

Primer

Play in the Peter Pan ape

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Baco, the alpha male of a foreign community on the east side of the local river, is sitting side by side with Jiro, a young adult male from the west side. They are watching each other closely while chewing on fruit. Seemingly out of the blue and with no hesitation, Jiro reaches up over his head, grabs a branch, and swings his whole body into Baco's with great force and kicks him in his midsection repeatedly. Baco, who is larger and stronger, sits back and takes the kicking for a few seconds. Then, having had enough of this 'teenage' behaviour, he leans forward, grabs Jiro's upper body, and overpowers him while biting his shoulder. Now the tables are turned — but only until Baco's grip lessens and Jiro escapes. Yet it doesn't end there. After having finally freed himself, Jiro returns for more. What is going on?

The next stage reveals the answer. Baco spreads his legs, displaying his genitalia to Jiro, who crouches down, extends his arm and starts poking the older male's testicles. Baco starts rocking his body, giving rhythm to this unique exchange. Then Baco starts hitting Jiro with open hands, and I see the alpha male is displaying the unmistakable, relaxed, open-mouthed play face.

This is not a fight, this is play: play between two adult bonobo males in their natural habitat, south of the river Congo.

Why do adults play?

We have mounting evidence that play is crucial for the healthy development of immature mammals and birds. Indeed play almost universally declines sharply as animals mature. So it is not surprising that play is typically considered a developmental scaffold needed for building an individual. And once that individual has been built — becomes an adult — the scaffolding falls away and so play disappears.

But this says nothing about why in some species the 'scaffold' remains beyond development — that is, why individuals of these species continue to

play into adulthood. Surely success as an adult is better served by engaging in more serious grown-up pursuits, such as finding food and mates and protecting their (playful) offspring from predators, rather than apparently wasting time and energy in playful antics themselves. Indeed, some have claimed adult play only exists as an epiphenomenon of development and has no utility other than hedonic value. But to leave it there seems shortsighted. In the very least, we know that the experience of positive emotion has beneficial effects on physical health, bonding and openness. Nonetheless, because play appears 'purposeless and risky' its presence in adults creates a challenging evolutionary question.

The clue to solving this biological puzzle emerges when looking at the common traits of the small cluster of species in which adult play occurs, such as elephants, primates, social carnivores, cetaceans, parrots and corvids. It is unlikely that there was a single origin for adult play, as these taxa do not form a clade with recent common ancestry (the last common ancestor of birds and mammals lived as far back as 280 million years ago). Yet these species do share an apparently coevolved 'adaptive package' of traits, namely intricate sociality, longevity and large brains capable of complex cognition. The relationship between brains and sociality is well known. Yet until now the relationship of those two traits with adult play has not been explored. Is the co-occurrence of intelligence and sociality with adult play only coincidental? Or...could it be that life-long play is a key adaptation that underlies complex sociality and intelligence?

This Primer provides an overview of the biology of fun in bonobos (*Pan paniscus*). It has a special focus on adult play and how it relates to social bonding and the flexibility component of intelligence. While most of what we know about bonobo play comes from the study of captive animals, I examine the how, what and with-whom of adult play in a community of wild, habituated bonobos. And contrary to claims that play in mature animals is an artifact of captivity, adult play clearly appears as a noteworthy part of the natural behavioral repertoire of these great apes.

Our Peter Pan cousins

Bonobos are important for understanding why adults play, as they are perhaps the most playful of all non-human animals. And like us, they are long-lived, highly social and have big brains. Bonobos share the spirit of Peter Pan's never ending youth. Like humans, they are neotenuous, meaning that they retain juvenile traits as adults. This delay in developmental timing lies behind their unusually high levels of playfulness and provides them with a long time for learning. Neoteny may also help explain why bonobos are more tolerant and less aggressive than chimpanzees, and more likely to share food with others.

Both bonobos and chimpanzees are male-philopatric — that is, females are the dispersing sex. But whereas chimpanzees are male-dominated, bonobo society is structured around bonded females. In contrast to other primate matriarchal systems, where female coalitions run down matrilineal, bonobo females bond strongly and form coalitions despite their *not* being related.

Peter Pan apes benefit from a tropical forest habitat that is rich in fruit, and this resource abundance boosts play in two ways. The first is via direct caloric contribution, as play is energetically expensive and dwindles in conditions of resource scarcity. The second is that resources allow female bonobos to aggregate in first place, which is a necessary precondition for their coalitions and bonding to occur. And it is female reproductive strategies that drive bonobo tolerance and cohesion, because strong social networks and low aggression protect offspring long-term survival. Thus, the by-product of female reproductive interest is a safe social environment.

