Play in evolution and development ☆

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Abstract

In this paper we examine the role of play in human ontogeny and phylogeny, following Surplus Resource Theory. We consider how juveniles use play to sample their environment in order to develop adaptive behaviors. We speculate about how innovative behaviors developed in play in response to environmental novelty may influence subsequent evolutionary processes. Play during this period of immaturity is especially important in the processes of development and evolution, because in play new strategies and behaviors can be developed with minimal costs and these strategies, in turn, can influence evolutionary processes. We posit that play influences these processes by supporting the development of new strategies in novel environments during the juvenile period.
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Invoking evolutionary theories to explain the human condition has a long history in psychology. Darwin (1871, 1877) himself applied his theory of evolution by natural selection to humans. Almost immediately this cause was taken up by others, for example Spencer (1878, 1898), in his book *The Principles of Psychology.* In the early 20th century, Hall (1904, 1916), the first president of the American Psychological Association, also applied variants of this theory to human's ontogenetic and phylogenetic development, perhaps most infamously hypothesizing, following Haeckel, that ontogeny recapitulates phylogeny. The importance of the roles of phylogeny and ontogeny in understanding human behavior

and cognition has continued as principles of evolutionary biology have been applied to the human condition, radiating from ethology (e.g., Blurton & Jones, 1972), sociobiology (Wilson, 1975), and evolutionary developmental psychology (Bjorklund & Pellegrini, 2002). In more recent cases, however, scholars have stressed the effect of ontogeny on phylogeny, as much as the reverse (e.g., Bateson, 2005; Bjorklund & Rosenberg, 2005; Hinde, 1983).

The study of play in both nonhuman and human animals has been an integral part of this venture for well over a century (e.g., Bateson, 1981, 2005; Groos, 1898, 1901; Pellegrini & Smith, 2005). For example, Groos' two volumes on the play of nonhuman (Groos, 1898) and human animals (Groos, 1901) suggested that play during animals' juvenile period, or period of immaturity, was "critical" in shaping later development. This notion of the deferred importance of juvenile play for subsequent development was later incorporated into Piaget's (1962) and Vygotsky's (1967) theories of play in human development.

Wilson (1975) anointed the study of play as one of the most important research topics in sociobiology. Robert Fagen (1981) rose to the challenge with his seminal examination of animal play. Fagen, like Groos, concluded that the importance of play, as a quintessential juvenile behavior, stems, in part, from the notion that an organism's early experiences are critical to subsequent development and functioning.

More recently, Burghardt (2005) examined the place of animal play in the phylogenetic order in light of his Surplus Resource Theory. For Burghardt, the extended juvenile period is crucial to the role of play in developing the complex set of skills necessary for survival and reproduction especially true for animals whose ecology is varied or unstable. From this position, individuals' behaviors are not triggered by an anticipated set of contingencies. Instead, juveniles use the resources afforded them (safety and provisioning by a parent) during this period to explore their environment and experiment with a variety of strategies that may be effective in that niche. These environmental and behavioral factors, in turn, should indirectly affect subsequent gene expression, frequency, and evolution.

In all the cases presented above, play behavior of nonhuman animals was of central concern, though each author speculated about the role of play in the human condition. Arguably, the study of play in humans from a broad phylogenetic and ontogenetic perspective has been less systematic. Rubin, Fein, and Vandenberg (1983) provided a thorough psychological overview in their chapter in volume four of the *Manual of Child Psychology*, and Smith's (1982) article and 1984 book compared animal and human play. This has not been taken up to any great extent in the subsequent 20 years, though recent work by Power (2000), Pellegrini and Smith (1998, 2005), and Sutton-Smith (1997) have included discussions of both human and nonhuman play. This is a puzzling state of affairs because, from our view, play during humans' period of immaturity represents a paradigm example of the place of a behavior in both ontogenetic and phylogenetic development.

During ontogeny, play is observed primarily during the juvenile period in forms that are qualitatively different from seemingly similar adult behaviors. For example, children often playfully enact adult roles other they have observed. These play behaviors, relative to more serious and functional adult variants, are typically exaggerated (Pellegrini & Smith, 2002) and have hypothesized importance for subsequent development (Smith, 1982).

