The Function of Play in the Development of the Social Brain

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Rough-and-tumble play, or play fighting, is common in the young of many mammals. Research on play fighting among rats shows that there are many levels of neural control over this behavior: subcortical mechanisms mediate the motivation and behavior of such play, and the cortex provides mechanisms by which the play changes with age and context. The cortical mechanisms help to explain the advantages playing offers the brain. The cortically induced modulations of the content of play with age ensure that exposure to particular kinds of experiences are enhanced during the critical juvenile period. These experiences, in turn, modify the development of other areas of the cortex. Such cortical changes appear to mediate the effects of play on the refinement of social skills. As a result, rats that play as juveniles are more socially competent as adults. This work was supported by the Natural Sciences and Engineering Research Council of Canada and the Alberta Heritage Foundation for Medical Research.

Introduction

Why do animals play? The question has perplexed scientists for over a century (Burghardt 2005; Smith 1978). Attempts to answer it have often confounded two definitions of why something happens in a biological system (Fagen 1981). The claim that play occurs because animals are happy and stress free usually makes reference to some of the psychological and physiological processes that foster play. In turn, the claim that animals play because it offers some beneficial outcome, such as the refinement of motor skills, points to the possible reasons such behavior evolved. Note that the two explanations are not mutually exclusive. An animal can play because it is happy and because its motor skills benefit from doing so. The first seeks to explain the behavior by the mechanisms within the animal or by the context that promotes it. The second seeks to explain the behavior by its beneficial consequences. These beneficial consequences, acted upon by natural selection, give an advantage to those members of the population that play over those that do not (Alcock 2005). Such a process leads to the spread within the population of psychological and physiological mechanisms that promote the occurrence of play, and the consequences of selective advantage can be thought of as the adaptive value of play.

While the two explanations are not mutually exclusive, real problems emerge within each category. There is a growing body of work that has identified and characterized many of the psychological and physiological mechanisms necessary either to produce play or modify its content (Burghardt 2001; Panksepp 1998; Pellis and Pellis 1998; Siviy 1998; Vanderschuren et al. 1997). Currently, there are many conflicting theories regarding the relative role or importance of any one of the factors, and some researchers wonder if stressful situations invariably diminish play or if such situations actually enhance play (Pellis and Pellis 2009). Even more difficult has been the quest to find explanations regarding the benefits of play. Many such benefits have been proposed (Baldwin 1986), but few have garnered convincing support (Martin and Caro 1985).

There are three likely reasons for this difficulty with identifying the adaptive value of play. First, play is likely to be multifunctional. That is, it may have more than one adaptive benefit, and any given species may evidence some, all, or none of the benefits. This being the case, cross-species comparisons can be troublesome. What may appear a promising explanation in one species may not be replicable in another (Burghardt 2005; Pellis and Pellis 2009).

Second, the benefits accrued from playing may be either immediate or delayed. Given that play most often occurs in immature animals, the majority of theories related to the adaptive value of play have focused on how playing in the immature stage of development fosters enhanced performance later in life, which means scientists have mostly concentrated on the delayed benefits of play (Fagen 1981). However, play can also be quite common in adulthood in many species, and any benefits at this stage of life are likely to be more immediate. One such benefit of adult play, especially socially, has been its use in assessing and manipulating social partners (e.g., Palagi 2006; Palagi et al. 2004; Pellis 2002a; Pellis and Iwaniuk 2000). And, there are likely immediate benefits for playing at all ages. Therefore, when examining the play of immature animals, those play behaviors important for their immediate effects need to be carefully teased away from those important for delayed benefits (Pellis and Pellis 2009).

Third, play tends to be a behavior engaged in only after all other needs are met, so the opportunity to engage in this behavior can vary with food availability and with other environmental stressors, both physical and biological. Even in free-living populations of the same species, the occurrence of play can vary from location to location, between seasons, and across generations (e.g., Baldwin and Baldwin 1974; Berger 1979; Barrett et al. 1992; Stone 2008; Pellis 1981). Thus, especially for delayed benefits, it cannot be that play is essential for proper development. Indeed, the absence of play does not compromise the emergence of species-typical behavior patterns, so play, when available, must only serve to refine or facilitate development (Martin and Caro 1985). If the role of play in development is contingent rather than essential, the likely benefits of play are small and subtle, making definitive experiments unlikely and cross-species replication difficult.

