

From curiosity to play: re-evaluating the evolutionary origins of play

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Abstract

The origins of play remain a profound puzzle in animal evolution. Play is often characterised as a seemingly non-functional behaviour that confers little survival or reproductive benefit. This characteristic makes the evolution of play appear paradoxical under Darwinian principles, which posit that traits must be beneficial to be selected. Given that the adaptive benefits are unclear even for the well-established forms of play in extant animals, it seems improbable that an incipient form of play in the earliest stages of evolution emerged due to a decisive selective advantage. The conventional view that has gained traction suggests that play evolved not as an adaptive trait but as a by-product of energetic, ontogenetic, ecological, and psychological facilitating factors. Building upon previous empirical and theoretical studies, this review discusses the evolutionary relationship between play and exploration. More specifically, it argues that relying on the classification dividing exploration into intrinsic and extrinsic types can help us articulate both the evolutionary and mechanistic continuities and discontinuities between play and exploration. Based on this distinction, this article proposes the following hypothesis: play originally evolved as a by-product of curiosity-motivated intrinsic exploration. This hypothesis is supported by recent empirical evidence indicating that play may have evolved by co-opting some of the mechanisms of curiosity, including (i) the commonality between stimuli that elicit curiosity and those that elicit play, and (ii) the shared neural basis of curiosity and play involving the reward and executive control systems. I also discuss new testable predictions derived from this hypothesis and outline future research directions, including comparative phylogenetic studies, eco-sociological analyses, and psycho-behavioural approaches.

Keywords

Boredom, By-Product, Curiosity, Exploration, Play, Surplus Resource Theory

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I. INTRODUCTION

Humans are notably playful animals, with some researchers asserting that playfulness is a fundamental characteristic of our species (Huizinga, 1949). Play is observed in many other mammals; however, it has not been reported in most other animal taxa. The label of ‘playful animals’ is limited to certain vertebrates, cephalopods, and arthropods (Burghardt, 2005). Why do some animals engage in play while most do not? This review addresses the evolutionary origins of play, exploring the possible pathways from ‘serious’ animals, which solely perform activities directly linked to survival and reproduction, to playful animals.

Defining play is often considered challenging (Fagen, 1981; Martin & Caro, 1985; Burghardt, 2005). One reason for this is that play involves action patterns that appear similar to other behavioural categories, such as aggression, predation, nurturing, and sexual behaviour. Many researchers have devised definitions of play and established criteria to distinguish it from ‘serious’ behaviour (Bekoff & Byers, 1981; Martin & Caro, 1985; Burghardt, 2005). For instance, Burghardt (2005) defined play as being: (i) incompletely functional; (ii) spontaneous; (iii) differing from ‘serious’ ethnotypic behaviours in form or timing; (iv) repeated but not stereotyped; and (v) initiated when an animal is free from severe stress. Many, but not all, definitions proposed thus far emphasise that play includes elements lacking direct and immediate benefits (e.g. Bekoff & Byers, 1981; Martin & Caro, 1985; but see Brownlee, 1954; Fagen, 1981). This characteristic of play appears to conflict with the Darwinian principle of evolution by natural selection, which posits that traits must be ‘beneficial’ in some way to be selected. If play is non-functional, why has it evolved?

It is widely assumed that play has evolved independently multiple times (Ficken, 1977; Burghardt, 1998; Chick, 2001) because playful animals are sporadically found across distantly related lineages, such as mammals, certain birds like crows and parrots, and octopuses. However, whether the evolution of play across various lineages resulted from convergent evolution, where each lineage was subjected to similar selection pressures, remains debated (Pellis *et al.*, 2015; Jensen, 2021). Further complicating the issue is that even if play in extant animals is shown to have some survival and reproductive benefits, its current utility might not be the same as its original function (Bernstein, 1982; Gould & Vrba, 1982; Burghardt, 1998; Pellis *et al.*, 2015). In the case of ‘serious’ behaviours (e.g. predation, sexual behaviour, parental care) with clear functions essential for survival and reproduction, the current utility is likely to align with the original function. However, when considering the evolution of behaviours with unclear functions, such as play, it is important to be particularly cautious not to confuse their current utility with their evolutionary origin (Bernstein, 1982; Gould & Vrba, 1982; Burghardt, 1998; Pellis *et al.*, 2015; Auerbach, Kanarek & Burghardt, 2015). With this caveat in mind, what evolutionary paths has play taken?