The more complex and flexible the organism, the longer the period of immaturity (Bjorklund, 2006; Bjorklund & Rosenberg, 2005). Humans have an extended period of immaturity, relative to other mammals. including nonhuman primates (Bjorklund & Pellegrini, 2002; Bogin, 1999; Kaplan, Lancaster, Hill, & Hurtado, 2000). Lancaster and Lancaster (1987) have argued that the long period of immaturity in humans (until sexual

maturity) was adaptive for an environment in which extensive parental-investment could pay off in terms of skill acquisition by offspring, in a situation in which immediate productive activity by children might be difficult due to hazards (e.g., hunting) or difficulty of extracting resources (e.g., foraging). Although in contemporary environments children learn mostly through formal teaching, in traditional human environments this was not the case. Learning mostly occurs through observation, exploration, and play (Lancy, 1996; Smith, 2004).

In modern society, formal schooling was created to educate children as an extension of the rationalizing associated with industrialization (e.g., social engineering, specialization, and efficiency) (Glickman, 1981). In pre-industrial times (Thomas, 1964), and currently in pastoral and foraging societies, learning is more integrated into the fabric of a child's daily life—not set off into a separate institution (Bock, 2005; Rogoff, 1994). For example, contemporary Botswana girls learn to process grain through a seamless process whereby they first play at pounding grain, where pounding with sticks and reeds is typically embedded in a fantasy theme. As girls become proficient in this activity in play, they move into "work" related grain pounding with mortars and pestles (Bock, 2005). From this position, one of the primary purposes of this extended period of immaturity is for organisms to sample their environment so as to development behaviors and strategies that are adaptive.

Play is a central component for the immature child. Indeed, an extended period of immaturity is typical when play is observed in most species. This correspondence between play and an extended period of immaturity is not trivial. We, following Fagen (1981) and others (Bateson, 2005; Sutton-Smith, 1997), posit that play during the extended period of immaturity is an important strategy used to develop behaviors that are adaptive to the niches that young children and adults inhabit. We posit that children sample their environment and through play learn and practice behaviors adaptive to that environment. Like Bateson (2005), we speculate further that play behaviors in ontogeny may be in the forefront of ways in which phenotypes affect subsequent evolutionary processes. We thus turn Hall's characterization of human development that ontogeny recapitulates phylogeny on its head by suggesting that ontogeny affects phylogeny.

This paper is organized as follows. First, we define play and then embed it in the phylogenetic order, following Burghardt's (2005) Surplus Resource Theory. Next we consider the role of play in human ontogeny and how immature organisms use play to sample their environment in order to develop adaptive behaviors. Lastly, we speculate about how innovative behaviors that develop in play in response to environmental novelty may influence subsequent evolutionary processes. Play during the juvenile period, as we argue, and following Bateson (2005), Burghardt (2005), Špinka, Newbury, and Bekoff (2001), is especially important in the processes of development and evolution, because in play, generally, new strategies and behaviors can be developed with minimal costs and these strategies can, in turn, influence evolutionary processes. We posit that play influences these processes by supporting the development of new strategies in novel environments during the juvenile period.

What is play and where does it occur?

The difficulties in defining play (e.g., Burghardt, 2005; Fagen, 1981; Hinde, 1974; Pellegrini & Smith, 2002; Sutton-Smith, 1997; Wilson, 1975) have not stopped a proliferation of definitions being proffered by animal behaviorists and psychologists. For

example, Fagen (1981) mentions close to 60 attributes of play listed by a variety of scholars. These attributes have been distilled down, across the varied disciplines, to the following (Burghardt, 2005; Špinka et al., 2001): Play is a seemingly "non-serious" variant of functional behavior. Playful behaviors resemble serious behaviors but participants are typically more concerned with the behaviors themselves (i.e., "means") rather than the function (i.e., "ends") of the behavior. Playful behaviors are also typically more exaggerated than their functional counterparts and the components of functional behavioral routines are often re-arranged in play. For example, playfighting, though it resembles serious fighting in some ways, is just that—playful, not serious, and participants generally do not aim to hurt each other. There are hits, but they are exaggerated and soft—not hard and participants typically reciprocate roles, alternating between the play aggressor and the play victim (Pellegrini & Smith, 1998). It follows that play behaviors, relative to non-play behaviors, stress means over ends, as well as self-selection and intrinsic motivation, and variable, non-stereotyped behaviors.

Given these criteria for play, "games" are not included in our discussion. Games, unlike play, require participants to follow *a priori* rules (Pellegrini, Blatchford, Kato, & Baines, 2004; Piaget, 1962). That is, participation in games requires participants to follow pre-set rules. If they do not follow the rules, they are penalized in some form. For example, in a game of baseball, a batter must relinquish his/her turn after three strikes or be excluded from the games. In play, children do follow rules, but the rules are flexible and are typically negotiated by children; for example, in pretend play, a child may decide that she's the mother and wants to cook a pretend meal. Her playmate, the pretend father, may disagree saying that "No, I want to cook." Plans are often changed to accommodate to different views so that play can be sustained (Pellegrini, 1982; Sachs, Goldman, & Chaille, 1984). This level of flexibility in play, that is absent in games, is crucial to behavioral innovation, as we will argue in this paper. Behavior in games, on the other hand, is more convergent and should not foster innovation.

