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The Genesis of Animal Play

Testing the Limits

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5 Nothing Is Simple: Studying the Hows and Whys of Play

5.1 Introduction

How did the many forms of play and playlike behavior originate? To answer this question, we cannot assume that all behaviors satisfying the play criteria have the same causal (neurobiological) mechanisms or that they are evolutionarily homologous and have common ancestral roots. The evidence presented in this chapter and throughout the rest of this book shows that the normal behavior, ecology, ontogenetic development, metabolism, neural organization, and phylogeny of a species influence the manner in which it expresses play. In fact, it is because play is, as part II shows, a heterogeneous category that arose repeatedly in the evolution of animals that we need clear criteria to help us sort out the processes and variables influencing playfulness and to point the way to experiments and critical phyletic comparisons. As the heterogeneous nature of play becomes recognized, it will become more acceptable to see play as a distinctive set of transitional behavior patterns linking a variety of behavioral phenomena with diverse qualitative and continuous attributes (Baerends, 1990).

Although many major concepts needed to understand play were extant near the beginning of the twentieth century (chapter 2), a half century later the most prominent comparative psychologist of the mid-twentieth century, reviewing animal play, concluded that “current views on the subject are considerably confused” (Beach, 1945: 523). Compartmentalization of play research (e.g., human versus nonhuman, neurological versus comparative, descriptive versus experimental, causal versus functional, field versus captive settings) is one reason for the slow progress in understanding play in mechanistic, developmental, or evolutionary terms.

Although there has been much relevant recent work on animal play (Bekoff & Byers, 1998; Burghardt, 1998b; Panksepp, 1998a; Pellis & Pellis, 1998a), a broader conceptual integration is needed. The preceding chapters have gathered some of the essential materials and tools needed to construct a framework for explaining the genesis of play.

In chapter 1 the need for an integrative approach built around the basic ethological aims was established. Chapter 2 reviewed early play theory, which, it turns out, contains the basic elements that can be used in a modern framework, although it took a century for theoretical clarification to occur. The necessary step of providing criteria for recognizing play was accomplished in chapter 3. A description of different kinds of play and play attributes was provided in chapter 4.

In this chapter basic biological factors helpful in the search for explanations of the origin and diversity of play are outlined. This is followed in chapter 6 by an attempt to join the causal mechanisms and developmental processes of play in individual animals within an evolutionary scheme. The goal is to explore how play originated in ancestral species and diversified in extant ones while gaining new functions that possibly facilitated behavioral, emotional, and cognitive complexity. In this chapter, which is updated from earlier analyses (Burghardt, 1984, 1988b, 2001), hypotheses and conclusions are emphasized. The model outlined in the next chapter is meant as a temporary tool to use in evaluating the diversity of behavior and species covered in part II. Empirical tests of the model's predictions, especially comparative ones, are thus not included in these two chapters.

I became professionally interested in play for two major reasons. The first was the difficulty researchers have had in demonstrating that play in any species has deferred benefits, in spite of appearing "purposeless." The second was that throughout my research career devoted to studying behavioral development in reptiles in both nature and captivity, I saw little that could be viewed as play in the traditional sense the concept was used (Burghardt, 1982, 1984). Yet reptiles are capable of considerable learning and complex sociality (Burghardt, 1977a,b). Why do they not play (Burghardt, 1982)? Most play theory in animals was focused on the most playful mammals, typically primates, ungulates, and carnivores (Bekoff & Byers, 1981; Fagen, 1981, 1993; Müller-Schwarze, 1978) along with laboratory rats (Hole & Einon, 1984). Thus the challenge was to try to understand why many mammals, but virtually no nonavian (ectothermic) reptiles, were considered playful (e.g., Fagen, 1981). Rather than the typical "top-down" approach to understanding the origins and radiations of playfulness, careful observations were needed of animals that seemed not to play (at least in obvious ways) or to play rarely, as well as of those animals that play a great deal. I have called this approach a "bottom-up" strategy versus the top-down view taken by most researchers on animal play (Burghardt, 1998a).

This chapter is not a review or detailed comparison of current theories of animal play, which are becoming increasingly sophisticated in trying to explain the role of play in animals that are highly playful (Bekoff & Byers, 1998; Caro & Alawi, 1985; Pellegrini & Smith, 1998; Pellis, 1993; Pellis & Iwaniuk, 1999a; Power, 2000; Spinka, Newberry, & Bekoff, 2001). Rather, it is an overview of issues related to searching for the origins of play constructed around the five ethological aims (chapter 1).

Table 5.1

General categories of proposed benefits of play

Benefit	Example
Motor development	Improve coordination in locomotion
Physiological development	Improve cardiovascular system and endurance
Perceptual-motor coordination	Improve integration of sensory modalities
Adult species-typical behavior	Improve prey capture or parenting abilities
Social-communicative skills	Improve ability to react appropriately to others
Social roles	Determine dominance-submission status or gender roles
Information	Learn what objects and other animals do
Neural development	Consolidate and integrate neural pathways
Cognitive abilities	Improve responses to environmental challenges
Creativity	Provide source of novel behavioral responses
Competence assessment	Allow parents to assess normative development

5.2 Searching for the Benefits of Play: Misplaced Priorities?

5.2.1 The Numerous Claimed Benefits of Play

For over a century claims have been made concerning the positive, perhaps crucial, role of play in the mental life and behavior of human and even nonhuman animals (Burghardt, 1999; Fagen, 1981). More than thirty functions have been proposed (J. D. Baldwin & Baldwin, 1977, 1981); table 5.1 lists the major (and overlapping) types of general benefits of play. These functions, derived from theory, have remained controversial and largely unsupported empirically (P. Martin & Caro, 1985; Power, 2000; P. K. Smith, 1988, 1996). Earlier writers concluded after reviewing all the factors influencing play in primates that multiple functions had to exist (e.g., Poirier, Bellisari, & Haines, 1978; Poirier & Smith, 1974), but the search for *the* major function of play persists. Claims have been made that play perfects instinctive behavior and facilitates learning (including reading and mathematics in children) and imitation of novel behavior, imagination, socialization, behavioral flexibility, mental agility, and creativity (e.g., Fromberg & Bergen, 1998; Hartley, Frank, & Goldenson, 1952; Miklosi, 1999). Conversely, lack of play can lead to disruptive, hyperactive children who need to be drugged (Panksepp, 1998a,b) or suggests, if it does not predict, children who later may be prone to violent criminality (S. Brown, 1998). Evolutionary arguments based on selected comparative data often accompany these assertions (e.g., Fagen, 1984). In spite of the lack of experimental support (Power, 2000), such claims have certainly been viewed as plausible by many who have studied play. Even those most responsible for disproving experimental results on the value of play in children find it difficult to completely dismiss these putative benefits (e.g., P. K. Smith, 1996).

Play actually may have an important role in the behavioral, social, emotional, cognitive, physiological, and developmental realms in the lives of many animals, including people. However, this role is likely to be multifaceted, variable, and often involve complex, indirect, and subtle processes, as indicated by the finding that there is some plausible evidence supporting almost every claim in table 5.1. It is this protean complexity that makes play an often paradoxical and socially controversial topic, as chapter 1 asserted and which the last chapter will revisit.

Although most views of play focus on the benefits of play itself, there are other possibilities as to its function, such as David Chiszar's view of play as a signal to parents that their offspring are competent and developing normally (Chiszar, 1985).

5.2.2 How Do We Demonstrate That Play Is Adaptive?

Much has been written over the past 20 years or more on the importance and adaptive significance of play in animals (Caro, 1988; Fagen, 1981; Petersen, 1988; Power, 2000). The sources cited are scholarly and critical. Much in the popular press and child development literature is uncritical, however, and bald claims are frequent that play is central to all childhood learning and thus play needs to be facilitated at all levels. What play means in many such claims, however, is often unclear, except that it must be "fun." It is doubtful that we have a better understanding of fun than we do of play.

What is needed are means of evaluating evidence on the benefits (and costs) of play, not confident assertions. Five basic methods have been used in evolutionary and ethological studies to investigate adaptive function. Although this book is not devoted to evaluating the evidence for the adaptiveness of play in the most playful species, each method is briefly described and named for future reference (cf. Rose & Lauder, 1996).

The first step in the ethological study of any behavior is to describe both the behavior and the context in which it occurs, such as how, where, and when a hawk captures and eats a mouse. Such observations reveal that the talons and beak play important roles in such predation and this may be why they differ from the comparable parts of a chicken or a hummingbird. It is thus almost irresistible to conclude that the design of the feet and beak is adapted to the feeding requirements of the species. This *design feature approach* can also be applied to details of the predatory behavior itself.

Similarly, researchers have looked at certain kinds of play and concluded that the form of the playful acts, their timing in the life of the animal, and the later behavioral needs of the animal show that the play is designed to function in a certain way for clearly adaptive reasons. Exactly what these reasons are, however, is seldom clear, because for any given play, several features could be enhanced. Does vigorous play fighting enhance fighting skills in general, offensive fighting skills, defensive fighting skills, social role learning, or various measures of physiological competence (Pellis & Pellis, 1998b)? An especially strong version of the design feature approach is to view the ani-

mal's current behavior or structure as having been optimized for the function it is serving. When the adaptive function is itself unclear, such an approach is misleading as well as largely useless.

The second approach to "proving" that play must be adaptive is to focus on the costs of play, which must be countered by corresponding benefits or otherwise play would be eliminated by natural selection. Here calculations are made concerning the energy and time costs of play as well as the risks of death or injury that play often entails (Fairbanks, 1993; P. Martin, 1984b). Caro (1988) lists numerous "survival costs" of play, including self-injury, increased predation risks, separation from parents, retaliatory aggression, and reduction of food intake. This *cost-benefit approach* is weaker than the design feature method in that it merely asserts that play must be adaptive to persist in the face of the costs involved. It does not directly imply what the benefits actually are, just that they must exist. However, if the play is a by-product of, or linked in some way (genetically, physiologically, behaviorally) with another feature of an animal, play might have costs or benefits that are not due to the playing itself.

The third approach is to show a correlation or association between the type or amount of play and either survival (nonhuman animals) or later abilities (animals and children). For example, do cats that play more with objects have more predatory success than cats that play less or not at all? Do rats that engage in more social play have more reproductive success than animals that do not play as much? Do children that show more sociodramatic play have more complex language skills or cognitive development than those that engage in less sociodramatic play and more of the less complex "functional" play (chapter 4)? Less direct correlations would be between the amount or type of play and measures of neural development, metabolic rate, or other features that presumably benefit the organism. I will term this the *adaptive correlational approach*.

A second type of correlational approach ignores individual differences within a population or species and seeks relationships among different species (or populations) in the amount or type of play engaged in and features of the organism, such as brain size (or development of parts of the brain), cognitive ability, social organization, or some aspect of ecology. I will term this the *comparative correlational approach*. In both types of correlational studies, a positive relationship can only suggest, but cannot prove, a causal relationship among the variables compared. To carry out the comparative correlational approach most validly, it is important to use modern comparative methods that control for the phylogenetic relationships among the taxa being compared. For example, finding a significant relationship between object play and diet by comparing only large predatory cat species with herbivorous ungulates is spurious. This is because the individual species of cats and ungulates could be viewed as components of a single radiation of cats and a single radiation of ungulates, since all cats are predators and all ungulates are herbivorous (Martins, 1996). We need to compare many

more groups to confirm that object play is associated with diet and not taxonomic group. Both adaptive and comparative correlational approaches are important because they can seriously question putative relationships about the value or role of play that abound in the literature, as well as suggest new ones (P. Martin & Caro, 1985; Pellis & Iwaniuk, 2000a; Power, 2000).

The fourth method of deciding what the adaptive value of play may be is to use mathematical modeling and simulations that draw on the power of modern computers and increasingly sophisticated methods of predicting outcomes based on the development of putative relationships among key variables and estimation of parameter values. This is being applied to everything from weather forecasting, the ecological consequences of global warming, neural networks and learning, and the effects of natural selection on almost every conceivable trait in plants and animals. The cachet of this *modeling approach* can be seen in almost any issue of the journal *Evolution*. Ultimately, formal mathematical modeling will be useful in understanding play, but the early models (Fagen, 1974, 1977, 1981) were premature (Burghardt, 1984). In any event, they often assumed the function of play rather than helping us to determine it. When and if various models for play can be contrasted and tested against empirical data, modeling will prove to be useful.