With regard to delayed benefits, the theories that contain the following assumptions, consistent with the above limitations, are most likely fruitful avenues of research: development need not include play; and under conditions where play is possible, its presence should enhance the skilled execution of capabilities otherwise developed independently of play. Two such theories have been proposed, and our work on the role of play in the development of social behavior in rats not only provides support for both theories but also suggests that the two may actually be connected at a metatheoretical level. That is, a third theory may be able to subsume both existing theories.

The Motor-Training Hypothesis

This hypothesis asserts that play during the juvenile period prepares the motor system of animals for engagement in adult behaviors (Brownlee 1954). The motor system includes the muscles and the nervous system. As predicted by this hypothesis, after vigorous play, modifications occur in muscles and the nervous system. While the changes in the muscles are typically short term, there is some evidence that exercise affects brain structure and function, and this effect may be longer lasting when it occurs early in childhood (Tomporowski et al. 2008). Byers and Walker (1995) noted an interesting correlation between the frequency of play with age-related changes in the anatomy of the cerebellum, a part of the brain critically important for motor performance, and the motor neurons of the peripheral nervous system.

One avenue of developmental change in the nervous system involves individual nerve cells differentiating into their typical adult form. A second avenue of developmental change relates to the fate of the cells and the branches—called dendrites—emitting from those cells. These dendrites provide the communication network of contacts—the synapses—with other cells. Initially, both cells and dendrites proliferate, but then they are pruned down to their adult-typical number and dendritic arbor (Rao and Jacobson 2005). Byers and Walker (1995) found that the critical period for cerebellar synaptic pruning and motor-neuron differentiation occurs at roughly the same time as the peak play period of the juvenile phase in three species of mammals—rats, mice, and cats.

The motor-training hypothesis raises the possibility that play in the juvenile period functions to shape brain development more broadly (Allman 1999). Indeed, this extended version of the hypothesis finds support in Fairbanks (2000), who has shown that different types of play peak at different times during the infancy of monkeys and that these peaks correspond to the times at which different—and presumably associated—brain areas mature. Such correlations suggest that peak periods of play and peak periods of maturation in different brain areas overlap. Again, the important point here is that, in the absence of play, these changes can still occur, and they must do so, since some species do not play at all (Pellis and Pellis 1998). The theory suggests that, when available, play can facilitate and refine neural systems. If so, then it should be the case that animals that have had the opportunity to play as juveniles should function at a higher level of sophistication in some skill sets than animals that do not have such opportunities.

A major problem for the motor-training hypothesis, however, is that its evidence rests on correlations, and correlations say nothing about causality. It may simply be that in the species studied, brain changes and occurrences of play are merely coincident, and play has no causal effect on neural development. Besides, in the species compared by Byers and Walker (1995), the play was predominantly asocial in one species and predominantly social in the others. Not only does this raise questions about which behavioral experiences are affecting the brain, but also about why such experiences are having their effect on any particular part of the brain.

The Training-for-the-Unexpected Hypothesis

This hypothesis posits that when animals play, they expose themselves to variations in actions, many of which lead to unpredictable outcomes. This, in turn, serves to train animals to cope with an unpredictable world (Špinka et al. 2001). In other words, animals that play are not as easily flummoxed when they encounter an unexpected impediment. If this is so, then one would predict that animals would include in their play movements that allow for the experience of losing control due to unpredictable events. And, indeed, there is some evidence that animals do so (Pellis et al. 2005; Petrů et al. 2008). Again, as with the motor-training hypothesis, play is not essential, but when available, it can lead to improved performance.

The training-for-the-unexpected hypothesis, however, is not the only hypothesis to predict variability in play. Baldwin and Baldwin (1977), for example, have suggested that exploration and play provide a vehicle for providing sensorimotor stimulation, and so play is a means of exposing an animal to new situations and of its testing new behaviors. This hypothesis predicts that as each type of play emerges during development, it should begin with a simple repertoire and gradually become more complex with age—a pattern investigators have reported in both monkeys (Baldwin and Baldwin 1977) and birds (Pellis 1981). Simply demonstrating behavioral variability during play, therefore, does not uniquely support the training-for-the-unexpected hypothesis. To confirm the hypothesis, we need specific evidence of variable actions performed at moments in play that ensure unpredictable consequences.