Play occurs in safe and familiar environments for animals with an extended and protected period of immaturity and in the presence of adequate, or even surplus, resources (Burghardt, 2005). Indeed, when organisms are under stress, such as during a food shortage (Müller-Schwarze, Stagge, & Müller-Schwarze, 1982) or extreme ambient temperature (Cullumbine, 1950; Pellegrini, Horvat, & Huberty, 1998), levels of play are reduced or cease altogether (Baldwin & Baldwin, 1976). That levels of play decrease under these conditions indicate that play may be "costly" in terms of caloric expenditure and survivorship risks (Martin & Caro, 1985). The cost of a behavior, relative to its benefits, has important implications for the function, and possible natural selection, of that behavior, as will be discussed below.

Forms of play are typically parsed by animal behaviorists along locomotor, social, and object dimensions, with the first two being more closely inter-related (Burghardt, 2005; Fagen, 1981; Martin & Caro, 1985). For example, playfighting, or rough-and-tumble play (R&T), has both physically vigorous and social dimensions (Pellegrini & Smith, 1998). Reliable sex differences have been observed in most forms of locomotor play, with males, more than females, engaging in locomotor play more frequently and at higher levels of intensity (Pellegrini & Smith, 1998).

Play with objects is typically sedentary and can be either social or solitary (Pellegrini & Gustafson, 2005). While boys engage in object play more than girls (e.g., Bock, 2005), girls engage in "constructive play," more than boys (e.g., Johnson, Ershler, & Bell, 1980).

However, constructive play, as defined in the literature, does not meet most of the criteria for play, as it is more "ends" than "means" oriented (Smith, Takhvar, Gore, & Volstedt, 1986).

Child developmentalists have usually neglected locomotor play, including play fighting (though see Pellegrini & Smith, 1998), and have mainly focused on fantasy play (Fein, 1981; Rubin et al., 1983; Smith, 2005). Fantasy, or pretend, play can be either social or solitary, though it tends to be social in young children (Haight & Miller, 1993). Girls, more than boys, engage in pretend play with domestic themes, such as "playing house," but boys engage in more pretend with physically vigorous themes, like "superheroes (Rubin et al., 1983). Whether nonhuman primates, especially those reared in their natural habitats, can engage in fantasy play is highly debatable and any such examples are certainly less complex than those typical of human 3-year-olds (see Gómez & Andrade, 2005; Tomasello & Call, 1997).

All forms of play follow exploration, ontogenetically. Infants spend more time exploring than playing and as toddlers their play increases to displace exploration in stable environments (Belsky & Most, 1981). Further, before infants, toddlers, and children can play with an object, they must explore it first (Hutt, 1966). In exploration individuals extract attributes of and uses for objects and individuals and then use those attributes as bases for play bouts. Take, for example, a child entering a preschool classroom for the very first time. In the initial weeks of the experience, the child is apprehensive and spends time (often cautiously) exploring the physical and social environment of the school—exhibiting, passive onlooker behavior (McGrew, 1972; Pellegrini & Goldsmith, 2003). Exploratory behavior is used not only to inventory an environment, but it is also used to identify dangerous aspects of an environment and discover how to avoid them (Špinka et al., 2001). Once it is determined that the environment is safe, then play occurs (McGrew, 1972; Pellegrini & Goldsmith, 2003).

All forms of play, for both human and nonhuman animals, also follow an inverted-U developmental curve, peaking during the juvenile period—a period where organisms have an abundance of resources and protection. Specifically, pretend, social, and locomotor play of children are first observed at the start of the second year, peak during the preschool years and then decline rapidly during the primary school years (Fein, 1981; Martin & Caro, 1985; Pellegrini & Smith, 1998; Rubin et al., 1983). The age-related trend for object play of nonhuman apes follows this pattern as well (Ramsey & McGrew, 2005), but the object play data for humans is more ambiguous, due to the conflating of object play with construction (Rubin et al., 1983), exploration, and tool use (Pellegrini & Gustafson, 2005). All of these factors converge on individuals using play to learn and develop new, and innovative, behaviors.