A fertile environment for play to flourish

One way that bonobo females bond is through frequent sex. Indeed bonobos have been called the 'make love not war' ape, as they use sexual interactions in all age and gender combinations to manage conflict, reduce stress, and solve social issues. But there is more to bonobo sociality than just sex. Like other primates, bonobos engage in long grooming sessions, and of course, they play both as immatures and as adults. But the colourfulness of bonobo sexual behaviour, in addition to the



Figure 1. Play and trust in bonobos: the 'hang game'.

In the hang game an adult holds a younger bonobo by a limb while swinging them. Note that the immature does not clasp to the adult in return, thus surrendering control of their safety to the adult. (A) Female with a male juvenile (not her son) of the E1 study group. (B) Mother-infant pair from the neighbouring community playing the 'hang game'. (Credit: Isabel Behncke)

perception of play as being only for immature individuals, has meant that our understanding of their ludic nature remains poorly understood.

Bonobos (together with chimpanzees) are our closest living relatives. We share a mosaic of around 98.7% of our DNA and a common ancestor that lived between around 7 and 8 million years ago. Bonobos are more neotenuous and playful in adulthood than chimpanzees, and our genetic closeness makes them ideal for bringing the biology of enjoyment into the human evolutionary story. This is important, as the role of play and positive emotion have been relatively ignored in evolutionary narratives of sociality and cognition.

Regrettably, despite bonobos' importance to the biology of fun, they are the great ape we know least about. They were only first described to science in 1933 — 'discovered' in a museum in Belgium, rather than in their wild habitat. Their natural distribution is restricted to remote primary forests south of the river Congo in the Democratic Republic of Congo (DRC), which comes with its own logistical challenges. The DRC has a long history of armed conflict, so research in the wild has been scant.

As a result, wild bonobos can only be closely followed in a handful of field sites. I have been fortunate to work in one of them: Wamba, the longest running field study of bonobo behaviour in existence. Wamba research camp (00° 11' 8" N, 22° 37' 58" E) was established in the early 1970s by Takayoshi Kano and today is run by University of Kyoto researchers led by Takeshi Furuichi. There, I followed the E-1 group of 30 individuals of wild, habituated bonobos during a three-year period where I collected thousands of play events. Most of that play occurred within the E-1 community, but remarkably it also occurred between individuals of E-1 and neighbouring bonobo communities.

The how and what of bonobo play

The Dutch historian Huizinga suggested in '*Homo ludens*' that the play drive underlies the most important forms of cultural expression humans have — from fashion to art, to competitive sports to exploration, whether artistic, scientific or geographic. In other words, play is at the heart of culture. So the examination of play reveals not just the nature of the behaviour itself, but extends beyond that into an understanding of what are the governing principles of

a given culture. It follows that when seeking to understand the nature of a given species we should ask: what are their favourite games? The different forms that shape-shifting play takes will tell us about the specific trade-offs of the animals we are looking at. Uncovering the nature of enjoyment in wild bonobos could tell us not just about play itself but also about bonobo nature overall. So: how do bonobos have fun in the jungles of Central Africa? True to play's protean nature, wild bonobos enjoy many different kinds of play, but themes do emerge. One theme is exploration and the generation of novelty, and the second is the dynamics of risk and trust.

Bonobo play in the wild

While most of adult play is social, bonobos also enjoy various forms of solitary play. One example is water play. Adults, as well as younger bonobos, play with water in Wamba. And there is variability in their styles: females trail their hands (and sometimes feet) in the water, typically with a more rhythmic, slower cadence than the males' more vigorous splashing (http://youtu.be/geWv5_I0jk). This game sometimes gives a sense of aesthetic exploration of water's properties and blurs the transitions between exploration and play. In other instances of solitary interactions with water, I have observed bonobos choose still water — a puddle of recent rain or a small pool in the swamp — to look at their reflection on the surface, sometimes stroking the water slightly as if to observe the resulting ripples.

One of the interesting things about water play in bonobos is that it differs from play with elements intrinsic to bonobo life, such as fruits or other bonobos. In a sense, water is a novel element to them: they do not drink water in the wild as they get sufficient hydration from the fruit and vegetable matter in their diets. They also don't seem to enjoy sitting or wading in water. Rain typically stops all bonobo activity until it passes. Voluntary interaction of bonobos with water seems to happen only in the context of play.