Enter the Rat

Play in rats mostly involves play fighting, where pairs of rats compete for access to the partner's nape, which if contacted, the rat then gently nuzzles (Pellis and Pellis 1987; Siviy and Panksepp 1987). Such interactions can involve complex sequences of attack, defense, and counterattack (figure 1). To protect its nape, a rat can use a variety of defensive maneuvers (Pellis and Pellis 1987), and these can be systematically scored (Pellis et al. 1992). A rat can evade nape contact by simply moving its nape and head away from the partner (e.g., swerve away, run, or leap away), or by turning to face its attacker. When turning to face the attacker, two major options are available to the defender: it can roll over onto its back, or it can remain standing. From either position, it can ward off further attacks. Once it has succeeded, it launches counterattacks of its own. Rolling over into a supine position is the most common defensive tactic a rat uses during its juvenile period (Pellis and Pellis 1987, 1990, 1997) and the one that most typically leads to the "pinning" configuration (one animal on the bottom, supine, and the other animal on top of it, ventrum to ventrum) (Panksepp 1981).

Some findings are relevant both to the motor-training hypothesis and the training-for-the-unexpected hypothesis. Depriving rats of play during their

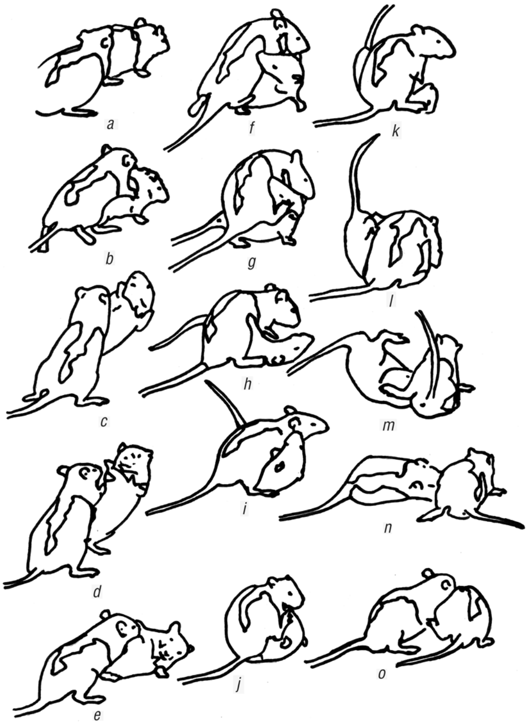

Figure 1. Two juvenile male rats, at about thirty-five days old, engage in a play fight in which they compete for access to the nape of each other's neck. The rat on the left begins by approaching from the rear (a) and pouncing at the nape of its partner's neck (b). Before contact is made, however, the defender rotates around the longitudinal axis of its body (c) to face its attacker (d). The attacker continues to move forward, pushing the defender onto its side (e), and then, onto its back, as the attacker continues to reach for its opponent's nape (f and h). From the supine position, the defender attacks its partner's nape (i), but it is blocked by its partner's hind foot (j and k). After another attempt to gain access to its partner's nape, the rat on top is pushed off (l and m), enabling the original defender to regain its footing (n) and again attack its partner's nape (o). (From Pellis and Pellis 1987, reprinted with permission of John Wiley & Sons, Inc.)

juvenile periods produces long-term cognitive, behavioral, and socioemotional deficits. While depriving young rats opportunities to engage in social play also limits other aspects of their social experiences, it could be argued that it is not the play itself that is important. Yet many studies—from many different laboratories using different procedures for encouraging rats to play—show that how much or how little rats play determines the amount of social contact they enjoin during the juvenile period. (For a review of the deficits in social contact and for the evidence implicating the important role of play in relation to them, see Pellis and Pellis 2006). One example will illustrate this point. Juvenile rats reared with adult females experience all the typical social behavior of rats such as social investigation, social grooming, and huddling. But these younger rats do not engage in play, because adult rats do not find juvenile rats attractive as play partners and because adult females, at the best of times, play very little. In contrast, a juvenile housed individually but given daily exposure to another juvenile for one hour per day experiences play in addition to the typical social behaviors. When tested as adults, the rats reared with an adult exhibit the above-mentioned social contact deficits, but the rats that had even limited exposure to other juveniles did not show the same deficits (Einon and Morgan 1977; Einon et al. 1978).