The phylogenetic place of play

Consideration of the evolution of play yields further insight into the antecedent conditions and possible functions of play (Tinbergen, 1951). Burghardt's (2005) Surplus Resource Theory is an evolutionary model which specifies the conditions necessary for play to develop in different species. They include: Parental care and correspondingly long periods of immaturity and ability to metabolize so as to thermo-regulate and engage in and recover from vigorous activity. From this view, play can be observed in those orders with surplus resources. Consistent with Surplus Resource Theory, play has been observed

predominantly in mammalian and avian species (Fagen, 1981), which generally have extended juvenile periods and relatively developed cerebral cortex. More controversially, Surplus Resource Theory posits that play exists in reptiles and fish, as well as some invertebrates (Burghardt, 2005), to the extent that these species have surplus resources and developmental plasticity and can use play during ontogeny to help shape their behavioral responses to their ecologies. Indeed, these are the same conditions that are important for increased behavioral plasticity and innovative responses to environmental change (Bjorklund, 2006), leading us to posit that play may be an important mechanism at the vanguard of behavioral innovation during the juvenile period.

Play in ontogenetic development

Consideration of ontogenetic development, in conjunction with phylogenetic development, function, and immediate causation, is crucial to understanding the meaning of a behavior or strategy (Tinbergen, 1951). The importance of ontogeny was highlighted by the differing views of Lorenz (1937, 1965) and Tinbergen (1951) on the role of environmental input in what was called "instinct." Lorenz argued that instinctual behavior was "innate" and that environmental influence was limited to a behavior being triggered by a stimulus during a critical period in development. Lorenz' observation of goslings imprinting to humans is perhaps the most famous example of this phenomenon. Instincts, from this view, were adaptive behaviors "built into genes" that required minimal environmental input (Bjorklund & Pellegrini, 2002).

Subsequent research on filial imprinting (e.g., Bateson, 1978; Gottlieb, 1976) demonstrated much more plasticity in young birds' responses than Lorenz envisioned. The variability of responses was influenced by experiences during "sensitive" periods of development during the juvenile period. The point of mentioning the imprinting debate is that understanding ontogeny is crucial to explicating the plasticity of development in terms of organisms adapting to their immediate environments, and possibly impacting evolution (Bateson, 1981, 2005; Bjorklund & Rosenberg, 2005).

The extended juvenile period, as argued by Surplus Resource Theory, is crucial to the role of play in developmental plasticity and to assembling the complex set of skills necessary for survival and reproduction. This is especially true for animals whose ecology is varied or unstable. From this position, individuals' behaviors are not triggered by an anticipated set of contingencies. Instead, juveniles use the resources afforded them (safety and provisioning by a parent) during this sensitive period to explore their environment and experiment with a variety of strategies that are effective in that niche, reflecting developmental plasticity.

When faced with a relatively novel or uncertain, but safe, environment, play affords opportunities for behavioral and cognitive innovation and subsequent practice of newly developed behaviors and strategies (Bateson, 2005; Bjorklund & Rosenberg, 2005; Bruner, 1972; Špinka et al., 2001; Stamps, 1995; Sutton-Smith, 1966, 1997). For example, when horses are observed in novel, but safe, environments they exhibit locomotive play, possibly to learn and practice new behaviors appropriate for such an environment (Stamps, 1995). Experimental evidence with mice suggests that locomotor play results in improved learning and plasticity, seemingly due to the increased synaptic plasticity and neurotransmission in mice engaging in play-like voluntary exercise, relative to controls (Van Praag, Shubert, Zhao, & Gage, 2005). More specifically, young and aged mice were housed with or without

a running wheel and injected with bromodeoxyuridine or retrovirus to label newborn cells. After one month, learning was tested using a Morris water maze and aged mice showed faster acquisition and better retention than controls. Further, running enhanced fine morphology of new neurons for both young and aged mice, supporting the hypothesis that locomotor play has immediate, not deferred, benefits, as will be discussed in greater detail in the next section (Pellegrini & Smith, 1998).