Why is this important? Positive emotion underlies play and motivates individuals to interact with novel elements that would otherwise be extraneous to their lives. This can sometimes generate further novelty, with new variations of a game. Indeed,

water play in Wamba appears to have been brought in by two females that immigrated in 2008 (Tetsuya Sakamaki, personal communication), and then to have spread through the group with new variations and styles. Incidentally, one of the females that might have kickstarted water play in Wamba is a female with a high play drive that manifests itself both in frequent and diverse social play (Fuku, central in the network of Figure 2), as well as other forms of more unusual forms of solitary play such as pretend play. I have observed her using a large fruit to hold and play ‘as if’ it were an infant for several minutes and detailed a variety of interactions with the pretend-infant: the use of an object ‘as if’ it were a different thing is another component of novelty leading to creativity.

Most of adult play is social, as first and foremost the Peter Pan apes enjoy playing with each other. And unlike chimpanzees, who regularly enjoy playing with objects, bonobo juvenile play is directed towards sex elements: erect penises, playful intromission and exploration of mature females’ swellings, touching, inspecting, and trying to climb of top of any dyads engaged in sexual interactions (<http://youtu.be/90blBZGLq5Y>). In short, sexual elements — and each other — seem much more fun for bonobos than objects or tools.

A striking example of play oriented towards sex-elements is the ‘ball game’ — as in play with testicles. This game is basically ‘ring around the rosy’, in bonobo fashion (http://youtu.be/DpVKLLWh_U). Typically, two individuals chase each other in circles, sometimes around a stationary object such as a young sapling, and the individual in front is male. The ‘chaser’ grabs the testicles of the male in front. The leading male often displays a play face and puts himself in position to reinitiate the game if the ‘chaser’ stops.

That bonobos find this fun is a remarkable example of the relationship between risk-taking and trust in play, as the individual could so easily ‘rip off’ the male’s testicles, but doesn’t. This observation becomes more poignant when we consider that in chimpanzees testicles are targeted during aggression: genital mutilation is not uncommon in lethal violence, especially in inter-group encounters where 66% of lethal violence occurs. Yet in bonobo inter-group encounters, testicles are a target for fun rather

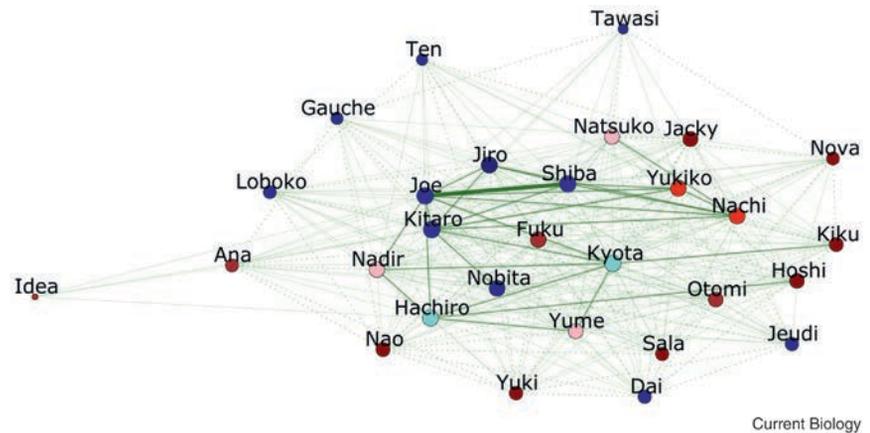


Figure 2. Network of play interactions in Wamba bonobos. The weighted network of play interactions ($n = 8,951$) of the E1 community of wild bonobos is highly inter-connected. It shows how bonobos play with a very high proportion of all available partners in their group. Blue nodes represent males, red nodes females, and color intensity increases to represent older age. The peripheral individual *Idea* was an incoming female that arrived in the last two weeks of observation (data Isabel Behncke, manuscript in preparation).

than mutilation. Indeed, the playful encounter I recounted between males from *different* communities would be extraordinary in chimpanzees, whose males are xenophobic and intolerant to males of other groups. In bonobos, low levels of aggressive conflict allow for rare forms of adult play — such as one male trusting a foreign male not to injure his genitalia (<http://youtu.be/0mk-RbFOBak>).

The ‘hang game’ in bonobos is a further example of the interplay between risk and trust (Figure 1). Games have rules and specifics. This game happens always in trees and always features a larger adult (male or female) with a smaller, younger individual. I have seen it played in a myriad combinations - by females and their infants, to old 41 year-old males with juveniles, and even by between the dominant male of one bonobo community with several youngsters of a neighboring group.