We think it important to note that because play fighting is an inherently social behavior, when juvenile rats do not do it, they become socially incompetent as adults (Pellis and Pellis 2007). Such rats overreact to benign social contact, such as social sniffing. This makes them hyperdefensive, and they are more likely to escalate encounters to aggression (Einon and Potegal 1991; Potegal and Einon 1989). Furthermore, when they are introduced into rat colonies, these rats fail to exhibit the appropriate submissive behavior when confronting dominant males, and they persistently attract aggressive attacks. They also fail to adopt strategies to circumvent attracting the ire of dominant rats (Hol et al. 1999; van den Berg et al. 1999; von Frijtag et al. 2002). Also, rats without juvenile play experiences remain overly stressed after encountering such situations (von Frijtag et al. 2002). Finally, these rats appear to have difficulty coordinating their movements with those of their social partners (Moore 1985; Pellis et al. 1999).

The litany of the social woes of rats deprived of play appears consistent with their deficient abilities in dealing with unpredictable social situations, and so it generally supports the training-for-the-unexpected hypothesis. However, as we said, these findings do not support only this hypothesis. For play in the juvenile period to function specifically to train animals to deal with the unexpected, it must be organized during the juvenile period in such a manner as to exaggerate the unpredictability—not just the novelty—of the experience. Similarly, if play serves to refine the development of the nervous system, the expanded version of the motor-training hypothesis would call for the brain areas that underpin these social skills to be different in some way from those of rats that have had no play experience. That is, brain systems specifically related to the skills being enhanced during play have to be affected by the play, and so they need to be malleable to modification at that age.

Testing the Hypotheses

Recall that in rats, play fighting involves competition for access to the partner's nape. Play fighting peaks in the midjuvenile period, thirty to forty days after birth (Thor and Holloway 1984), but it begins about a week before weaning (Bolles and Woods 1964; Pellis and Pellis 1997) and continues well into adulthood (Pellis and Pellis 1987, 1990). The age-related changes in the frequency of play fighting follows changes in the number of playful attacks launched. The likelihood of such attacks eliciting a defensive response, however, remains relatively constant (80 percent or more) at all ages (Pellis and Pellis 1990, 1991a, 1997; Thor and Holloway 1983). What *does* change at different ages is the kind of defensive tactic used (Pellis, 2002b; Pellis and Pellis, 1987). Generally, at all ages, evasive defense is used about 20 or 30 percent of the time. However, the relative use of the supine tactic rather than the standing defense tactics, changes markedly with age. The sex of the rat further complicates these changes.

For both sexes, from the onset of play, standing defense is the most common tactic before the juvenile period. When male and female rats reach their juvenile period, they most commonly use the supine defense. Then, with the onset of puberty, males revert mostly to using the standing defense, whereas females, as adults, continue mostly to use the supine defense (Pellis and Pellis 1990; Smith et al. 1998). Thus, there are two transitions: one for both sexes from weaning to the early juvenile period and the other, for males, at around puberty (Pellis 2002b). With puberty, a further complication arises for males as they form dominance relationships. While dominant males invariably show the adult-typical pattern of play, subordinates vary their pattern depending on the identity of their play partner (Pellis and Pellis 1991b). Subordinate males playing with other subordinates or with females primarily use the standing tactic, but when they play with a dominant male, they primarily use the supine tactic (Pellis and Pellis 1992; Pellis et al. 1993; Smith et al. 1998). Since play fighting is most common among juveniles and the absence of play at that age has devastating effects on the development of social competence, closer inspection of these age-related changes offers potential insight into the function of play.

Training for the Unexpected

Given that rats of all ages are capable of executing the standing defense, the question arises: Why do rats favor the supine defense in their juvenile period? Indeed, from the point of view of an effective defense against nape contact, a standing defense is superior to a supine defense. From the standing defense position, the defender can readily shift to other patterns of defense—like hip slams and foreleg boxing while upright—and more readily execute successful counterattacks to the partner's nape (Pellis and Pellis 1987). In this regard, rolling over to a supine position and blocking access to its own nape relinquishes the initiative to the partner on top. Perhaps the predominant use of the supine defense in the juvenile period ensures that the defender experiences loss of control over its own movements and over those of its partner—an interpretation consistent with the training-for-the-unexpected hypothesis.