The most powerful method, the “gold standard” to many, of establishing causal relationships between play and other features of animals is the *experimental approach*, in which subjects are placed in different groups and given different experimental or control treatments. Does raising kittens without giving them opportunities for object play lead to less proficient killing of prey? Do rats deprived of opportunities for play fighting have less successful social lives than those who can play? Do experimental groups of animals that are reared in complex environments develop larger brains or better immune systems than those that are raised in simple environments? Do children given the opportunity for free play with objects later use them more creatively in problem solving than children who are never exposed to the objects or children who are allowed to use them only in specified ways? Certainly there are data that seem most convincing. Polecats (*Mustela putorius*) raised without opportunities for play fighting, which involves neck biting, were relatively incompetent at both mating and rat killing (Eibl-Eibesfeldt, 1970).

Unfortunately, there are great logistic difficulties in doing such research, and it is often hard to vary only the single aspect that one is interested in evaluating. This is particularly a problem in social play deprivation studies, which are difficult and controversial (cf. Caro, 1988; Müller-Schwarze, 1984; Power, 2000). Furthermore, given the great diversity of species, types of play, and possible independent and dependent measures, it is necessary to use plausible, but grounded and cautious, inferences based on methods other than direct experimentation to devise the experiments. Diversity among species and populations (including human cultural and ethnic groups, Avedon

& Sutton-Smith, 1971; Blurton-Jones, 1993) and even genetic differences within populations may lead to differences in the effects of variables or to contradictory experimental results. For example, social isolation can have different effects on play fighting in different inbred strains of laboratory rats, even those derived from the same outbred source (Siviy, Baliko, & Bowers, 1997; Siviy et al., 2003).

Furthermore, play may be only one path to an adaptive outcome: demonstrating that play, or variations in play, has limited effects in an experimental setting does not rule out the role that it may have in normal settings. For example, play may provide physical exercise benefits that could also be obtained by other activities (hunting, fighting over resources, stereotyped movements in confinement, etc.). Thus, even experimental studies may have limited value in determining the utility of play outside of very narrowly specified boundaries. In short, rather than being the gold standard or benchmark for a science of play, experiments are often rather limited and open to as many interpretive problems as the other methods. To understand play then, both comparative and experimental approaches need to be used to jointly test hypotheses generated from the cost-benefit and design feature approaches to the control, ontogeny, function, experience, and phylogeny of play.

5.2.3 Immediate versus Delayed Functions of Play

Characterizing play as behavior with no immediate function or contribution to survival and then inferring that the benefits of play are delayed has led to much theory, from Groos (1898) to the present (Power, 2000), on what these benefits are and how they are to be obtained. In spite of considerable research, the evidence for delayed benefits based on the adaptive correlational and experimental approaches is sparse (P. Martin & Caro, 1985; Power, 2000). Perhaps more interest should be taken in evaluating whether play has immediate current benefits, not long-term delayed benefits. There is good reason to suspect that this might be a more useful way to begin an approach to understanding the role of play in animals' lives.

In the past, the study of behavioral development in animals, including human children, was focused on development to an end point—the adult stage of life. Less focus was placed on the fact that animals go through different stages of life, with their own social and ecological demands. Their size, physiology, morphology, diet, and other traits change as they proceed through ontogeny. Many of the behaviors that they perform are better viewed as adaptations to the life stage they are in (such as use of the “egg tooth” to facilitate hatching in birds), rather than as behavior preparatory for the future. Many tadpoles have mouth parts and behavior specialized for eating plant matter, whereas their adult forms have jaws, tongues, and behavior specialized for capturing insects (McDiarmid & Altig, 1999). These tadpoles have features adapted to their juvenile ecology and there is little evidence that, beyond survival to metamorphosis, these feeding adaptations have any specific influence on adult feeding. In

short, the details of juvenile feeding behavior are designed for current problems tadpoles face. Similarly, the behavioral processes involved in neonatal mammalian suckling behavior seem quite separate from those involved in eating solid food. So, even in mammals a form of behavioral metamorphosis can occur, and recognizing this phenomenon (including the role of play) may be crucially important in understanding behavior in mammals (P. Bateson, 1981; Coppinger & Smith, 1989).

Thus, the question now arises for all features of behavior seen in early development: Which behavior patterns serve juvenile functions and which are preparatory for later life? For example, secondary sexual characteristics and hormonal changes in females may be largely preparatory if the females cannot yet mate or have offspring. However, such changes could have immediate effects on the social life of young females and these may themselves have consequences later in life.

Instead of looking for long-term or delayed benefits of play, then, it is probably more useful, certainly initially, to focus on immediate benefits that play may provide (P. Martin & Caro, 1985). Of course doing so immediately discounts “purposeless,” “non-functional,” and other typical defining traits of play. Some of these immediate benefits include providing important physical exercise that develops endurance, control of body movements, or perceptual-motor integration. Other immediate benefits could include testing objects that represent food or danger, or establishing social roles and communication skills that contribute to current survival in the juvenile stage. Such immediate benefits might be even more evident in play in adult animals, a phenomenon too often neglected in animal play research (S. L. Hall, 1998; Pellis & Iwaniuk, 1999a). The emotional benefits of play in enhancing psychological and physiological well-being and resilience might be important as well (Sutton-Smith, 2003a). Ruling out the immediate benefits of play should, in typical scientific approaches, precede the more problematic study of delayed benefits. However, the typical definition of play as behavior with no immediate function has conspired against such research or even asking the proper questions.

5.2.4 The Processes of Play in the Origins of Play

In addition to evaluating whether the benefits of play are immediate or delayed, it needs to be asked whether play originally evolved, or currently serves, to aid in survival at all. The null hypothesis has been strangely absent in the study of play and is rarely even proposed. Play may not have any direct role, *as play*, in aiding either individual survival or reproductive fitness. As pointed out in chapter 1, play may have its ambiguous status in children as “good” or “bad” for valid reasons. One way to resolve this good-bad, benefits-costs opposition is to distinguish between primary processes, or the setting conditions through which “play” first evolved in ancient animals and their modern descendants, and derived secondary processes. These latter may currently provide, or in an earlier evolutionary time period did provide, physiologi-

cal, behavioral, social, cognitive, or emotional advantages to those animals engaging in play. Thus, it would not be expected that playful-appearing acts that were due to primary processes would have either immediate or delayed benefits. They could be truly nonfunctional initially (and in some instances maybe still are), perhaps as the outcome of several processes described below. In trying to explain the possible origins of play, it is useful to divide play into three types that outline a broad evolutionary scenario.

Primary process play This is play behavior (meeting the five criteria) that is an outcome of factors not related to any direct action of natural selection on the play behavior itself. Identifying primary process play is crucial to understanding the origins of play. Play of this type may have no role in subsequent behavior or may serve as a “preadaptation” or “exaptation” providing variation that can be selected (Burghardt, 1984, 2001).

Secondary process play This is play behavior that, once it occurred, evolved some role, although not necessarily an exclusive or even major one, in the maintenance or refinement and normal development of physiological and behavioral capacities (question M in Burghardt, 1977c). Just as certain experiences are important in the maintaining (preventing atrophy) of many other motor and sensory systems, such as suckling or visual perception, play may serve to maintain the precision of predatory, defensive, and social skills; neural processing; and physiological capacities.

Tertiary process play This is play behavior that has gained a major, if not critical, role in modifying and enhancing behavioral abilities and fitness, including the development of innovation and creativity. There is not too much support for this seemingly commonsense interpretation (Fairbanks, 2000; P. Martin & Caro, 1985). The transition between secondary and tertiary processes, in particular, is probably on a continuum and graded, but the distinction seems important in resolving the issue of the evolution and current function of play (figure 5.1).

Primary process play is most likely to be found in animals that play rarely or simply. Secondary and tertiary process types of play have been selected to perform some adaptive functions, such as those outlined in table 5.1. These functions are both diverse and often difficult to evaluate; it is enough to state that if play serves even a small number of these adaptive functions, then this in addition argues for the multiple origins and heterogeneous nature of play phenomena across taxa. It also needs to be recognized that just because a behavior serves a function does not mean that it was directly selected to perform it. Which came first in the evolution of birds: feathers for insulation in incipient warm-blooded reptiles or feathers as lightweight devices for flying?

Primary processes for play are the proximate conditions, such as lowered thresholds for eliciting behavior as a result of stimulus deprivation, that underlie many “playlike” performances (see later discussion). Animals that have much tertiary play may also still

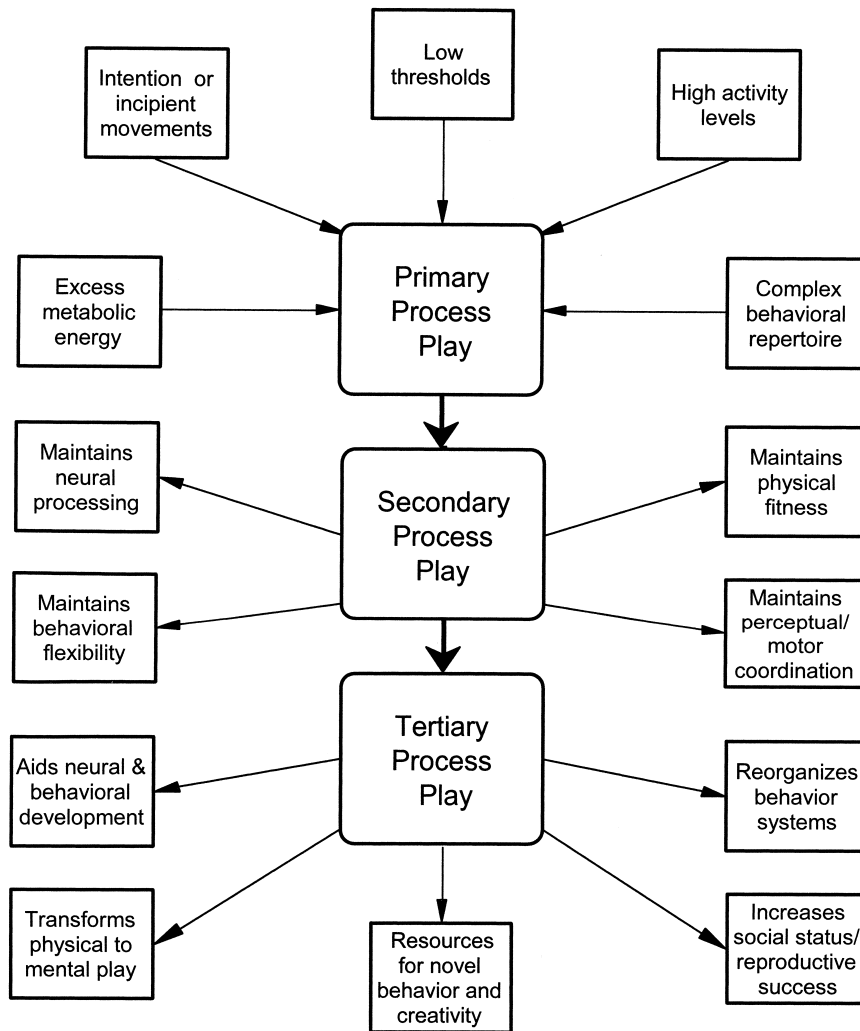


Figure 5.1
Attributes of primary, secondary, and tertiary play processes.

produce primary play because many of the factors are still present. In any event, primary processes provide an essential base upon which the highly diverse and complex structures of mammalian play can be built through the selective actions of secondary processes that provide important cognitive, emotional, and motivational functions useful in foraging, defensive, and social contexts (Burghardt, 1998a). For example, the exaggerated movements, role reversals, and testing of the individuals or objects being played with may allow an animal to learn about the reactions of other entities as well as aiding control of the animal's body. The distinction is similar to that underlying the process of behavioral ritualization, in which autonomic, thermoregulatory, defensive, or feeding responses are incorporated into social displays and can become essential for successful courtship, for example (Burghardt, 1973; Grier & Burk, 1992; Tinbergen, 1951).