Focusing on the role of play during human ontogeny, we must ask why should children play to learn or develop innovative behaviors and strategies when they might more efficiently learn them through either direct adult tuition or, less directly through observational learning. Part of the answer to this is that actual adult tuition has been rare in human history, until recent times (Smith, 1982, 2004; Lancy, 1996; Gosso, Otta, Morais, Ribeiro, & Bussabb, 2005). More fundamentally, however, adult tuition and observation of adults will only transmit existing practices. The possible benefit of play, relative to other, adult-directed strategies, is that behaviors generated in the context of play, especially social play, can be more innovative. Juveniles can observe behaviors and strategies performed by adults but then recombine elements of these behaviors in novel routines in play (Bateson, 2005; Bruner, 1972; Fagen, 1981; Sutton-Smith, 1966). For example, the levels of children's symbolic functional and oral language production are more varied and complex in peer play, relative to when they are interacting with an adult (Pellegrini, 1983). Additionally, and as we will explicate in more detail below, play is a low cost and low-risk way in which to learn new behaviors during periods of immaturity and to impact subsequent evolutionary processes. The safety inherent in a protected and prolonged juvenile period supports this sort of innovation. This approach would not be efficient for adults to use for skill development, as they do not have the benefits of others protecting and provisioning them. Indeed, even during the juvenile period, play will not be optimal if the conditions are stressed and unsafe (Burghardt, 2005). Thus, play occurs primarily during the juvenile period when resources are abundant, but the benefits may be reaped either then or later in development.

Benefits of play for ontogeny and phylogeny

The benefits associated with play during the juvenile period may have either deferred effects, at maturity, or immediate effects, during the juvenile period, or a combination of the two. The most common prediction for the role of play in the human development literature is that it will have a deferred effect (e.g., Fagen, 1981; Groos, 1901; Piaget, 1962; Vygotsky, 1967). Indeed, the logical conundrum that play is simultaneously a non-serious behavior and one that has a function, can be solved by predicting that the benefits associated with a "purposeless behavior" are deferred, not immediate (Martin & Caro, 1985). From this view, playfighting and pretend as a juvenile should relate, respectively, to improved fighting/hunting skills and skills related to adult economic activity, respectively, as an adult (Bock, 2005; Smith, 1982; Smith, 2005).

An alternative view, advanced initially by students of animal play (Bateson, 1981; Bekoff, 1976; Martin & Caro, 1985) and more recently voiced by some child developmentalists (Bjorklund & Pellegrini, 2002; Pellegrini & Smith, 1998), hypothesizes that play has an immediate effect during the juvenile period, and the benefits are not necessarily deferred until adulthood. This prediction is based on two premises. First, it assumes that natural selection works on all periods of development, not only at maturity. Second, in order for a

behavior to be selected, the benefits associated with it must be greater than associated costs.

Considering the first premise, in order to live to maturity and reproduce, organisms must survive the infancy and juvenile periods, and play may be one way that organisms learn and develop skills that enable them to survive the juvenile period. A corollary is that some adaptations may be age/stage specific. The importance of this position for developmental psychologists is that children's behavior should be primarily evaluated in terms of the specific age period they are in (not necessarily for the benefit of that behavior for the adult). Consider three examples: (1) in infancy, sucking is functional and selected for during the period of infancy, while chewing food, not sucking, would be adaptive in the juvenile period; (2) in middle childhood, over-estimation of one's cognitive abilities may help a child sustain interest in an activity that they might not otherwise engage in if their engagement was contingent upon approximating an adult ideal (Bjorklund & Green, 1992). Similarly, over-estimation of one's strength may give a child more confidence in peer relationships (Omark & Edelman, 1976). What might be viewed as immature (such as over-estimating one's own strength), is in fact functional for children during this period; (3) in adolescence, increased risk-taking and distance from parental authority may be functional in raising status in the peer group and attracting the opposite sex, and more so than in earlier childhood or in adulthood (Arnett, 1992; Pellegrini, 2003).

Regarding the second premise, in order for a behavior to be selected, the benefits associated with the behavior must be greater than the costs (Martin & Caro, 1985). Moderate cost behaviors incurred during the juvenile period should result in benefits which are reaped immediately because there is a relatively high survivorship risk (i.e., of not surviving to sexual maturity) associated with this period; benefits should be reaped immediately, when they can.

Costs (caloric, time, and survivorship) of animal play during the juvenile period, across social, locomotor, and object play have been estimated by Fagen (1981) as moderate (2.5–10%). Costs of human play are less commonly documented but where they have been, they are consistent with Fagen's (1981) estimates. Specifically, Pellegrini et al. (1998) found that locomotor play, separated from non-play locomotion, accounted for 2.5% of juveniles' caloric budget, similar to that observed in domestic cats, for example (Martin & Caro, 1985). Object play, distinct from construction, exploration, and tool use, for American pre-schoolers observed in an object-rich nursery school accounted for a rather high 25% of children's time budget (Pellegrini & Gustafson, 2005), while the object play of pastoral children in Botswana was more in line with moderate levels observed in other forms of play at 16–17% (Bock, 2005), a level similar to chimpanzees (McGrew, 1981). Fantasy play, when observed primarily in university laboratory preschools, accounts for about 15% of observed time (Field, 1994) and among two groups of Parakanã Indians, hunter-gatherers in Brazil, ranges from 1.5% to 10.8% of time budgets (Gosso et al., 2005). These estimates are consistent with moderate costs, as is found in much of the animal literature, and suggest that under general conditions, play probably serves an immediate function.