In this game, the adult sits on a branch anything from 5 to 40 or more meters above the ground, grabs a juvenile’s arm or leg, and swings them back and forth. Notably, the juvenile does not clasp the adult’s arm or hand, so the adult has complete control of the juvenile’s fate (a long fall could result in injury or death). This voluntary surrendering to a more powerful individual graphically demonstrates the dynamics of voluntary risk-taking (by the immatures in this case) and trust (towards the adult) so often seen in play. Moreover, there is visible joy in this trusting risk-taking as the youngster

being swayed often displays full open-mouthed play-face. In other words, the unfulfilled risk becomes the point of the play. There is enjoyment in risk-taking as there is trust in the play-partner.

Bonobo fun and games highlights the relationships of play to the generation of novelty (an important component of creativity and adaptability) and trust (a crucial component of social bonding). Which brings us back to the original question of whether play might have a crucial role in mediating the relationship between sociality and brains.

Flexibility through sociality

To further explore the relationship between brains and sociality we have to look not just at how bonobos play, but also with whom they play. Bonobo social cohesion is an ideal environment for fun to be enjoyed, not just one-to-one, but *one-to-many*. Which means the network of play interactions in wild bonobos is highly interconnected as play occurs in all age and sex combinations (Figure 2): adult males play with adolescent males, adult females with subadult females, juvenile males with adult females, and so on. Bonobo play-partners even extend outside their immediate communities to inter-group play (such as adult male-juvenile and adult male-adolescent pairings). In fact, despite their well-known sexual promiscuity, bonobos actually have more diversity of partners in play than they do in sex (and grooming). This remarkable diversity contrasts with higher conflict social systems, where the number of

play partners of an individual is more restricted as only few can be trusted as play-mates. For bonobos, it seems it is safe to play with anyone.

Play-partner diversity is important when thinking about adaptability: playing 100 times with the same individual requires less variation and adjustment of behaviour than playing 10 times with 10 different individuals. Playing with individuals of different sizes, personalities and sex requires learning about contextual-dependent behaviour: with whom and when a bite is appropriate, a chase over a push, a gentle tickle rather than a stomping slap, and so on. An example is self-handicapping — when individuals self-adjust their strength in order to maintain playful interactions with animals of different size, status and ability. In short, because social play only happens when individuals learn to adjust to each other's differences, diversity of play partners boosts experiential complexity and thus behavioural repertoires.

There is another fundamental aspect to social play that is relevant to adaptability: positive emotion that is *salient*. Driven by positive emotion, play rewards engagement with the world, and in doing so it increases yet further the complexity to which adult brains are exposed. While this is of course very important for the development of immatures, we know that adult brains remain plastic and indeed match even slight variations in environmental enrichment. Complex systems (such as brains!) tend to show increased flexibility of responses with increased complexity. Interactions other than play can have the same result of course, but *salient* emotion makes play a particularly time-efficient mechanism of creating complexity — partly because is so rewarding. Emotional salience has a strong effect in learning, memory and bonding intensity. So play — short in duration, diverse in expression — can serve as a 'fast-track' cognitive and bonding boost (which is especially useful given adults' constrained time budgets). The human equivalent would be the efficacy that a good laugh or dance session has in bonding us with others compared to less salient activities such as plain conversation by the water cooler. Adult play can be an intense 'fast-track' creator of experiential complexity.

The rewards of adult play

Understanding the Peter Pan apes gives us insights as to why socially complex species may play into adulthood. Since the social world is necessarily unpredictable, cognitive flexibility is key for successful context-dependent strategies. This is true for immatures and I believe it to be particularly important for adult individuals that face decades of living in complex societies, where responding appropriately to changing contexts is crucial. I have termed this view of play 'the Adaptive Joker hypothesis' — play behaviour is the jester, a joyful shape-shifter, a *biological wild card* whose value and form changes according context. Play makes individuals more adaptable *because* it makes them more social; and more successful in their sociality *as a result* of being more adaptable. Life-long play is a bridge between sociality and adaptability.

Play also rewards interaction with the world, driving cognitive complexity and adaptability. In the course of hominid evolution there has been an up-regulation of the reward system — which underlies positive motivational drives such as exploration and novelty-seeking. Thus humans and other highly social, big-brained animals are particularly fond of finding myriad ways to amuse themselves. Heightened positive emotion rewards *seeking* that complexity, and result in more adaptable brains — *at all ages*. Hence the biology of fun does not only belong in childhood.

Further reading

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