The distinction between primary and secondary processes also allows recognition that both the surplus energy theory popularized by Spencer (1872) and the recapitulation theory of play popularized by G. Stanley Hall (1904) largely dealt with primary process in play. Neither explicitly addressed the derived (secondary and tertiary) processes of play that Groos (1898) and the modern proponents of play contend are the major reasons for play (chapter 2). Recall that the surplus energy theory held that play occurred when well-fed "higher" animals had an excess of energy and needed to release it through vigorous activity. The recapitulation view held that juvenile play, which resembled adult serious behavior, was a necessary biological developmental process that animals, including people, went through; it incorporated behavior patterns once necessary for survival in earlier times, but in and by itself it had no long-term effects. The instinct-practice theory held that play was important solely as a means of perfecting adult behavior in species with long periods of immaturity and extensive parental care.

The tendency of most early, and even some current, writers on play to confuse proximate mechanisms and adaptive value led to much needless controversy and especially a neglect of the former in evolutionary theorizing on play (Burghardt, 1984). *We now recognize that play can be viewed as both a product and cause of evolutionary change; that is, playful activities may be a source of enhanced behavioral and mental functioning as well as a by-product or remnant of prior evolutionary events.* It is probably a mistake to think that play originally evolved in order to provide such advantages, and this mistake may have hindered a more accurate and scientifically supported analysis of play.

If the distinction between primary, on the one hand, and secondary and tertiary processes, on the other, is appropriate, it becomes critical to ground the phenomena of play in a phylogenetic context. What are the processes leading to playfulness throughout vertebrate evolution? The answer to this question may be critical in the search for the putative consequences of play.

5.2.5 Studies on the Costs of Play

Although the controversial research on the possible functions of play is not reviewed in depth in this book, the costs of play have recently received renewed attention (Caro, 1995) and deserve mention. Play has costs in time and energy, although the extent of these costs has been debated (Bekoff & Byers, 1992; P. Martin, 1984b). Young mammals may spend 5–10 percent of their time in play and several percent of their metabolic energy (Fagen, 1981; P. Martin, 1984a). In a series of experiments with school children ages 7 and 10, Pelligrini, Horvat, and Huberty (1998) measured heart rate, movement speed, and behavior ratings to estimate caloric costs of physical play. They found outdoor play more costly than both indoor play and classroom behavior. Even though total play time was limited, the authors calculated that play consumed about 6 percent of the childrens' total energy budget. At some age periods, in some species, and in captive settings, the relative amount of play may be much higher than 10 percent; the amount of social behavior in adolescent chimpanzees that is devoted to social play may exceed 30 percent of their time (Paquette, 1994). Play thus uses metabolic resources and time that could be devoted to more "important" or "serious" activities. Pronghorn antelope fawns (*Antilocapra americana*) expend a steady amount of play until weaning at week 6, during which play decreases significantly and only recovers after the fawns shift to substantial independent browsing (Miller & Byers, 1991).

As noted earlier, play has costs in addition to time and energy, such as increased risk of predation and physical injury from performing vigorous activities. Harcourt (1991b) has shown that twenty-two of twenty-six fur seals (*Arctocephalus australis*) that he observed being killed by sea lions (*Otaria byronia*) were attacked while playing, although play only occurred during about 6 percent of their waking hours.

Wariness in exploring and foraging in environments populated with predators has been shown to increase survival (Sih, 1992). An interesting suggestion as to why animals spend so much energy in play is that by doing so they become exhausted and rest more, becoming less conspicuous to predators (Müller-Schwarze, 1984). No research seems to have tested this idea, but it is very similar to one of the theories for why animals sleep (Grier & Burk, 1992). However, becoming conspicuous through play to become subsequently inconspicuous does not, on the surface, seem very plausible.

A remarkable long-term field study of play in cheetahs (*Acinomyx jubatus*) was based on 2600 hours of observation of forty families during their cubs' first year of life (Caro, 1995). Locomotor play, object play, and contact (e.g., wrestling) and noncontact (e.g., chasing) social play were distinguished. This study shows both the strengths and weaknesses of the design-feature, cost-benefit, and correlational approaches. Caro found that the risks of injury, maternal separation, and predation were minimal in cub play. Mothers showed no increased "unease" when their cubs played. That energy expenditures during play may be a significant cost was shown by the positive rela-

tionship between time spent eating and playing. The possible benefits of play were modest. There were positive relationships between the amount of time spent in object play and contact social play and the number of contacts made with live prey released by the mother for her offspring to play with. Noncontact social play measures such as stalking, crouching, and chasing showed some subtle age-related changes.

Another recent field study of play in golden lion tamarins (*Leontopithecus rosalia*), a small South American primate, also was designed to test various hypotheses and resulting predictions about play using an approach similar to that in the cheetah study (de Oliveira et al., 2003). Juveniles 2–5 months old in nine social groups were observed. Some animals were reintroduced and given supplemental food. Play occupied 3.8 percent of the activity period and social play was more frequent than solitary object and L–R play. Highly energetic play occurred in short bouts, presumably to avoid overheating or excess energy depletion, but play did occur most during midday when it was hottest. Food-supplemented animals did not play more than wild non-supplemented animals, but this could have been due to less efficiency in foraging rather than having better nutritional resources available, so it does not contradict the squirrel monkey studies cited earlier. The predation risk hypothesis was supported since animals played more when in the center rather than the periphery of their group and they also chose less physically risky or exposed (to predator) locations for play. The authors also found that animals preferred to play with older partners rather than siblings (tamarins are often twins); they concluded that this supports the cognitive training for the unexpected model (Spinka, Newberry, & Bekoff, 2001) rather than the self-assessment model (K. V. Thompson, 1998). Injuries to young animals playing with older ones were nonexistent, suggesting that older play partners self-handicapped. Finally, some individuals and groups played extensively with juvenile and subadult common marmosets (*Callithrix* sp) found in the same habitat.

5.3 The Ontogeny of Play

5.3.1 Timing, Deprivation, and Critical Periods

Elements of play can appear remarkably early in an animal's life: as early as 2 hours after being born in wild beavers (*Castor canadensis*) in Canada (Patenaude, 1984). Ontogeny, then, is an important arena for addressing primary and secondary processes in the role of play. Play is typically found in juvenile animals, although in some, including human beings, it can endure throughout life. Most studies of ontogeny have looked at the course of play throughout the juvenile period: the type, context, frequency, duration, and targets of play. Among the many animals studied have been laboratory rats (Panksepp, 1980), olive baboons (*Papio anubis*; Chalmers, 1980), cats (P. Bateson & Young, 1981), canids (Biben, 1983), gazelles (Gomendio, 1988), and fur seals (Harcourt, 1991a). Different kinds of play or play movements may appear and

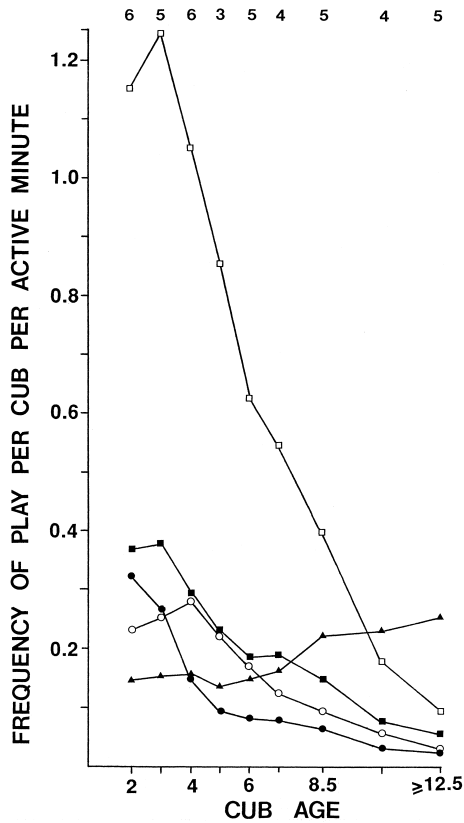


Figure 5.2

Occurrence of different play behavior patterns in young cheetah cubs in the wild at different weeks. □, contact social play; ■, noncontact social play; ●, locomotor play; ○, object play; ▲, exploratory (sniffing objects). (From Caro, 1995)

then wane at different time periods, suggesting that play behavior reflects different behavior systems in development. In slender-tailed meercats, *Suricata suricatta*, object play begins in week 4, wrestling with litter mates and play with adults in week 5, play soliciting signals such as head-rolling and stiff-legged walking during weeks 9–10, and vigorous play with juveniles and yearlings during weeks 11–14 (Doolan & Macdonald, 1999). In cheetahs, locomotor play peaks before social and object play (figure 5.2) and it has been argued that this is because of the need to perfect flight responses at a time of maximal vulnerability to predators (Caro, 1995). In spotted hyenas (*Crocuta crocuta*), the cubs are very aggressive in the natal den until they are moved, during weeks 2 and 3, to a communal den (Drea, Hawk, & Glickman, 1996). Social play emerges during week 2 but locomotor play begins at week 3 and object play at week 4. The

authors conclude that the timing of the changes supports the socialization role of play in the clan. However, similar arguments for the role of play in integrating juvenile howling monkey (*Alouatta palliata*) clans (Carpenter, 1934) have been questioned as both sexes emigrate fairly soon from their natal groups (Zucker & Clarke, 1992).

Such studies of differences in timing of various play responses can, thus, provide clues for answering questions concerning the function, motivation, physiology, and evolution of play. However, mere observation that the type of play changes throughout life may lead to uncritically concluding that play has a formative role at certain times in the life of an animal, does its work, and fades away. For example, all mammals show a decline in play fighting after puberty. This is one of the main design feature arguments for the importance of play. Nonetheless, the fact that play appears at a certain point, such as play fighting in rats during the fourth and fifth weeks of life, does not mean that it (1) functions to perfect fighting behavior for use in adulthood or (2) necessarily has some other delayed function. It could have a function of giving a rat enduring experience with the defensive and offensive moves involved in fighting or even courtship (Pellis & Pellis, 1998b), but it may have neither of these roles (also see Paquette, 1994, on play and aggression in chimpanzees).

Studies that manipulate variables such as social contact, the presence of the mother, nutritional status, and presence and type of objects are subsequent steps in the analysis of ontogeny that have much promise, but they are still too infrequent. The reason such studies are needed is the possibility that play criterion one (incompletely functional) and the temporal or structural aspect of play criterion three (play as imperfectly organized behavior that appears before it is actually needed) have a simple explanation.

Good examples of careful developmental research on play are available for young domestic cats, one of the most extensively studied species. In an early study of social play in kittens from birth to 2 years of age, West (1974) isolated eight play behaviors first seen at different ages from 21 days (belly-up) to 42 days (face-off) with others such as pouncing, chasing, and leaping appearing at intermediate ages. The overall amount of play increased threefold from weeks 4–12 and then declined threefold by week 19. She claimed that the different play elements could have different functions and was one of the first to point out the potentially misleading use of the term *play fighting*. The development of all types of play in twenty-eight kittens was followed for the first 12 weeks of age (P. Bateson, 1981). Stalking, rearing, neck arching, neck flexing, wrestling, and object contact were six play elements followed during this period (mere contact between cats was also considered a play category, but I consider it ambiguous by itself). Of these six behaviors, rearing, arching, and neck flexing (performed in the presence of siblings) increased from weeks 4 to 7 and then declined rapidly. In contrast, stalking showed a marked increase at 7 weeks and stayed high thereafter. Wrestling continuously increased from weeks 7 to 12. Object contact play showed about a fivefold increase from 6 to 8 weeks and remained high thereafter. Patrick Bateson

concluded that “Play is heterogeneous, and it seems likely that the factors controlling one system of play are not the same as those controlling another” (1981: 287). This is an important conclusion that argues against a unitary “play drive” or “play instinct.” While there were positive correlations among all six play behaviors in the 4–7-week period, several were negative in weeks 8–12. This discontinuity suggests that after weaning, which begins at 6 weeks of age, a major behavioral reorganization is taking place and behavioral systems are becoming differentiated. Thus object play increases as exploration and independence from the mother occur. Some aspects of social play also have elements of predation (e.g., stalking).

Bateson and his colleagues were also able to shift the timing of the alteration in play behavior frequencies by enforcing early weaning at 4 weeks of age (P. Bateson & Young, 1981). Thus contextual factors might be important in the ontogenetic timing of various play behaviors.