The behavior of the partner that assumes the position on top during play fighting supports the training-for-the-unexpected hypothesis as well. Usually, when a rat has rolled over into the bottom position, its partner on top continues to grasp and restrain the movements of the supine animal and maneuvers to gain access to its nape (figure 1f–k). Typically, the animal on top keeps both its hind feet planted on the ground, anchoring itself so that it can move its torso and forelimbs to counter the maneuvers of its partner on the bottom (figure 2a). However, in the juvenile period, something seemingly peculiar happens. The animal on top more often stands on top of its supine partner with all four of its feet (figure 2b) (Foroud and Pellis 2003). It is not that rats are simply more playful at this age, but rather, it seems they genuinely prefer to stand so (Foroud and Pellis 2002). Standing on top of a squirming, supine partner with all four feet makes an animal less able to maintain its own posture. Indeed, the likelihood of the supine rat successfully launching a counterattack is much greater when one stands on top with all four of its feet (Pellis et al. 2005). Thus, both attacker and defender behave in ways that diminish their dominance over the partner's actions, increasing their loss of control and their experience of unpredictability.

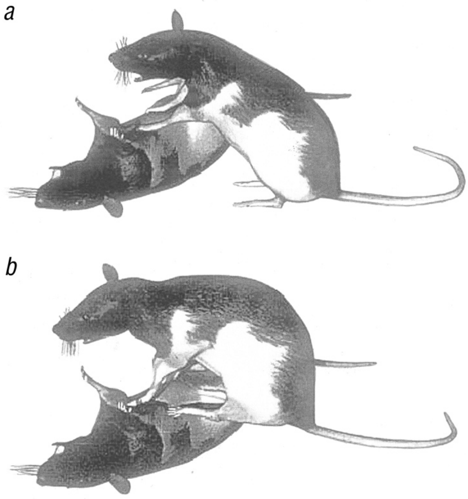

Figure 2. When engaged in play fighting, rats often adopt a posture where one animal stands over the other rat, which is lying on its back. However, the posture of the rat on top can take one of two forms: it can hold its partner down with its forepaws while standing on the ground with its hind paws (a) or, it can stand on its partner with all four of its paws (b). (From Foroud and Pellis, 2003, reprinted with permission from John Wiley & Sons, Inc.)

The existence of highly specific neural mechanisms that regulate these age-related changes in patterns of defense also supports the training-for-the-unexpected hypothesis. If you remove the entire cortex of neonatal rats, they remain playful, they use all the tactics of attack and defense, and they—like rats with intact cortices—exhibit the age-related changes in the frequency of play (Panksepp et al. 1994; Pellis et al. 1992). The rats that have had their cortices removed, however, do not exhibit the age-related changes in defense tactics or the age-related change in how they stand on top of the supine partner (Foroud et al. 2004; Pellis et al. 1992). These rats do not undergo the unique reorganization of play in their juvenile period the way normal rats do. Furthermore, it appears that even more selective damage to the motor cortex blocks these age-related changes in defense (Kamitakahara et al. 2007). The fact that other rodents do not undergo such age-related changes in defense (Pellis and Pellis 1998) suggests there is a specific neural switch in rats that seems to have no effect other than to reorganize play in the juvenile period. These findings suggest that play fighting in rats is designed to ensure that juveniles frequently experience an unpredictable loss of control. Again, this is as one would predict from the hypothesis of training for the unexpected.

The Motor-Training Hypothesis (Extended Version)

The prefrontal cortex (PFC) of the brain regulates social skills such as using and recognizing appropriate social signals in appropriate contexts (Kolb 1990). Damage to areas of the PFC in both humans and other animals leads to a variety of deficits, but not to altered, age-related changes either in the frequency or content of play fighting in rats. It does, however, lead to changes in the animals' social skills. Rats that do not play as juveniles apparently develop two major social deficits: they cannot change their behavior with different partners; and they fail to coordinate their movements with their partner (e.g., Moore 1985; Pellis et al. 1999; van den Berg et al. 1999; von Frijtag et al. 2002). Damage to one area of the PFC, the orbital frontal cortex (OFC), makes a rat unable to modify its behavior in relationship to its partner's identity (Pellis et al. 2006). Damage to another area, the medial prefrontal cortex (mPFC), appears to dampen the rat's ability to coordinate complex sequences of movement with its partner (Bell et al. 2009). Therefore, damage to the PFC of rats that have had normal play experiences leads to the same kinds of deficits in social skills typical of rats with intact brains that have not had the opportunity to play as juveniles. For the motor-training hypothesis to be correct—and, especially, the extended version that links behavior to relevant areas of the brain—we would expect that the absence of play-derived experiences in the juvenile period leads to an altered development of the PFC.