Innovative behavior as an immediate benefit of play. We posit that a primary immediate benefit to play during the juvenile period relates to the generation of innovative behavior and strategies. Play enables juveniles to sample their environments and develop behavioral responses in a relative low-risk fashion. When children are in a new but safe environment they are able to experiment with a variety of behavior routines and sub-routines. Like Sultan in Köhler's (1925) experiments, they construct through play varied responses to novel

environments. The costs associated with constructing and practicing new behavioral routines are low because they are in a safe environment and the behaviors are non-serious. Risks are also minimized by the extended parental care characteristic of the human juvenile period. That play is characteristic of the juvenile period suggests that it is used during this sensitive period to gauge and construct behaviors that will be useful during this period and throughout their development. From this view, play during the juvenile period is a low-risk strategy for developing phenotypes that will be adaptive to individuals' current and subsequent environments. That play is especially important in individuals' developing innovative and novel behavior seems important to it impacting evolutionary processes and phylogeny as any mechanism that creates phenotypic variation is the very stuff of natural selection (Bjorklund, 2006).

The role of play in the development of innovation was formalized by Špinka and colleagues (2001) in their "training for the unexpected hypothesis," by positing how the locomotor and social play of animals helps them to prepare for unexpected and novel environmental and social circumstances. The gist of the hypothesis is that in the safe context of play, animals appear to place themselves into unconventional and often disorienting positions. These novel behavioral situations afford opportunity for them to experiment with a variety of routines in relatively safe circumstances and generate novel, and possibly adaptive, responses. With practice in play, individuals become facile at enlisting these processes and thus they become more accessible in times of need, such as during an emergency. Take, for example, cases of mother-child play, where mothers' physical play with their infants may relate to lower levels of stress and reactivity in infants (Field et al., 1996). Infants' lower reactivity, in turn, is related to their subsequent social behavior being more regulated. Being more socially regulated certainly has implications for individuals' immediate well being in specific environments, as well as later adaptation.

In the area of locomotor play, Povinelli and Cant (1995) provide an interesting example of the role of an uncertain environment in the evolution of behavioral flexibility. They compared the degree of behavioral flexibility in long-tailed macaques (*Macaca fascicilaris*) and orangutans (*Pongo pygmaeus*). Their hypothesis was that behavioral flexibility (i.e., having a variety of non-stereotyped locomotor behaviors in their repertoires) was a result of encountering uncertain environments on which to move (in these cases- arboreal clambering). Orangutans are physically larger than macaques, thus the niche of the orangutans is relatively unpredictable. For example, an animal the size of an orangutan (~40 kgs) clambering from tree to tree will experience tree limbs and vines that are relatively unpredictable because they bend extremely or could break. In order to locomote successfully in these areas, orangutans had to develop a very flexible behavioral repertoire so as to adjust to their unpredictable environment. Macaques, by contrast, are much smaller (~5.5kgs) and their locomotor repertoire through a similar environment is more predictable. Their weight does not perturb their travel as it does with orangutans; consequently their locomotor repertoire is much more stereotyped than the larger orangutan.

An example of the importance of play in developing social competence has been demonstrated in the development of both normative behavior (Lewis, 2005) and in psychopathology (Suomi, 1991, 2005; Suomi & Harlow, 1972). The experimental evidence from Suomi's laboratory suggests that the behaviors of monkeys bred for high aggression and reactivity can be changed when they have enriched social play experiences with conspecifics and adults, and this may have had an effect on evolution and gene frequency. Specifically, highly aggressive and highly reactive individuals are at a disadvantage, relative to