Stamps (1995) has pointed out that locomotor play could be important in motor learning related to escape in familiar territories. If so, simple experiments involving transplanting animals to unfamiliar areas at different ages could test the function of play in general vs. age and context-specific escape ability.

The fact that vigorous behavior typical of play appears at a certain time could have more general long-term consequences unrelated to the specific behavior patterns seen in play. It is known that certain experiences in early life are essential for later behavioral expression and in fact may have to occur during certain sensitive or critical periods in life if they are to be effective. This is true of song learning in some birds, parent-offspring attachment and imprinting (Harlow, 1964; Hess, 1973), and in people, mastery of spoken foreign languages and the playing of many complex musical instruments. Could play have the role of facilitating the performance of certain essential behavior patterns at certain developmental periods?

A specific research question would be the following: If motor training or physical exercise is involved in the function of play, then why is play limited to a short period of time in most animals’ lives? In a review of the functions of play, especially the exercise or “getting in shape” theories, Byers and Walker (1995) point out that none of sixteen different physiological exercise effects posited for play, such as increased oxygen-carrying capacity in the blood, increased blood volume, and increased endurance, have permanent effects. Once a long-distance runner shifts to the couch, he or she cannot keep the fitness accrued by prior exercise in the body’s “bank,” let alone accrue interest. By looking at the ages when play peaks in three domestic species (mice, rats, and cats), Byers and Walker found that these play peaks coincided closely with the ages at which permanent experience-dependent synaptic development occurred in the cerebellum and important muscle fibers were innervated (figure 5.3).

Although the Byers and Walker theory is based on a comparative correlational approach using a small sample size ($n = 3$ species) and the design feature approach,

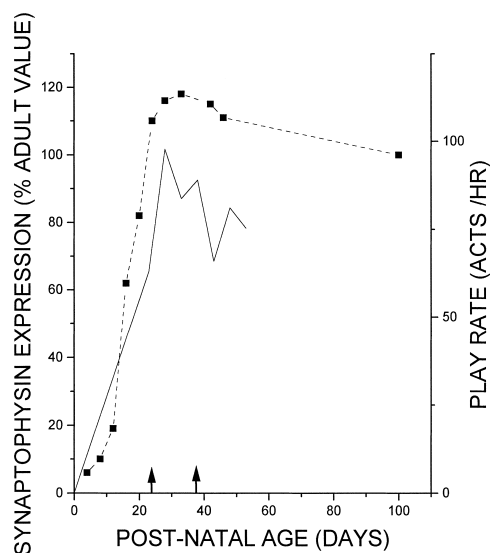


Figure 5.3

Timing of play (solid line) and cerebellar synapse development in rats. Arrows point to age range that muscle fiber differentiation occurs. (From Byers & Walker, 1995)

the idea that play is associated with a sensitive period for neural integration may be a key to understanding the timing of play (Byers, 1998). A study with male rats who were prevented from engaging in social play as pups found a decrease in the amount of social interaction as adults when the rats were not able to play during a period comparable to the period that Byers and Walker (1995) argued is critical for cerebellar synapse formation (van den Berg et al., 1999).

As indicated earlier, depriving animals of play and not interfering with other systems has proven very difficult. There is still no solid experimental evidence that play deprivation per se has long-lasting consequences for behavioral ontogeny (Caro, 1988; Power, 2000). However, a recent study in rats based on social isolation (Hol et al., 1999) found that social deprivation at week 4 but not week 5 reduced adult social interaction, suggesting a sensitive period. More refined tests are needed. Other critical changes may also be occurring. For example, bone growth and bone “remodeling” are known to be affected by events such as dietary experience, and it could be that prepubertal play functions in skeletal development.

The ontogenetic organization of play may have more specifically behavioral consequences. When 6-week-old experienced rats play, pinning is performed by the winners having their hind feet firmly anchored on the ground, whereas 30-day-old rats often pin by trying to balance their hind feet on the supine rat’s body (Foroud & Pellis, 2002). Yet the obvious conclusion that such a skill must be learned does not hold

as weaning rats (25 days old) anchor frequently as soon as they begin to play. So why the ontogenetic shift? The authors argue that by not anchoring the animals may be increasing the opportunity to gain experience in play tactics that may be developmentally beneficial, although they have no good idea as to what the benefits are (Foroud & Pellis, 2002). Nevertheless, this self-handicapping merits more detailed study.

The timing of primate play may also provide information on functional issues (Fairbanks, 2000). Fairbanks followed the development of several kinds of play in captive vervet monkeys (*Cercopithecus aethiops sabaues*). She thus extends the Byers and Walker analysis and makes a strong case for extending it to all play and many functions.

Careful consideration of the developmental timing of primate play leads to the conclusion that each of the different play types influences later capacities via the process of neural selection, by increasing relevant experience during the time when the neural and cognitive mechanisms involved are undergoing ontogenetic modification. Thus, primate play contributes to the development of fighting skills, object handling abilities, and motor performance by selectively enhancing the basic neuromotor structures that will be later available to perform these tasks. (Fairbanks, 2000: 1578)

Unfortunately, this is still too much a just-so story, especially since these claims immediately follow a section in the chapter labeled "Play is not essential!" Certainly all these play types can "influence" later behavior, but the plausible must be made more convincing. In addition, adult play is ignored. As pointed out early in chapter 1, extravagant claims for play that have led to its lowly status in many scientific quarters and uncritical claims in the media also need to be considered (R. A. Thompson & Nelson, 2001).

If play is primarily a phenomenon of infancy and juvenile periods, then the amount and importance of play might be related to the length of such periods. Indeed, the famous statement from Groos that "animals do not play because they are young, but they have their youth because they must play" (1898: 76) leads to the claim that the longer the period of "youth," the more important play must be. Life history factors do play a role in differences in the amount and nature of play seen among animals, but Groos's statement is not supportable when the comparative information in part II is looked at even superficially. Nonetheless, the relative degree to which animals have their sensory, skeletal, and motor systems operational at birth or hatching (precocity) versus the amount of postnatal development needed for independence after birth or hatching (altriciality) is an important distinction that will prove useful later. Precocity and altriciality are themselves related to the amount of parental care needed by animals, which is why parental care is often considered an important factor that can help explain the amount of play seen.

The rapidity of postnatal development is also important. Some birds and mammals born in a very altricial state mature very quickly to independence, in a matter of weeks,

while some animals born in a more mature state may stay with the parents a much longer time (S. T. Parker & McKinney, 1999). Thus the timing and duration of the parental care period may be more important than the degree of immaturity at birth. In some mammalian species the mother has only one or a few precocial neonates. These offspring are generally larger and entail more prenatal maternal investment per individual than species that have large numbers of smaller altricial young. The relationship of play to altriciality is not simple because phylogeny, physiology, body size, reproductive investment style, and other factors can preclude simple relationships. That is why the parental care system as a whole needs to be considered. Nonetheless, altriciality may be a useful marker in identifying animals in which play is prominent because species with altricial young often play more, or more complexly, than even close relatives that are more precocial (Burghardt, 1988b; Fagen, 1981; Ortega & Bekoff, 1987; Pellis & Iwaniuk, 2000b).

5.3.2 Is Learning to Walk a Model for Play?

An early type of secondary process in play may have been the maintenance or modification of basic species-typical motor activities by young animals. In altricial species, compared with precocial species, a more drawn-out process in the appearance of various behavior patterns would be expected, and there would be a greater window of time for incompletely functional performances to be influenced by playlike performances. However, even in human beings, the motor components of species-typical behavior (facial expressions, reaching, grasping, biting) may be only modestly influenced by experience, although their contextual deployment and perceptual-motor control may be influenced to a considerable degree.

A good test case in which the first type of secondary process (maintaining “instinctive behavior”) in play may be relevant is learning to walk in human children. McGraw (1943) emphasized the importance of maturation; infants do not really learn to walk, they walk when the neuromuscular system is ready. Thelen (1995) has confirmed that human infants do indeed have many precocial locomotor skills, such as coordinated stepping movements at 1 month of age if they are held on a treadmill. Nevertheless, she argues, these congenitally highly complex behavior patterns still need much experience in order to develop fully, and walking and other behaviors should be viewed in a “multicausal” framework. Although hard evidence is limited concerning the basic features of locomotion in infants, it can be granted that practice is as important for perfecting locomotion in children as it seems to be for predatory behavior in some young snakes (Burghardt & Krause, 1999; Halloy & Burghardt, 1990).

Thelen argues that “new views of motor development emphasize strongly the roles of exploration and selection in finding solutions to new task demands. This means that infants must assemble adaptive patterns from modifying their current movement dynamics” (1995: 85). Although Thelen attempts to challenge the operation of genetic

and neural inputs in behavioral development by emphasizing the role of the body's biomechanical features in producing "self-organizing" behavioral change (Metzger, 1997), a softer version in which the adaptive deployment and altering of much motor behavior may involve considerable ontogenetic input (growth and learning) has value. Aiding this process are motivational factors (as when an infant keeps trying to stand alone, crawl up stairs, or cross a room to get to a parent or toy), accompanied by the joy of success, which facilitates the learning of a novel means of accomplishing a behavioral outcome (see sections 5.4.1 and 5.4.2).

Central to Thelen's view is that action and perception are linked and "that each component in the developing system is both cause and product" and that "cognition is emergent from the same dynamic processes as those governing early cycles of perception and action" (Thelen, 1995: 94). Even "higher order mental activities, including categorization, concept formation, and language, must arise in a self-organized manner from the recurrent real time activities of the child just as reaching develops from cycles of matching hand to target" (Thelen, 1995: 94). She formulated a conceptual model for how sophisticated motor activities, often involved in play, are derived from the same kind of processes as those involved in the development of advanced mental abilities.

Applying the five criteria of play, including incomplete functionality, repetition, endogenous motivation, and structural or temporal factors, all speak to learning to walk and other behavioral tasks in altricial mammals as more than superficially playlike. The task now is to forge this link between the two kinds of secondary processes and go beyond the vague multicausal ("nonlinear") framework (B. Goodwin, 1994) that Thelen advocates. We need analytical research that separates and evaluates the various putative influences. For example, Meer, Weel, and Lee (1995) showed that spontaneous arm movements in newborn (10–24-day-old) infants are more frequent when the infants can see their arms. Furthermore, visual information is used to counteract external forces (weights, strings) on their limbs in maintaining a reference position. The authors speculate that such early developmental processes may be critical in the development of more purposeful reaching and grasping skills 3 months or so later. Playlike behavior may be important in many of these developmental transitions in human and nonhuman species.

Comparable experimental work with animals in which controlled and long-term manipulation of sensorimotor integration during social, locomotor, and object play is carried out could be an entrée to the analytical work that has been so lacking in play research. In later chapters, evidence that animals have a neural template like that found useful in understanding song learning in birds will be presented. Play may be a means to activate the behavioral work needed for certain necessary skills to be acquired and operate in behavioral systems, such as walking, which are rarely considered playful.

5.3.3 More on Play Sequences and Sequences in Ontogeny

Piagetian and neo-Piagetian developmental research in children and nonhuman primates (S. T. Parker & McKinney, 1999) focuses on research showing that the four periods of cognitive development (sensorimotor, preoperations, concrete operations, and formal operations; see chapter 4) build on one another sequentially, as do several stages within each period. Play, as characterized earlier, is an integral and important component in cognitive development (Piaget, 1962). For example, the sensorimotor intelligence series involves a sequence of stages that include circular and secondary circular reactions. The latter consist of repeated actions, such as repeatedly striking a mobile or shaking a rattle; similar actions are found in many species and usually considered playful. A famous example popularized by Piaget was the fact that infants from about 7 to 12 months of age who are shown a toy in one location persist in reaching toward that location even after the toy has been moved to a different location that the infants can see. This persistence is considered an error (the A-not-B error) that must be overcome, and Thelen has applied her field theory to this problem as well (Thelen et al., 2001). The controversial explanation she provides is an attempt to break down the dualism between cognitive and bodily movement processes. However, comparative evidence shows that many other animals show this phenomenon and it might very well be adaptive in situations where the object is not viewed as unique (Hailman, 2001).