Researchers, in fact, have examined the anatomy of the neurons of the PFC in adult rats, some that had play experience as juveniles and some that did not. The researchers found in their rat subjects critical differences in the degree of arborization of the dendrites of their cells. Rats that had been reared with adults as juveniles—and had thus experienced social interactions but few, if any, play fights—had neurons that differed from rats that had been reared with peers as juveniles and had thus experienced play in addition to other forms of social behavior (Bell et al. 2010). Three complications, however, mar the simplicity of this relationship. First, as we noted earlier, during development, brain maturation typically involves a pruning of the number of cells and dendritic branches. While this is generally true, in some areas of the nervous system, development can involve an increase in complexity, and this applies to the different dendritic fields of the different areas of the PFC (Douglas et al. 2004). Furthermore, the two areas of the PFC appear to undergo complementary changes: increases in the complexity of one are coupled with decreases in the complexity of the other (Kolb et al. 2004). Second, neurons have one cluster of dendrites that project upward from the top of the cell (i.e., apical) and dendrites that project downward from the base of the cell (i.e., basilar). Altered dendritic arbor can occur in one or both sets of projections. Third, these two areas are affected differently by different social experience during the juvenile period. The experience of play is critical for the pruning of the apical dendrites of the neurons of the mPFC, and the experience of multiple social partners is critical for the proliferation of the basilar dendrites in the OFC (Bell et al. 2010).

How these changes in dendritic arbor and neural connections lead to changes in the way these areas of the PFC function remains to be determined. Indeed, we do not know whether these cellular-level changes in anatomy are directly responsible for the changes in behavioral function or whether they are incidental byproducts of the relevant changes. Nonetheless, given that there are a number of different learning and memory tasks that are differentially dependent on OFC and mPFC function (Kolb 1995), rats with anatomical changes in these brain areas coming from differential social experiences in the juvenile period could be tested to evaluate whether or not these anatomical changes map onto cognitive, emotional, and behavioral differences in performance. Also, if changes in the PFC that lead to supposed improved social skills are the reason natural selection favored this form of play experience in the juvenile period of rats, it should also be the case that such play-derived improvements in performance would lead to improved survival and reproduction. One experimental approach could be to create colonies of rats with known differences in juvenile play experience and evaluate whether those that are supposedly more socially skilled actually sire more offspring.

Despite the complexities of changes in cellular structure during different experiences early in life (Kolb 1995), several pieces of converging evidence point to the importance of social experiences, especially those derived from play in the development of the PFC. First, we know that the PFC matures during the juvenile period (Kolb 1990) and that the number of neurons in this area is modified by peer-peer interactions occurring during this period (Markham et al. 2007). Second, the dendritic arbor of cells from this area is affected by the experience of peer-peer play interactions in the juvenile period (Bell et al. 2010). Third, during play, growth factors that promote neural development are released in these same brain areas (Gordon et al. 2003). Therefore, the extended version of the motor-training hypothesis finds support—juvenile play experience is organized in a manner to promote the development of those brain areas associated with the skills used during play.

A caveat here is that the differential effects on the OFC versus the mPFC should alert us to both direct and indirect effects of play on brain development (Pellis and Pellis 2009). For the dendritic changes to occur in the mPFC, it is critical for an animal to experience rough-and-tumble play with at least one peer. This suggests that the mPFC neurons are directly susceptible to the experiences derived from play itself. In contrast, for the OFC neurons, it is not the experience of play itself that matters but, rather, the opportunity for the animal to engage in social interactions of any kind with multiple partners. Given that in colonies of free-living rats, the impulse to play likely provides juveniles with the opportunity to interact socially with multiple animals, the role of play for the development of this area of the brain remains important but is likely to be an indirect one. Future studies need to separate those effects specifically due to the experiences derived from the act of playing itself from those encountered because the animals play. Regardless of the precise mechanisms, the evidence appears strong that play fighting in rats promotes the development and refinement of those brain areas that are involved in the very social skills crucial for play and other social behavior.

