, prefrontal damage mimics some of the typical social deficits from being reared in isolation, providing strong evidence that play and other social experiences (e.g., interacting with multiple partners) during the juvenile period are critical for refining the neural circuits of the PFC that are involved in producing a socially competent adult (Pellis, Pellis, and Bell 2010).

The PFC and several subcortical structures we believe to be involved in the neural circuitry for executive function are activated during playful interactions (Cheng, Taravosh-Lahn, and Delville 2008; Gordon et al. 2002). This includes the amygdala, which is essential for the expression of emotion (van Kerkof et al. 2014). Given the play-induced structural changes in the neurons of the mPFC, we could expect that the cells in the amygdala would also undergo structural remodeling, but preliminary data suggest that this is not the case (Himmler, unpublished observations). As noted previously, rats that are socially isolated and so denied the opportunity to engage in playful interactions during the juvenile period exhibit deficits in emotional regulation (e.g., da Silva et al. 1996; von Frijtag et al. 2002). Therefore, it seems possible that the play-induced changes in emotional regulation may arise from improved control of subcortical systems by neurons coming from the cortex, like those from the mPFC, that are changed structurally by the experience of play. Because there are strong connections between the mPFc and the subcortical neural systems that make up the executive-control complex, the play-induced activation of both the cortical and subcortical circuits may strengthen their connections. While this possibility remains to be tested, closer consideration of the anatomical links between the mPFC and selected subcortical circuits makes it a plausible hypothesis.

The mPFC has strong excitatory connections with multiple nuclei in the amygdala, including the intercalated (ITC) and the basolateral nuclei (BLA). A majority of the connections from both of these nuclei are then sent to the central amygdala (CeA), which then projects to a variety of structures in the limbic system. Whereas cells in the BLA are excitatory (McDonald et al. 1989), the cells in the ITC are inhibitory (Nitecka and Ben-Ari 1987; McDonald and Augustine 1993; Paré and Smith 1993). Therefore, information sent through the BLA (excitatory) and the ITC (inhibitory) neurons are likely to have different effects on the target systems. Given that mPFC has strong connections to both these nuclei in the amygdala, some of the deficits seen in emotional regulation due to play deprivation may arise from reduced regulatory control of the amygdala by the mPFC. In part, the mPFC may exert regulatory control by modulating the activation of the excitation and inhibition of the specific nuclei in the amygdala (Rosenkranz and Grace 2002). Regardless of the specific mechanisms, the play-induced changes to the mPFC likely have an effect on the regulation of the amygdala.

The dorsal raphe nuclei (DRN) constitute another subcortical area activated by playful interactions (van Kerkof et al. 2014). The majority of the neurons that innervate the DRN come from the mPFC (Peyron et al. 1998; Vertes 2004), and these connections act to inhibit serotonin neurons (Jankowski and Sesack 2004; Hajos et al. 1998). The DRN is strongly activated if animals encounter uncontrollable stress and this is coupled with heightened levels of fear and anxiety (Grahan et al. 1999; Maswood et al. 1998). However, the strength of this activation and behavioral response can be reduced if animals are exposed to mild controllable stressors earlier in life. The attenuation of DRN activation likely arises from improved regulatory control from the mPFC (Amat et al. 2005; Amat et al. 2006).

Linking these neural connections with play suggests the following model. Engaging in playful interactions, young rats are exposed to both controllable and uncontrollable situations (Pellis, Pellis, and Foroud 2005), and it is these experiences that are hypothesized to influence the development of the mPFC (Pellis, Pellis, and Bell 2010). In turn, these play-induced changes to the mPFC may improve the regulatory control of the mPFC over subcortical regions such as the amygdala and the DRN. These play-induced changes in neural organization are the basis for the improved executive control present in rats that have played as juveniles.

## Conclusion

Why do rats have complex patterns of play fighting that contribute to the juvenile experiences that, in turn, refine the development of the neural circuits that regulate executive function? And, why do mice not have these patterns of play? Mice and rats have much of their behavioral repertoire in common, but for a wide range of naturally occurring behaviors and in tasks requiring motor and cognitive-skill acquisition, mice appear to be a pared-down version of rats (Whishaw et al. 2001). Quite simply, mice have a behavioral repertoire that is only modestly capable of being refined. Possibly, this results from mice having a shorter life span and achieving sexual maturity at a younger age than do rats, so that the capacity for excessive refinement of skills would be counterproductive—i.e., the cost of such a capacity would exceed the benefit. For their part, rats live in a somewhat more complex social system, have a longer lifespan, and reach sexual maturity at a later age, increasing the benefits that arise from an increased capacity to be more flexible in dealing with unpredictable events (Whishaw et al. 2001). There is support for such a hypothesis.

It has been shown that in rodents, primates, and birds more complex patterns of play correlate with longer juvenile periods (Diamond and Bond 2003; Pellis and Iwaniuk 2000b), and, in turn, longer juvenile periods are correlated with larger brain sizes and a greater variety and flexibility in species typical behavior (Joffe 1997; Walker et al. 2006). Moreover, innovative ability correlates with increased brain size, especially in those brain areas associated with executive function (Lefebvre, Reader, and Sol 2004; Reader and Laland 2002).

When comparing primate species, those that have more complex social systems require more nuanced social cognition and actions, and these are the species that are also more likely to use play in adulthood as a social tool for assessment and manipulation (Pellis and Iwaniuk 2000a; Ciani et al. 2012; Palagi 2006). Importantly, with regard to the role of play in the juvenile period promoting improved executive function, the juveniles of such species have a modified pattern of play that exaggerates the experiences shown to be important for the development of such capabilities (Reinhart et al. 2010). Indeed, these changes in the pattern of play, such as increasing the movements that lead to loss of control (Pellis, Pellis, and Foroud 2005), are associated with changes in factors related to the timing of development—they extend the juvenile period (Palagi and Cordoni 2012). These age-related changes in development, which lead to longer juvenile periods and to the retention of more juvenile-like features into adulthood, are the same kinds of processes that underlie domestication (Hare, Wobber, and Wrangham 2012). Interestingly, domestication in rats has made them more playful and more likely to engage in wrestling (Himmler et al. 2013), whereas the play fighting of domesticated mice (Pellis and Pasztor 1999) is little different from that of the wild type (Wolff 1981).

Thus, like other transformations in play (Burghardt 2005), there are likely important enabling factors, such as an enlarged brain, a long juvenile period, and complex social systems, that create the conditions that make it beneficial to change the pattern of play to refine the brain's executive functions. It is among such species that we can find the role of play in making the brain more adaptable.

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