Play behavior, as is true of many other behavior patterns, also has several sequential components that may have different causal bases. Even a circular reaction can be divided into sequences. For example, if an object such as a ball is introduced into a kitten's environment and play with it ensues, we observe the following: orientation to the object (initiation); running over to the object (approach); hitting it with a paw, perhaps several times in a row (engagement); and leaving the ball and switching to another activity (termination). Such sequences may occur repeatedly in bouts.

Recently Willingham (1998, 1999) has put forth a general model of motor skill learning that postulates a specific set of four processes involved in motor control of just the first part of the above sequence. Consider the process of reaching for and moving an object, such as when a cat reaches out to a dead mouse and pulls it to her mouth. This entails a "decision" to perform the act (strategic process), a translation of the spatial locations of cat, paw, and object into an "egocentric space" (perceptual-motor integration), a sequential ordering so that the paw is moved to the object (the "goal location") before being retrieved (sequencing), and finally the translation of these steps into appropriate muscle firing (dynamic process). In each of these four stages, learning of different kinds may be involved in enhanced behavioral performance. Play could be a means of ensuring that behavior patterns are both practiced and deployed in effective manners to either maintain skills removed from the operation of natural selection by

parental care or to enhance performance beyond that which could possibly be anticipated by innate wiring.

Even the most congenitally perfected behaviors (such as predation) may have to be employed in widely varying environments and with widely disparate objects to increase the chances for survival, especially when environments change. Perhaps, however, object play in kittens is so exaggerated or otherwise so different from real predation that such “unrealistic” practice interferes with predatory behavior. If so, then object play has no secondary function related to predation and exists for other reasons (e.g., compensation for stimulus deprivation, exercise of diverse body parts). Evidence suggests, however, that predatory play in cats is linked to motivational systems that involve predation (S. L. Hall, 1998; Pellis et al., 1988).

An alternative conception, the possibility that play is just neurologically or motorically immature behavior in the process of being prepared for its “serious” deployment, must always be considered as a default hypothesis of primary play. Such a view would explain the greater prominence of play in species with long developmental periods or immense physical changes before adulthood (Burghardt, 1984; Ewer, 1968a). In other words, play as behavior that has no current adaptive function or only a limited one may be a consequence of developmental necessity. Play is seemingly nonfunctional because it is, in fact, a largely nonadaptive consequence of other factors in the lives of the organism. The most common examples of precocial behavior as play may be play as a temporary maturational intermediate, an ontogenetic by-product of adult behavioral necessity. These examples, such as wing flapping, have also been termed prefunctional behavior (Hogan, 1988; Kruijt, 1964). Although some have argued that such behavior is not true play (Fagen, 1981), others have argued that this is all that play really is (G. C. Williams, 1991). George Williams (1991), for example, points out that, just as with anatomical traits, much species-typical behavior (courtship, fighting, predation) in animals with parental care only becomes necessary after a juvenile period. However, there may be a rapid onset of the need to include such behaviors in the animal’s behavioral repertoire if it is to survive and reproduce. Since natural selection will operate to ensure that the nervous system and other mechanisms underlying such behavior are available in functional form at this abrupt developmental transition (postweaning solo hunting, first courtship), and if the costs (and hence selection against) of precocial performance of behavioral elements are low, such temporary maturational intermediates are to be expected. Thus play is something that animals can afford to perform if the costs are low and the benefits are great if the behavior is performed adequately as soon as it is needed. The more complex the behavioral systems needed, the less likely it is that they will be functionally integrated when first performed. This is certainly one way to explain the occurrence of primary process play in development, but to dismiss all play as prefunctional adult behavior is highly simplistic.

5.4 The Control of Play

5.4.1 Behavior Systems and the Question of Motivation

As mentioned at the end of the preceding section and in previous chapters, motivational issues have been at the heart of many controversies about play (Eibl-Eibesfeldt, 1970; Meyer-Holzappel, 1978; Müller-Schwarze, 1978) and resemble those concerning exploration (Hughes, 1997). Early studies trying to demonstrate a relatively autonomous drive for play by depriving animals (deer and goats) of social play had mixed results (Chepko, 1971; Müller-Schwarze, 1968) and were challenged on methodological grounds (Fagen, 1976, 1981). These early studies were based on short-term deprivation, however, and avoided many of the social and environmental deficits that long-term social deprivation can create (Müller-Schwarze, 1984). In male rats, the ability of even short-term opportunities for social play to override the effects of isolation rearing (van den Berg et al., 1999) has been shown repeatedly (Ikemoto & Panksepp, 1992; Panksepp & Beatty, 1980). Rats are much more ready to play if they are separated from a partner for some time.

Motivation concerns itself with basic drives underlying physiological and reproductive behavior (e.g., feeding, drinking, mating, fighting, parental care) as well as extensions to social and cognitive behavior (e.g., altruism, achievement, status, addictions, social roles). All of these have been implicated in play. Nevertheless, despite a long history in psychology and ethology (Baerends, 1976; Mook, 1996), motivation has not been a central focus of recent work in animal behavior. Modern ethologists and behavioral ecologists have minimized the study of “drives.” Behaviorist psychologists prefer to talk about “setting factors,” such as environmental context or hours since last eating. Physiologists avoid the term and would rather measure body fluids (blood glucose, hormones). Neuroscientists image brain states and measure neurochemical concentrations to obtain their objective facts about psychological states. However, the fact remains that motivational analyses are still both common and needed (Mook, 1996).

A feature of play is its repeated nature and the persistence with which animals often pursue opportunities to play (Hole & Einon, 1984) and even learn tasks in order to gain a play partner. Repeated behavior patterns in moderately changing contexts might be particularly conducive to learning or improving complex skills and negotiating complex habitats. A descriptive behavioristic theory that has utility in relating play and other responses is the Matching Law (Herrnstein, 1997). At behavioral equilibrium, matching assumes that the ratio between any two behavioral responses (B) matches the ratio of the respective reinforcement (R) obtained such that $B_1/B_2 = R_1/R_2$. This also should hold for time allocation (t) such that $R_1/t_1 = R_2/t_2$. From this it should be possible to calculate the subjective (to the animal) value of different alternative

behavior, since, to Herrnstein R_i is subjective value. It is interesting that behavioral ecologists have recently “discovered” the relevance of conditioning, matching, and other psychological models for understanding why animals persist in, for example, competing over space (Sih & Mateo, 2001). However, the motivational mechanisms underlying such persistence and their comparative, physiological, feedback and ecological correlates have barely been considered, which Herrnstein (1997) allows is necessary “before any actual behavior can be predicted” (Herrnstein, 1997: 76). Play could very well be a “safe” means of beginning such competition and learning behavioral and spatial tactics (e.g., Pellis & Pellis, 1998b).

A brief review of the traditional ethological model of behavior may be useful here. Animals are often predisposed to respond to rather specific stimulus cues from biologically important items in their environment (such as food, predators, potential mates, or offspring). These stimuli are often extractions from the complete set of stimuli an object possesses and, depending on the species, may be an odor, a sound, a color, a shape, a specific movement, or even a tactile stimulus, as well as a specific combination of stimuli. Such stimuli (often termed cues, sign stimuli, or releasers), when perceived, may elicit a response that is also instinctive (often termed fixed or modal action patterns, unlearned or instinctive movements, etc.), such as flight, attack, eating, courtship behavior, or care of young (e.g., retrieval of a pup upon hearing a high-pitched vocalization, movement toward the mating call of a male frog, capturing an insect). These stimulus-response units often occur in a series in which the animal first appears to “search” for the stimuli to which it can respond with the instinctive response. This initial phase is termed appetitive behavior (Craig, 1918) and is followed by the more stereotyped “consummatory acts” after the animal perceives the stimulus object (prey, mate) that “releases” the consummatory action sequences.

From Craig’s pioneering work through the refinements of Lorenz, Tinbergen, and others to sophisticated newer models (Hogan, 2001; Timberlake & Silva, 1995), the appetitive phase is where the most learning and adaptability is found. In most learning experiments with nonhuman animals, quite complex responses are taught, from maze running to counting and deception (Bekoff, Allen, & Burghardt, 2002), while much less attention is devoted to teaching animals how to eat, mate, and flee. Learning for most people focuses largely on how to obtain important resources such as food, drink, shelter, and mates; how to chew and swallow food, how to sleep, or how to copulate receive far less attention. The performance of these behaviors is itself, in the ethological system, rewarding.

But why should animals strive to obtain stimuli that elicit adaptive behavior patterns even before they “know” that performing them is important to their survival or reproduction? A general drive might not accomplish this and so the ethologists postulated individual drives for different behavioral systems (reproductive, predatory), which

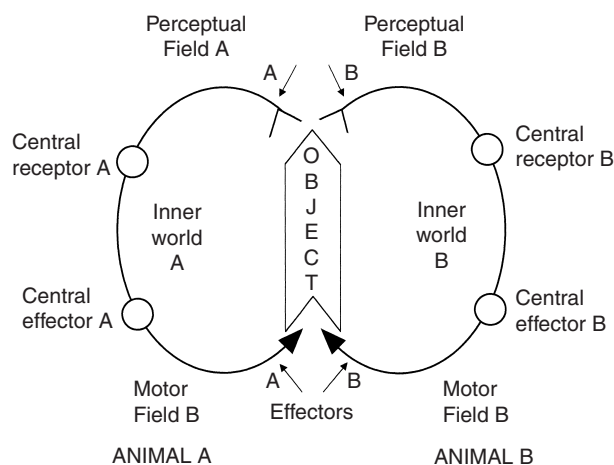


Figure 5.4

A double functional circle derived from the single actor circular system developed by Jacob von Uexküll. In social play the partner is both object and an experiencing actor/reactor. (From Burghardt, 1998c)

could in turn exist at rather fine-grained levels. Thus the reproductive drive could consist of a series of drives that involves establishing territories, courting mates, building nests, and giving parental care, each of which may have further stimulus-behavior connections and its own motivational system (action-specific energy) (Lorenz, 1981; Tinbergen, 1951). Positing a drive for every response is, however, overly reductive and minimizes the value of the concept of motivation itself, which is used as a shorthand for behavioral systems that contain a group of behaviors with common functional features (Mook, 1996).

Responses by an animal to an object or another animal can in turn alter the features of the object or produce responses by the object (e.g., a ball or rattle) or the mate, prey, baby, or predator and lead to a fairly complex series of interactions. Social play is precisely one of these types of interactions. Von Uexküll's (1921) concept of the unity of external and internal stimuli in a "functional circle" is a useful way to keep motivation from being viewed only as an internal mechanism (Burghardt, 1998c). Figure 5.4 shows a double functional circle illustrating the interactive nature of the functional circle when two animals interact (social play). Removing the right hand circle gives the original functional circle (object play, locomotor play) in which the cue bearer can be the physical environment as well as a specific object. The more complex the species' behavioral repertoire, the more complex the motivational system that would be present. In fact, William James, America's first great psychologist, asserted that humans

have more instincts, not fewer, than any other species (James, 1890). It may be this complexity that makes possible the countless combinations of behavioral responses more frequently seen in animals with rich repertoires.

The “behavior system” approach (Baerends, 1976; Timberlake & Silva, 1995) is being employed today as a counterpart to the concept of modularity in evolutionary psychology (Buss, 1999). This approach is particularly useful in that it incorporates learning into the sequential organization of motivated behavior at certain points, a concept termed constrained variability (Timberlake, 2001). It derives, as we have seen, from the analysis of motivated behavior by Craig (1918) in which it is in the appetitive phase of behavior that most variation and openness to experience exists, whereas the behavioral organization of the end point of a sequence (drinking, killing, eating, copulating) is more impervious to modification. It is within this appetitive phase that most play occurs. In fact, the absence of the final consummatory acts has often been used as a major characteristic of play (chapter 3).

Clever recent experiments have shown that rats, even up to 4 weeks of age, do not show the appetitive responses for food or water until experienced with both food-deprivation or dehydration. Thus appetitive responses (drives) for basic biological substances may need to be learned (Hall, Arnold, & Myers, 2000; Changizi, McGehee, & Hall, 2002). If so, play may serve as a means to establish or enhance motivational systems and responses to stimuli in various behavior systems.