low-aggressive and low-reactive individuals, in competing for mates, reproducing, and protecting and provisioning offspring until sexual maturity in environments where close relationships between mothers and offspring and between conspecifics is normative (Suomi, 1991, 2005). Phenotypes associated with these genotypes can be changed by social play rehabilitation regimens (i.e., peers or nurturant adults) during the juvenile period. A hallmark of these social rehabilitation regimens involves social play, first between juveniles and mothers and then between juvenile peers (Suomi, 1991, 2005; Suomi & Harlow, 1972). For example, monkeys bred for high reactivity that were cross-fostered by a nurturant female were more playful, cooperative, and socially competent, relative to peer-reared monkeys. In play bouts with adults and peers, juveniles learn the appropriate social behaviors to function in their peer groups and eventually mate. These behaviors are used to establish close relationships with both adults and peers during a juvenile's sensitive period of becoming socially competent. Additionally, these initial close relationships, such as an attachment relationship between the high-reactive monkey and a surrogate mother, enable the juvenile to establish close relationships with different adults in new social groupings, not unlike findings in the human attachment literature (Sroufe, Egelund, & Carlson, 1999). For example, in new social groups rehabilitated monkeys established relationships with nurturant foster grandparents who not only protected the reactive monkeys but also conferred their dominance status on the juveniles (Suomi, 2005). The rehabilitated monkeys retained this dominance status, even when the older individuals left the group.

The behaviors of reactive individuals can be changed during the juvenile period if they are reared by a nurturant mother. Following the notion of competitive exclusion (Bateson, 2005), these competent behaviors will be learned during this sensitive period, rather than less competent behaviors, such as stereotypic behaviors and social withdrawal, if the individuals are kept in a stable social environment, as was documented by Suomi and Harlow (1972).

Play affecting evolutionary processes

Scholars from psychology (e.g., Bruner, 1972; Sutton-Smith, 1966, 1997), biology (e.g., Bateson, 1988, 2005; Bekoff, 1995), and philosophy (Carruthers, 2002) have posited links between play and creative responses to the environment for at least 40 years. However, we take this further by hypothesizing that because play affords opportunities for the generation of new, and possibly adaptive, responses to novel environments, it is an excellent candidate as an exemplar of behavior affecting evolutionary processes. The position that experiences during ontogeny affect phylogeny is broadly derived from theory dating back to Spalding in 1873 (Bateson, 2005), Baldwin (1896) and the "Baldwin Effect", and Lloyd Morgan (1896). More recently epigenetic theory has been advanced to formalize the ways in which genes and the environment affect each other, suggesting that immature organisms, especially, are responsive to environmental perturbations and adjust their behaviors in response to these changes (Bjorklund, 2006; Gottlieb, 2003).

More specifically, epigenetic theories suggest that behavioral changes of the developing organism can lead the way to phylogenetic change. Changes during the infant and juvenile periods are especially likely to launch organisms onto new developmental trajectories for the rest of their life span. At root, these theories assume that organisms possess substantial unexpressed genetic variability and that extreme environments activate, or deactivate, those genes. The environment affects genetic expression in at least

two important ways, however: The range of reaction and the norm of reaction views (Gottlieb, 2003).

The reaction range is a high and low limit of responses to a "usual" environment and is set by the genotype, suggesting that behavioral responses at different times in ontogeny were naturally selected to be activated by a variety of environmental stimuli. So, given a variety of environments, but similar genotypes, the reaction range view would predict similar phenotypes. While genes and the environment do interact, the effects are linear. This position is consistent with both sociobiology and evolutionary psychology.

By contrast, and more consistent with epigenetic theory, the "norm of reaction" view does not specify similar changes in behavior, or phenotypes more generally, when different genotypes encounter different environments. There is a true, non-additive interaction between genotype and phenotype, so that the relative phenotypic position of different genotypes may vary substantially and non-linearly, in different environments. Bjorklund (2006), Gottlieb (2003), and Stamps (2003) provide many examples of such interactive outcomes.

The epigenetic view posits that genes do not link directly to behavior; genes actually code for the production of proteins, initially in the micro-environment of the fertilized egg. There are many steps between genetic activity and behavior (see Gottlieb, 2003). Thus there is a complex system with possibilities of short-term and long-term feedback loops between phenotypic behavior and development in the next generations. It follows from this position that individuals' behaviors actively contribute not only to their own development, but to subsequent evolution in a number of different ways (Bateson, 1988, 2005; Stamps, 2003; Waddington, 1959).

Organic selection is one such form of change consistent with epigenetic theory, positing that organisms are capable of change in their own lifetimes when exposed to environmental change. Such may be the case of Suomi's (2005) high-reactive individual monkeys being reared by a nurturant foster mother in a novel social environment, who may pass this change on to their offspring by extra-genetic means. The social behaviors they learn in this relationship are generalized to other social groupings, even when that adult is no longer present. Indeed their dominance status is closely associated with the dominance of nurturant adults with whom they have a relationship. It is this elevated dominance status that should translate into the rehabilitated monkey mating with females with different genotypes. That is, dominant males, relative to subordinate males, are more likely to access females with "good genes," as evidenced by specific female positive morphological features, such as symmetry and physical attractiveness (Thornhill & Gangestad, 1993). Attractive females, in turn, choose to mate with dominant males (Pellegrini & Long, 2003). This sort of mating should result in selection favoring the genes associated with social competence over high reactivity. Bjorklund and Rosenberg (2005) outline a similar scenario involving the cross-fostering of chimps with human caregivers, and they speculate about numerous mechanisms capable of instantiating epigenetic inheritance in response to novel environmental conditions.