A Metatheory: Experiencing the Unexpected Improves Self-Regulation

Data on the development of brain and behavior in rats as it relates to the role of play provide support for both the training-for-the-unexpected and the extended motor-training hypotheses. It is important to remember that, as we noted earlier, play varies dramatically across species, and it is likely multifunctional. Thus, while both rats and mice have complex patterns of locomotor play (Pellis and Iwaniuk 2004), social play in mice is impoverished when compared to that of rats (Pellis and Pasztor 1999). Therefore, as Byers and Walker (1995) originally proposed, in both mice and rats, the locomotor experiences derived from play may function to refine the areas of the brains intimately involved in the coordination of movement, such as the cerebellum, although it is unlikely that the rudimentary pattern of play fighting present in mice is useful for refining the anatomy and function of the PFC (Pellis and Iwaniuk 2004) as the more complex pattern of play fighting appears to do in rats (Bell et al. 2010; Pellis and Pellis 2009). By considering such differences between species, the question becomes one of identifying how particular play-derived experiences can modify the development of specific areas of the brain. This inquiry requires identifying and characterizing the relevant experiences and the molecular mechanisms by which these experiences exert their influences on the cells of the neural circuits involved. Then, in turn, we must understand how these altered neural circuits change the functional capabilities of these brain areas. The pattern that has emerged from rats suggests a possible framework for the further exploration of these mechanisms. This framework emerges partly from bringing together the two hypotheses for the adaptive function of play we have explored in this article.

Training for the unexpected posits that animals with play experience are less affected by unpredictable events (Špinka et al. 2001). This may occur because play somehow dampens the emotional reaction to a novel, unpredicted situation. Several lines of evidence converge on this possibility. First, we know rats that have not had play experience as juveniles overreact to situations, such as encountering another rat; and when confronting such situations, they have an exaggerated physiological stress response (von Frijtag et al. 2002). Second, rats deprived of play as juveniles exhibit an increased fear response when tested in novel environments, even nonsocial ones such as an open field (Arakawa 2003). A common instrument used to test fear or anxiety in rats is the elevated radial-arm maze. As the name implies, the maze is elevated above the ground (about a meter), and several long, thin platforms radiate from the center. While some of these arms are covered, some are open. In such a maze, the more fearful or anxious rats avoid moving from one arm to another and tend to remain in the covered arms rather than in the open ones—that is, they go where they would be most protected (Walf and Frye 2007). Yet, when given an anxiolytic, such as an anxiety-reducing drug like diazepam, rats that have been deprived of play explore all the arms of the maze just as much as rats that had the opportunity to play (da Silva et al. 1996). Third, we know that, when stressed, rats are less capable of using their cognitive and motor skills effectively (McEwen and Sapolsky 1995; Metz et al. 2001, 2005; Roozendaal 2002; Smith and Metz 2005). Thus, rats cannot perform well if their emotional reaction to a situation proves too great. But if as juveniles they have had the opportunity to play, they seem better able to restrain their emotional response.

One way, then, play experiences in the juvenile period may enhance performance in adulthood is by dampening the fear of novel situations. Supporting this possibility is that a major brain structure known to regulate fear and its related, negative affective states is the amygdala, a bilateral structure that is situated beneath the temporal lobes and under inhibitory control of the PFC (LeDoux 1996). The PFC dampens the activity of the amygdala, thus preventing emotional overreaction. Given the findings reviewed in this article, which strongly suggest that the experience of play directly and indirectly influences the development of the PFC, this mechanism may be the vehicle play uses to train animals to be more resilient in the face of an unpredictable world. Thus, for rats, the two hypotheses—training for the unexpected and extended motor training—converge into one process: play trains animals to be resilient by modifying the neural circuitry that regulates emotional responses. Whether the two hypotheses diverge for other forms of play, such as locomotor play, and for other species, such as mice, still has to be evaluated empirically. Nevertheless, the evidence for rats does suggest that these are two potentially useful hypotheses for guiding further research to connect the peculiarities of play with the brain mechanisms that are modified by them.

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