The main issues in motivation and play revolve around these four questions: Is play controlled by a separate or unitary motivational (or behavioral) system for playful behavior that is separate from the internal states underlying serious performance? Is play incomplete, unperfected, or simulated behavior that is derived from the same motivation as that underlying the serious version? Does play behavior involve a blending of both serious and play systems? Does play result from mixing two or more independent serious systems?

These questions are partly subsumed in the distinction between primary and secondary processes in play. It is possible that each alternative may underlie some forms of play and thus the diversity of play is best viewed as a continuum on which any separate motivational components of play are secondary processes, although they need not be. Thus, in learning to walk, at a certain age an infant seems very motivated to accomplish first crawling, then standing, then walking with support, then walking independently, then rapid walking and running. Piagetian and mastery-type processes can be involved. Here the motivational source is probably identical to that involved in locomotion itself. In play fighting, however, the motivational sources may be quite different from those underlying serious fighting. Motivational concerns are probably important in the evolution of play and underlie play as ritual as discussed earlier. Recall that the autotelic theory and the view that play is behavior done for its own sake are motivational constructs.

One way to study the question of the behavioral systems underlying play is to look for marker behaviors. Play signals (chapter 4) are often useful, but do not necessarily give unambiguous cues as to the behavior system being invoked. A rare exception is found in dwarf mongooses, which have a distinctive play vocalization that pulses 3–12 times per second throughout a play bout with an object (Rasa, 1984). The repetition rate is related to the intensity of play and associated behavior patterns. More typical is the finding that social play increases after feeding. For example, Pellis (1991) found that changes in object and social play occurred as a function of hunger in a group of captive oriental small-clawed otters (*Aonyx cinerea*). The typical object play sequence resembled the gathering, handling, fragmentation, and chewing of food. Typical social play involved attempts to gently bite a conspecific's cheek. As feeding time approached, the otters increased their object play and decreased their social play, even threatening each other over objects. Once the animals fed and were satiated, object play declined and amicable social play significantly increased. Such studies suggest that different kinds of play are linked to primary motivational systems rather than a separate play drive or instinct. Studies on the effect of hunger on play have led to a more complex picture of motivation and object play such that varying prey and toy size, type, and movement as well as satiation/hunger can lead to conflicting results (see Hall, 1998). Furthermore, different components of predation and other behavior systems may have separate thresholds and drives underlying the types of play performed and their sequential organization (Leyhausen, 1979). In this way the rarity of the final consummatory stages such as killing bites in play can be explained (Burghardt, 1984). Leyhausen's "drive surplus" view of play has been unduly neglected.

What we need are more detailed observations of play from the viewpoint of the various systems involved within what seems to be a single kind of play, such as play fighting. Play fighting in rodents has been most informative in this regard. Early work by Pellis and co-workers (Pellis, 1993; Pellis & Pellis, 1987) showed that the targets of play fighting were not those used in serious fighting, but those used in precopulatory encounters between males and females (see also Eibl-Eibesfeldt, 1970). Thus the view that play fighting represented a low level of aggression, but derived from the social aggression behavior system, was disproved at least in these species. In cats, both serious fighting and predation involved the same target (the nape of the neck) and thus other behavior patterns involving stalking, leaping, etc. were employed to decide whether the play represented predatory or conspecific fighting systems.

A recent study of the grasshopper mouse (*Onychomys leucogaster*), an unusual carnivorous rodent, showed that play fighting in this species involves the mixing of both predatory and nonpredatory (sociosexual) behavior systems (Pellis et al., 2000). Thus attacks to the nape of the neck are predatory and the other kinds of play behavior, such as nosing and allogrooming of the nape and nearby regions of the partner, are part of the precopulatory behavior system. Detailed observations of the sequential

organization of attack and defense in play fighting support this view. In another rodent, Richardson's ground squirrels (*Spermophilus richardsonii*), close analysis of play fights found that most (86 percent) could be readily classified as either sexual or aggressive play fighting, and most of these were sexual in both sexes (Pasztor et al., 2001). Furthermore, it was found that a play bout that began as sexual play fighting ended that way; the same was true for agonistic play fighting. This suggests that play fighting in other species also may only superficially appear to represent a unitary behavior system and questions the view that play is, by definition, a phenomenon of mixed motivations. Furthermore, in the ground squirrels, agonistic play fighting did not differ between the sexes, whereas sociosexual play did differ; males initiated more attacks.

Play in the most highly playful species involves multiple behavior systems, but they may remain largely separate causally. Mapping such diversity in the systems underlying play across taxa may be essential for tracing the evolution of play in its most highly developed forms. The transfer of elements from one behavioral system to another through ritualization (Grier & Burk, 1992; Tinbergen, 1951; Leyhausen, 1979) may also have happened in play (Loizos, 1967). This complexity may be a major reason for the lack of progress in understanding the evolution of play among playful families of mammals prior to the careful comparative work instituted by Sergio Pellis, Marc Bekoff, and others.

Can the motivational processes underlying social play be distinguished? Specifically, when dogs play with human beings is the same system being expressed as when they play with other dogs? Rooney, Bradshaw, and Robinson (2000) compared the details of play with toys when the partner was another dog or a human. They found less interest in the toy and more time spent in interacting with the partner in dog-human play. They also studied more than 400 dogs being walked by their owners and found that dogs who had the opportunity to play with other dogs played as much with their owners as dogs being walked alone. Dogs in multi-dog households played somewhat more with humans than dogs in single-dog households. The authors suggest that these differences mean that play with each kind of partner is motivationally distinct and cannot be used to predict levels of play with another type of partner. Clearly this is not a definitive study, but it might point the way to more experimental testing of this and related hypotheses. Still, the development of play from precursor behavior patterns cannot be ignored, as shown by the work of Chalmers (1980) with baboon (*Papio anubis*) infants (figure 5.5).

5.4.2 Emotion and Affect in Play

Whereas motivation is concerned with the "push" and the decision-making processes underlying the choice among alternative behavior patterns available to an organism, emotion and affect are viewed more as consequences of external stimulation or of the behavioral performance itself. The joy, fun, thrill, or pleasure attributed to playful acts is surely real in many cases and is an important and perhaps critical issue in the anal-

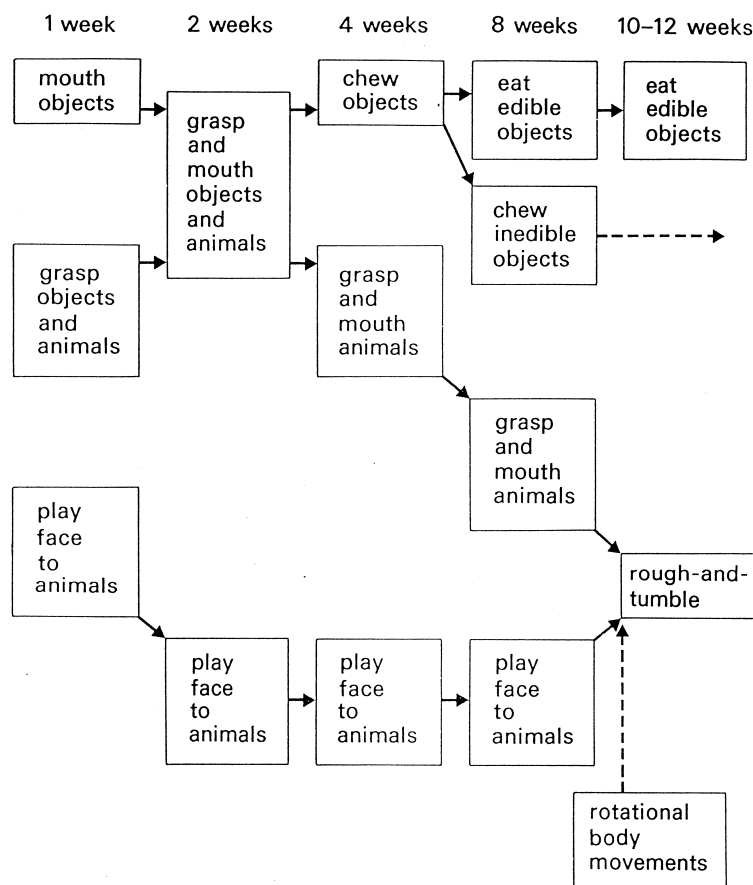


Figure 5.5

The emergence of complex play from precursor behavior patterns and the interaction among behavior systems in young baboons, *Papio anubis*. (From Chalmers, 1980)

ysis of play (Csikszentmihalyi, 1991; Spinka, Newberry, & Bekoff, 2001; Sutton-Smith, 2003a). For example, the positive (reinforcing) emotions associated with play have been interpreted as facilitating training to deal with more serious events when they occur (Spinka, Newberry, & Bekoff, 2001). Unfortunately these emotional attributes of play are not easily measured in diverse species, which is why affect, as well as motivation, were incorporated as alternatives in play criterion two. Certainly, any comprehensive theory of play will need to deal with affect and the way animals experience play, as the fifth ethological aim (private experience) posits. The performance of play, however, may not be conventionally “fun,” as shown by the concentration and even fear involved in voluntary thrill-seeking behaviors in which humans often engage

(Sutton-Smith, 2003a, b); whether these are found in other species is less certain but it is probable because stress may accompany play fighting (L. K. Smith, Fantella, & Pellis, 1999). Although the emotional and experiential aspects of play are not emphasized in the comparative survey that follows, ultimately we will need to do so.

Not only are motivational and emotional issues difficult to study in play, they suffer from a more general problem. Mainline psychologists downplayed motivational and emotional aspects of play for much of the twentieth century as a focus on species-typical behavior (instincts) became unfashionable. This is shown in the review of play by E. D. Mitchell and Mason (1934), who were at pains to accept the then-ascendant “modern” anti-instinct perspective (Bernard, 1924) and stated that “Out of habits and attitudes arise motives and desires. These are the drives that lead to play” (E. D. Mitchell & Mason, 1934: 70). Thus emotions and drives are mere learned behaviors that have no special status. Modern research questions such dogma, but the effect it had still lingers.

Having fun seems to be the major characteristic of play to many. Humor is often associated with fun, and laughing; a repetitive and easily recognized vocalization is one good sign that children are playing. As in children, there is evidence that great apes laugh when they are tickled and played with gently (Provine, 2001). Using ultrasonic detectors, we now know that rats too perform a laughterlike repetitive chitter response when tickled, and seek out opportunities to be tickled by a familiar person; they also perform the behavior in social contexts with other rats (Burgdorf & Panksepp, 2001; Panksepp, 1998a, 2000). Panksepp feels that such positive emotions aid social bonding and that the neurochemistry of such systems is a core mammalian attribute.

Is fun as a positive emotion an essential trait of play? It is not an essential part of play criterion two for a very good reason. Even if play is fun at times, this attribute is not only hard to measure in nonhuman animals in a noncircular manner, but it seems not to be true. Animals, including people, can be quite immersed in playful activities that arouse emotions other than benign fun or pleasure, such as intense fear, surprise, anger, and even grief as the play activity proceeds. Play may serve as a means of arousing emotions in settings where their serious deployment is muted through comfortable and socially constrained contexts. Sutton-Smith (2003a) has argued that much play in humans may be a means of triggering “virtual emotion” in safe contexts. In a sense, the psychoanalytic theory of Freud (Wälde, 1978) is a narrower version of Sutton-Smith’s formulation. Regardless, play may be proximally controlled by a broad array of emotions, not just fun. If this view is valid, then the often rapid transition from play to serious behavior (fighting, sex) can be understood. Once the virtual emotion is aroused, the serious one is more readily triggered. Social play fighting, particularly in older juveniles, can escalate into serious fighting, as in black bear cubs (Burghardt & Burghardt, 1972).

Perhaps the discouragement of recreational dancing by many conservative religious groups, especially at church social events for adolescents, derives from a recognition

that a transition from courtship play to consummated mating is a real danger and an unwelcome test of the efficacy of their moral teachings.

5.4.3 External Stimulation

Curiosity and exploration are directed to environmental stimuli, generally novel ones. Play, as discussed in chapter 3, can also be a response to stimuli in the environment, although novelty is not the key criterion. Play is clearly facilitated or even made possible by the presence of appropriate stimuli, be they objects or social play partners. Obviously locomotor play requires the appropriate environment—water for otters, trees for arboreal monkeys, fields for antelopes—as well as sufficient room. Object play is facilitated by items that provide appropriate interactive opportunities or “affordances” (J. J. Gibson, 1978) for the species involved. Much evidence supports the conclusion that animals often habituate to objects in their environment and increase their investigation and manipulation of novel objects when they are introduced (e.g., Renner & Seltzer, 1991). Social play partners of the appropriate age, size, and sex may be important, although social play between species is common, particularly in captivity.