In the longer term, there are processes that allow environmentally acquired behaviors to influence the genotype without invoking discredited Lamarckian ideas. Ideas of what are broadly called organic selection date back to at least Lloyd Morgan (1896) and Baldwin (1896). The basic idea is that environmental challenge activates or deactivates certain genes or alleles (Bjorklund & Rosenberg, 2005) responsive to that challenge. But individuals with different genotypes may acquire or learn this new behavioral response with varying ease or

efficiency. Although in each generation the new response is socially learned, or at least environmentally acquired, over a number of generations natural selection will favor those genotypes that more readily acquire this new behavior, especially if the environment that elicited these changes remains relatively stable. Natural selection will favor individuals possessing these traits, relative to those who do not, and the trait will spread throughout the population.

The importance of play in impacting evolution relates to it being a relatively low cost way in which to develop alternative responses to new and challenging environments. By low cost we mean one that has low-risk and likely to be incorporated into the behavioral repertoire and eventually into the genotype. Genetic mutations, of course represent one very low cost way in which the genotype is changes. Change via play, we hypothesized, is realized through the epigenetic processes outlined above.

This is not to say that adults cannot also learn and develop alternative strategies, but it is probably less costly, and consequently more likely to spread through the population, if it is accomplished through play in childhood (Bateson, 2005). As noted above, organisms, especially complex ones like humans, are especially sensitive to environmental perturbations early in development. Novel behavioral responses to these environments lead them to develop new, and more flexible, phenotypes, than less flexible conspecifics. During infancy, mothers afford opportunities to learn and develop new phenotypes (Bjorklund, 2006; Harper, 2005) as demonstrated in Suomi's research (2005). During the juvenile period, this is likely to occur through peer play (Suomi & Harlow, 1972). That play during periods of immaturity is less costly than other strategies during other periods of development is predicated on organisms having surplus resources, as described above. These conditions afford opportunities to develop novel behaviors early in ontogeny and these new behaviors, in turn, influence subsequent development. The ease (or low cost) with which play and play-related behaviors spread through the population should relate to them being naturally selected.

Innovative behaviors associated with play during the juvenile period should be especially prone to this process because of the protection and provisioning associated with play during the juvenile period. Later periods in development, such as adolescence and maturity, are not typically characterized by "surplus resources"; thus at these stages of the life cycle, play would be less effective in skill learning than a more direct strategy, such as observational learning. Further, the behavioral variability associated with play should make it especially sensitive to natural selection (Bjorklund, 2006).

One version of how the innovative behaviors developed in play might impact evolutionary processes was described by Waddington (1957) as genetic assimilation. Waddington's experiments were with fruit flies, and involved developmental modifications to adult flies as a result of early stressors (such as heat shock) and subsequent artificial selection; but more naturalistic examples of this effect are available (see also Bjorklund & Pellegrini, 2002). At least in Waddington's prototypic experiments, genetic assimilation involved delayed phenotypic responses and rapid genetic change. However, organic selection as described by Bateson (2005) is seen as distinct from genetic assimilation. It involves rapid concurrent phenotypic change to a stressor and delayed genetic change via the occurrence of mutations. Mutational change can allow an adaptive, acquired characteristic to be expressed more easily. As we have argued, however, the innovative behaviors associated with play during the juvenile period, provides another low cost way in which innovative behaviors spread through the population.

Conclusions

There has been a marked increased in the invocation of evolutionary theories in the study of human development. In this paper we use the case of play during the juvenile period as an example of a behavioral construct that is important in ontogeny and also possibly affecting evolutionary processes. Exploration and play in one's niche can enable individuals to forecast what their developmental niche will be, a strategy that may be especially important in novel environments. Play enables individuals, after they have sampled their environments, to generate, in a rather low cost manner, a repertoire of innovative behaviors that may be adaptive to their specific niche. This point was illustrated with gene x environment interactions derived from experimental studies of cross-fostered rhesus monkeys of differing genotypes. The initial phenotypical changes associated with play, such as increased exploration and cooperation, decreased aggression and stereotypic behavior, and dominance status were sustained across development. Selection should favor individuals exhibiting these new phenotypes, relative to those who do not.

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