Different species rely on different sensory systems, and this may influence the type and amount of play. Collared peccaries, as mentioned in chapter 3, rely heavily on olfaction, and in a field study playing was almost always accompanied by olfactory investigation and contact. This often took place in a 4 m diameter “playground” heavily scent marked (Byers, 1985). Play in the playground often involved many herd members in boisterous bouts four times longer in duration (about $6\frac{1}{2}$ min.) than play occurring elsewhere. Nocturnal primates rely on tactile, vocal, and chemical signals for communication more than on visual signals. If nocturnal and diurnal prosimian primates are compared, the former engage in much more play fighting than the latter, with New World monkeys and Old World monkeys continuing the trend toward use of visual cues in short-range communication, along with decreasing social play. It has been suggested that this is due to the use of play as a social evaluation and assessment method when visual cues are less available or less evolutionarily developed (Pellis & Iwaniuk, 2000a).

This finding is in line with much research suggesting that animals require certain types and amounts of stimulation for proper sensory, structural (muscle, skeletal), motor, and cognitive development. The environmental enrichment movement for captive animals is built on this premise (Burghardt et al., 1996), a premise so convincing that more and more legislation is being passed in the United States requiring that facilities provide not only adequate space for laboratory animals, but added structural features; varied diets provided in novel ways; and objects to manipulate, climb over, or push around. The concept of a range of necessary and optimal stimulation is central to this view. Clearly, apparatus, objects, and play partners are important in facilitating play. The notion that chemical, auditory, and tactile cues should be considered in

enrichment schemes that are in line with a species' biology and life history needs to be formally addressed (Lampard, 2002). Too often enrichment is based on providing satisfying visual displays for humans rather than dealing with the needs of the species being maintained in captivity (Burghardt, 1996). Nonetheless, experiments that attempt to evaluate the role of specific sensory modalities, such as olfaction, in the development and performance of play can lead to confusing results, especially when neural circuits are manipulated (e.g., Loranca & Salas, 2001).

Excessive stimulation (crowding, too much noise), not just insufficient stimulation, can lead to increased stress and decreased play, as noted in play criterion five. But stress is best measured from the perspective of the animal and not just environmentally. For example, in one study, high-density housing of chimpanzee groups led to less agonistic behavior, less mutual grooming, and fewer submissive greetings, but more juvenile social play (adult social play was very low in both conditions) (Aureli & de Waal, 1997). In rats, social play was also increased in small cages (Siegel & Jensen, 1986) and small boring environments might be a reason for the common observation that well-cared-for animals play more in captivity than in the field (Burghardt, 1984). For juveniles, the increased availability of nearby play partners may have facilitated social play more than crowding inhibited it.

Although spare and sterile environments may inhibit play, animals are not passive reactors to environmental constraints. They can actively alter their level of stimulation, and this may be a crucial factor in the origins of play (Burghardt, 1984). Animals in stimulus-deprived (boring) environments may engage in various activities to relieve sensory and response deprivation and to increase arousal. Such boredom might be expected in the well-provisioned and protected environments (e.g., nests, burrows) provided by endothermic parents. This factor may be the critical one in the consistent finding that well cared-for captive animals play much more than their wild counterparts (Burghardt, 1988b). If juveniles are buffered from the demands of survival, and the species possesses a complex repertoire of evolved and active behavior patterns, then the animals have a behavioral resource to draw on when they are deprived of stimulation. Lowering of the stimulus threshold and reorganization of behavior sequences into less precise adultlike forms could result. Since the simplistic views of a unitary nonspecific arousal system are no longer accepted, having been replaced with a conception of functionally different neural systems mediated by monoaminergic and cholinergic neurotransmitters "contributing to different forms of behavioral activation" (Robbins & Everitt, 1995: 703), the plausibility of such processes has increased. For example, polecat (*Mustela putorius*) young, when reared alone, engaged in more than three times the social play than socially reared animals, and the author argues that the threshold for play sequences was lowered (Diener, 1985).

Related to this is the finding that many mammals that typically engage in social play may, if deprived of a play partner, respond to less-preferred partners or even play with

inanimate objects as if they were a social play partner. If a preferred play partner is present, such object play responses are reduced (Power, 2000).

5.4.4 Genetic Differences in Playfulness

If play is subject to natural selection, then individual differences in playful behavior should be at least partially attributable to genetic differences, irrespective of sex or species. Laboratory rats from different strains play fight to different extents, and this play can be differentially affected by experience (Siviy, Baliko, & Bowers, 1997; Siviy et al., 2003). Individual differences in locomotor play in laboratory mice are heritable (C. Walker & Byers, 1991) and suggestive evidence exists for horses as well (Wolff & Hausberger, 1994). As noted earlier, temperament differences among individual animals from fish to snakes to humans are increasingly reported (D. S. Wilson et al., 1994). Such individual differences, as well as those in the level of neurotransmitters such as dopamine, are related to the occurrence of play and exploratory behavior in mammals (Burghardt, 2001; Depue & Collins, 1999; Siviy, 1998; Vanderschuren, Nie-sink, & Van Ree, 1997). Consistent with this theory, C57BL6 mice have more dopamine neurons than DBA2 mice and show more novelty-induced exploratory behavior than DBA2 mice (see also Cabib, Puglisi-Allegra, & Ventura, 2002; Depue & Collins, 1999). Rats would be the prime animals to test for exploratory and object play differences since different strains also vary in their dopamine concentrations (Depue & Collins, 1999). Recently, rats have been genetically selected for immature behavior (Brunelli & Hofer, 2001) and such a process, which may be prevalent in domestication, also shows the potential role of genetics and individual differences in playfulness. Rats have been bred for their laughter response when tickled, showing a marked change from baseline rates in four generations (Panksepp, Burgdorf, & Gordon, 2001).

Finally, if playlike behaviors can be selectively bred, then it is possible to begin looking at a host of associated changes in other behavior patterns—development, sociality, physiology, anatomy, and so forth. Silver foxes (*Vulpes vulpes*) bred just for social tameness showed many seemingly unrelated changes in morphology and behavior and became more playful, even doglike in their attachment to people (Trut, 1999). That this is not an isolated finding is suggested by studies such as those by Gariépy, Bauer, and Cairns (2001). These authors selected mice for high or low social aggressiveness. In a very detailed and careful study, they found that selection led to developmental changes in timing of behavior (heterochrony) so that low aggressive lines showed greater differences early in ontogeny (days 28 and 42) than as adults (day 280), especially early in the selection process. The authors point out that this is an example of neotenzation of behavior, and it would be interesting to see how play behavior was altered, especially since domesticated laboratory mice are not very playful compared with rats (Pellis et al., 1991; Poole & Fish, 1975). Mink (*Mustela vison*) selected for approach (confident) reactions to people explored people more quickly and

maintained much closer distances to them than did mink undergoing selection for avoidance (fear) of people (Malmkvist & Hansen, 2002). More interestingly, confident selected mink approached and played with novel objects more, explored tubes in a maze more, and would more readily approach and eat a new food.

Such studies may not always have clear results, but the differences can be illuminating as well. Girard et al. (2002) selectively bred mouse strains for high and low wheel-running activity and found, rather surprisingly, no effects on offspring size, litter size, growth, maternal behavior, or other life history measures. However, the mothers did not have access to running wheels during the time they were raising babies and the authors predict that when they have such an opportunity, reproductive performance in the high-running strain will suffer.

5.4.5 Neural Substrates of Play

Does play have its own neural underpinnings, a play module as it were, as suggested by Panksepp (1998a) and advocated for most behavioral systems by evolutionary psychologists (Buss, 1999)? Such play would most likely be tertiary play. Or is play a product of a special set of circumstances that could arise in almost any behavior system? Indirect evidence supporting the modularity view comes from studies indicating a specific motivation for play of certain types (Rasa, 1984). Contrary evidence comes from those who see play as derived from incipient behavior (intention movements; Lorenz, 1981), the emergence of prefunctional behaviors in ontogeny (Hogan, 1988, 2001; Kruijt, 1964), or conflicts between behavior systems (Pellis et al., 1988). These views would all reflect primary process play. We are far from an answer, but neural play circuitry would have evolved from the latter processes and thus we might expect both specific and more diffuse neural underpinnings for play of different types, different phases of the sequence, and in different species, as suggested in section 5.4.1.

The role of the brain in play has been reviewed repeatedly, although unfortunately most neuroscience research on play is based on play fighting in rats (Panksepp, 1998a; Panksepp, Siviy, & Normansell, 1984; Pellis & Pellis, 1998a; Siviy, 1998; Vanderschuren, Niesink, & Van Ree, 1997). Integrating this work with the literature on exploration and responses to novel objects led to the following conclusions (Burghardt, 2001), which are updated here with more recent studies.

The brain is central to behavioral performances as well as the cognitive, emotional, and motivational attributes of a behavior. The role of play in cognitive processes is often supported by pointing out that play is found most commonly in those birds and mammals that have large brains relative to their body size and are considered “intelligent” (Fagen, 1981). In fact, recent claims by primatologists make it sound as if we have all the answers and the skepticism underlying this book is misplaced: “The bigger the brain, the longer the life, the more the need for social living, the more complex the environment (including the social environment), the greater the importance of play”

(Poirier & Field, 2000: 262). The passage continues with all sorts of bald claims about the adaptive value of play, although the only reference for these claims is 30 years old (Poirier & Smith, 1974). Regardless, play and curiosity could be marks of intelligence as well as necessary for the development of a sophisticated mind. The view that play is most common in large-brained animals is rarely evaluated rigorously; what we find when we do such an assessment has not been very encouraging to date.

First, we need to determine if species with larger brains *are* more intelligent. This certainly is an attractive hypothesis: "The larger the brain, the more likely that the animal's behavior will appear highly intelligent. Large-brained species will have large motor repertoires and will construct complex, variable, goal directed motor sequences. They will recognize foods, mates, and other objects by means of object images constructed from varied perceptual features. Large-brained species will also exhibit greater ability to accommodate motor actions to environmental stimuli, and their behavior will appear more volitional" (K. R. Gibson, 1990: 109). Such putative relationships were at the heart of much comparative psychology; the problem was the lack of a general measure of learning ability that could be used across species with widely differing morphological, ecological, social, neural, and phylogenetic attributes. Thus a more limited emphasis on behavioral specializations of an ethological and ecological nature became popular (Burghardt, 1973). Nevertheless, the general pattern of increased brain size relative to body size among those mammals and birds considered most intelligent or adaptable in behavior is hard to ignore. Efforts to develop a comparative measure of intelligence that can cut across species are still under way; a recent attempt claimed to be promising for primates from prosimians to *Homo sapiens* is the transfer index, a measure of an animal's ability to learn from prior learning (Beran, Gobson, & Rumbaugh, 1999). The correlation with brain size is high enough (0.83) that the authors used it to predict the intelligence of extinct hominid species.

Even if we accept that animals with larger brains are, in some important senses, smarter or more cognitively adept than other species, does this relate to play? Claims are frequent that play seems more common in, if not limited to, species with large brains (Fagen, 1981). Whether this holds across diverse species in a taxonomic group will be explored in later chapters. However, play frequency and complexity can differ among even closely related species (Pellis et al., 1991; Poole & Fish, 1975) and among those with similar relative brain sizes. Thus one needs to look at the kinds of play shown and all the other factors enumerated earlier.

Additional complications arise. Domesticated species generally play more frequently than their wild counterparts (Burghardt, 1984), but they actually have considerably smaller brains, controlling for body size. Indeed, domestication seems to lead to a decline in brain size of about 30 percent (Kruska, 1987a,b; R. W. Williams, Cavada, & Reinoso-Suárez, 1993). A comparative analysis of relative brain size and play showed that while at the level of order or family, a relationship may hold (chapters 8 and 9,

Byers, 1999a), when studies controlled for phylogenetic effects or focused on closely related species differing in playfulness, the correlation largely disappears (Iwaniuk, Nelson, & Pelles, 2001). The ratio of neocortex size to play in primates does appear to be positively related to social play but not locomotor or object play (Lewis, 2000). Thus overall brain size may not be a crucial factor in variation in playfulness (Burghardt, 1999).

There are also some other problems with the putative relationship between play and cognition. Dogs raised in social isolation appear to be more social and curious than normally reared dogs, especially in novel situations; they are less neophobic. However, Melzack and Thompson (1956) showed that such dogs are rather stupid; even the most trivial items amuse them persistently. There is also considerable evidence that habituation—rapid boredom with stimuli—is a good measure of intelligence and can be used to test preverbal infants with considerable success (Colombo, 1993). If becoming bored is a sign that one has mastered what there is to know or do with an object, then choosing stimuli that are more complex might be a way to maintain play. This is exactly what Piagetian mastery play is directed toward. K. V. Thompson (1998) has advocated a similar process that she terms self-assessment; animals play to perform and “practice” a skill until it becomes mastered or too easy (habituated, boring).

However, curiosity killed the cat. Rodents, fish, and tadpoles that stray too far from secure retreats for food have been shown to be more at risk of predation (e.g., Sih, 1992), and evidence for predation as a cost of play was documented earlier. Thus prudent behavior has some advantages over the exuberant “joy of life” excitement many view as the essence of play. Clearly, some ecological contexts might have facilitated play in some contexts and opposed it in others.

It is also becoming increasingly apparent that external stimulation, including environmental enrichment, can enhance brain development in many domestic species (Kolb & Whishaw, 1998). In humans, the role of experience in brain development, including critical periods, is not very well known and there are fears that making large claims in this area in the public news media is both premature and could backfire (R. A. Thompson & Nelson, 2001). Nevertheless, Thompson and Nelson provide a summary graphic (figure 5.6). Play may be one of the ways that such enrichment has neural effects, although the diversity of types of play and the extent of play in mammalian species that have been studied preclude generalizations. What is interesting here is that the plasticity seen in the ontogeny of individual animals can be mimicked by rapid genetic changes in several thousand years of domestication (Ebinger, 1995) or even several generations (Trut, 1999). Perhaps, however, the role of the brain in play is not tied to the development of the “higher” brain centers, but true to its resemblance to instinctive behavior, is more accurately traced in its origins to the brain systems that underlie motivated and emotion-laden instinctive behavior: the striato-pallidal complex (basal ganglia) and the limbic system (Burghardt, 2001). These areas, along with

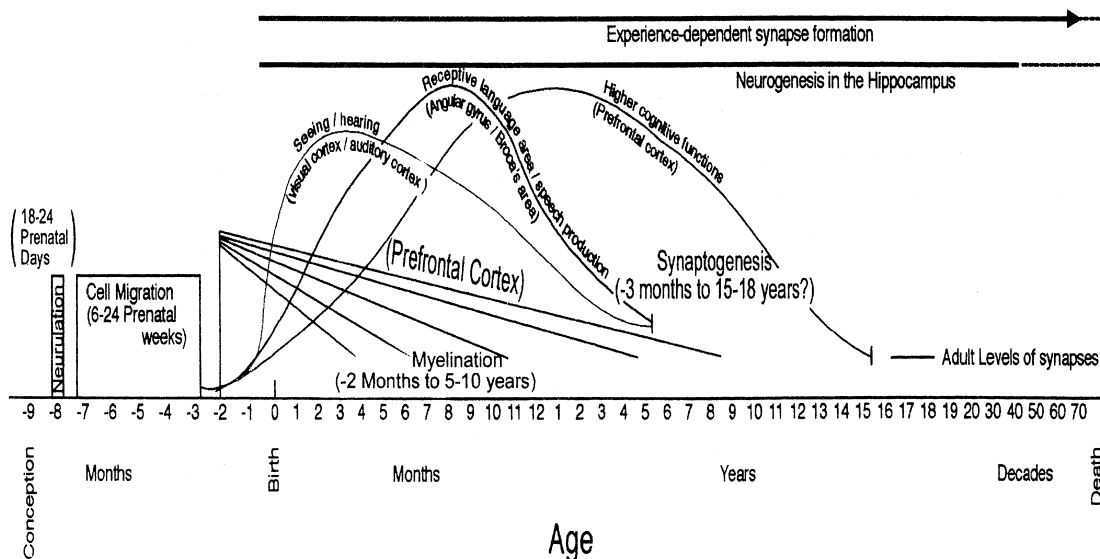


Figure 5.6

The course of human brain development showing the differential pacing of different brain regions and psychological processes. (From R. A. Thompson & Nelson, 2001)

the prefrontal cortex, link emotion, motivation, and reward conditioning (Cardinal et al., 2002). Some neuroscientists vigorously maintain that the mammalian brain evolved conservatively and while “Special [natural?] selection for specific functions does occur, . . . it is a minor factor compared to the large-scale covariance of the whole brain” (Finlay, Darlington, & Nicastro, 2001). However, convincing evidence for a more modular “mosaic” evolution of brain structures based on function exists (e.g., Barton & Harvey, 2000) and play may be a tool to investigate the “play module” idea.

The amygdala may be particularly important in social play. For example, lesions of it in male rats on days 7 or 21 led to decreases in social play one or two weeks post operation compared to sham and ventral hippocampus lesions (Daenen et al., 2002). However, social behavior deficits in adult rats were seen only in rats lesioned in the amygdala on day 7, suggesting a neurodevelopmental defect. This and other studies (Burghardt, 2001; Pellis & Iwaniuk, 2002) suggest that the amygdala and social play may be related. A phylogenetically controlled comparison of adult social play and brain size in primates found that amygdala size was correlated with sexual but not nonsexual play, whereas nonvisual neocortex was related to both play types (Pellis & Iwaniuk, 2002). Brain imaging studies will become much more feasible with small animals in the future and the possibilities are intriguing. For example, not only is

laughing a stereotyped fixed action pattern response in people (Provine, 2001), the amygdala of the limbic system is itself activated when people hear laughter (Sander & Scheich, 2001) regardless of their mood or attentional state, suggesting that markers of play (as well as of distress such as crying) are neurologically and developmentally largely preprogrammed responses in behavior systems.

The basal ganglia, prefrontal cortex, and dopamine systems are critically involved in the reward, anticipation, memory, social modulation, and goal orientation seen in the often fast-paced, contextually sensitive, and anticipatory responses (Pellis & Pellis, 1998a; Kolb, Pellis, & Robinson, in press) of locomotor, object, and social play. Dopamine is the main neurotransmitter involved in play and is heavily concentrated in the basal ganglia and its associated structures implicated in play. In fact, the substantia nigra and ventral tegmental area (involved in motor systems) have perhaps the highest concentrations of dopamine in the brain (Butler & Hodos, 1996). Dopamine is involved in reward, pleasure, arousal, and motor patterning systems of motivated behavior. Exploiting the sequential organization of play sequences (i.e., initiation, engagement, and termination) may be useful in clarifying the role of dopamine in play. This literature cannot be explored in depth here, but it is important to note that the studies of Siviý and others suggest that dopamine antagonists reduce play, but agonists do not always facilitate play. To resolve this inconsistency, Steve Siviý proposes that dopamine might be involved in the initiation of play through anticipated reward systems and summarizes suggestive experimental evidence. He speculates that:

Stimuli which predict a playful experience would result in increased activity in the dopaminergic mesolimbic pathway. This would result in an increased release of dopamine in mesolimbic terminal areas, such as the prefrontal cortex and nucleus accumbens, resulting in energization of the animal and behavior patterns that would increase the probability of a playful interaction. Because of the diffuse nature of noradrenergic, serotonergic and opioid pathways, these systems are likely to exert a more modulatory influence on how the play bout will unfold. Increased noradrenergic activity may enhance the ability of a rat to focus its attention on the task at hand (i.e., playing), while increased opioid activity may enhance the pleasure associated with playing. For all this to happen, serotonin levels must also be low. (Siviý, 1998: 232)

However, these systems are also involved in many nonplay activities, suggesting that the pathways involved may overlap, converge, or reinforce a variety of behavior systems. This supports the plausibility of the hypothesis that play originated in the initiation and execution of instinctive behavior sequences in which motor performance was itself rewarding. Repeating the behavior could enhance performance through practice in changing contexts and produce modifications of sequences based on experience. It turns out that the neural circuits underlying species-characteristic behavior may be very conservative and just a single gene may alter regulatory neuromodulation (Katz & Harris-Warrick, 1999). We also now know that 30 minutes of social play in rats can affect gene expression and lead to measurable changes in a variety of brain areas,

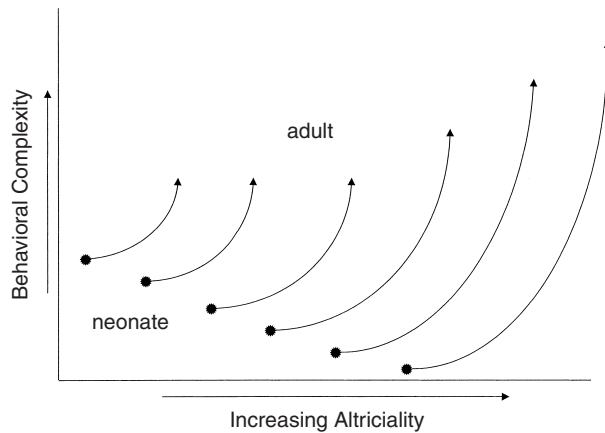


Figure 5.7

Behavioral complexity as an adult is often greater in animals born in a more altricial state and with a longer period of dependency on parents. Juvenile play then has a greater opportunity to become developmentally important.

including those in the striatum, tectum, somatosensory cortex, and hypothalamus (Gordon et al., 2002). Further work showed that such play experience leads to elevated levels of brain-derived neurotrophic factor (BDNF) in the amygdala and dorsolateral frontal cortex (Gordon & Panksepp, in press). BDNF is a key modulator of neuronal development and plasticity, and the authors suggest “that play may help program higher brain regions involved in emotional behaviors,” a tertiary play process, even though decorticate rats can still play. Soon brain imaging during play may be possible. Child developmental psychologists are now attempting to study how to “turn on” genes that promote favorable outcomes (B. Brown, 1999). Although these initial discussions are based on the effects of stress, poor nutrition, and other markers of poor environments, a focus on the value of more active behavior such as play may not be far behind. Solid experimental work here will result in perhaps the most powerful tool available to assess the role of play in our lives.

Nevertheless, the difficulty in isolating specific long-term benefits of play may lie in the fact that play may provide only one of several ways to enhance behavioral, physiological, and cognitive performance, a facilitation that is not essential in every case (Burghardt, 1984; Fairbanks, 2000). In any event, neural systems underlie playful acts and may be affected by them. However, the origins of play do not solely lie within the brain itself. The brain is the mediator of animals’ responses to their environment as well as a record of a long evolutionary history. If adult behavioral complexity, not just intelligence, is important in playful species, then slower rates of behavioral development,

and opportunities for play, may both relate to behavioral complexity (figure 5.7) and be involved in the transition between primary and secondary play (see figure 5.1).

If play is closely linked in the brain to the many behavioral systems that underlie the repertoire of any species, then it is not surprising that play in any species resembles its normal behavioral repertoire, and that it often shares the motivational, perceptual, behavioral, and emotional pathways of these systems. The shift from play fighting to serious fighting can be thus understood in neural terms, although the detailed mechanisms are still not known.

The research discussed in this chapter and in part II supports the view that locomotor, object, and social play derive from different behavioral systems associated with the species-characteristic behavior of animals. The nature and the amount of play are not random, but are tied to a species' phylogeny, ecology, ontogeny, and normal behavior. Object play is typically predatory in carnivores and manipulatory in extractive foragers (such as cebus monkeys). Social play can be composed of chasing, stalking, wrestling, and other behavior patterns that may be derived from sexual, aggressive, or predatory behavioral systems. Many of the most playful species show all three major types of animal play, although the mix may differ. This level of complexity seriously hampers attempts to uncover the ancestral forms of play. It is because of such complexity in the internal dynamics of play that it is necessary to turn to other factors that may explain the origins and early evolution of play.