This review aims to provide insights into addressing the questions raised above. Section II first provides an overview of the classic debates and recent empirical studies concerning the function (i.e. current utility) of play in extant animals. Section III focuses on discussions regarding the origin of play, particularly outlining the ‘Surplus Resource Theory’ (Burghardt, 2005), a prominent theory on the origins of play. This theory posits that play did not evolve as an adaptive trait *per se* but as a by-product of other characteristics. In Section IV, building on the Surplus Resource Theory and the pioneering work of others (e.g. Berlyne, 1960; Hutt, 1966; Pellis & Burghardt, 2017), I will discuss the evolutionary relationship between play and exploration. More specifically, I argue that we can articulate better both the evolutionary and mechanistic continuities and discontinuities between play and exploration by clearly distinguishing between extrinsic and intrinsic exploration. Based on this distinction, I propose the following hypothesis: that incipient play in the earliest stages of evolution originally emerged as a by-product of curiosity-motivated intrinsic exploration. I introduce several pieces of evidence supporting this hypothesis.

II. THE SERIOUS ISSUE OF PLAY: FUNCTIONS OF PLAY IN EXTANT SPECIES

(1) Classical debates: Spencer *versus* Groos

The assertion that play is a useless behaviour with little adaptive benefit for survival or reproduction is highly unsettling to modern biologists familiar with Darwinian evolutionary theory. Play involves obvious costs, such as the risk of injury, potential social conflicts, energy expenditure, and increased risk of predation due to heightened visibility (Fagen, 1981; Iki & Kutsukake, 2022). If play were not only non-adaptive but maladaptive, then animals that engage in play would soon be removed from the population by natural selection, leaving only ‘serious’ animals to survive. The literature on play often avoids making definitive statements about its function by using expressions such as play ‘*appears* to be purposeless’ (Bekoff & Byers, 1981, p. 299, italics added) or ‘*appear[s]* to have no obvious purpose or immediate benefits’ (Martin & Caro, 1985, p. 64; italics added). However, this cautious phrasing does not particularly help resolve the question of the evolution of play. The function of play has remained obscure and ambiguous, unlike ‘serious’ behaviours with clear and robust adaptive functions, throughout evolutionary history.

The question of the function of play has long captivated researchers. Two prominent theories were proposed during the early days of Darwinism and continue to influence the study of play significantly, particularly in non-human animals.

In the second edition of *The Principles of Psychology* (Spencer, 1872/1920), Herbert Spencer developed a theory of play later termed the ‘Surplus Energy Theory.’ In essence, this theory adopts a non-selectionist stance on play. According to Spencer, play does not ‘subserve, in any direct way, the processes conducive to life’ (Spencer, 1872/1920, p. 627). Spencer's answer to why animals play also relates to why play is observed only in some animals. According to Spencer, play does not yield any long-term benefits, and ‘the proximate ends are the only ends’ (p. 628). Spencer identified this ‘proximate end’ as the release of surplus energy. He posited that ‘inferior kinds of animals’ (p. 628) must expend all their energy to sustain their vital activities. By contrast, ‘animals of high types’ (p. 628) with more efficient and sophisticated functions, such as mammals, can sustain life without expending all their energy. Consequently, these ‘more-evolved creatures’ (p. 629) accumulate surplus energy that is not entirely consumed. Spencer argued that play occurs when this excess energy, accumulated over long periods, overflows in the form of bodily movement. Thus, according to the Surplus Energy Theory, play is merely the result of excess energy expenditure in animals that have achieved a highly efficient lifestyle and play itself does not confer any benefits to the performer.

By contrast, the German philosopher and psychologist Karl Groos pioneered a theory that actively sought adaptive significance in play with his ‘Instinct-Practice Theory’ (Groos, 1896/1898). Spencer's theory, which did not recognise the adaptive importance of play, was seen as inadequate for explaining the evolution of play at a time when Darwinism was gaining ground (Burghardt, 2005; Schank, Lutz & Wood, 2023). In *The Play of Animals* (Groos, 1896/1898, p. 63), Groos stated ‘[i]n the explanation of instinct (and of play) we need consider only natural selection’. His Instinct-Practice Theory thus embraced a selectionist perspective on play. While acknowledging the value of Spencer's Surplus Energy Theory, Groos expressed dissatisfaction with it, noting, ‘a state of surplus energy may not always be even a *conditio sine qua non* of play’ (p. xix). The main issue Groos identified in Spencer's theory was its failure to explain why a state of excess energy would lead to species-specific play patterns rather than other behaviours. He argued, ‘while simple overflow of energy explains quite well that the individual who finds himself in a condition of overflowing energy is ready to do something, it does not explain how it happens that all the individuals of a species manifest exactly the specific kind of play expression which prevails with their own species, but differs from every other’ (p. 12). Groos addressed this problem by proposing the existence of a ‘play instinct’ that drives animals to

engage in species-specific play. This instinct drives animals to practice skills necessary for survival, such as predation and fighting, through play. Since the specific skills crucial for survival vary among species, the type of practice (i.e. play) required also differs from species to species. According to Groos, each playful species possesses a practice instinct shaped by natural selection to provide opportunities to learn skills important for later life, and this instinct leads to a specific way of playing tailored to each species' unique needs.

(2) Contemporary studies on the functions of play

Groos's idea that, even if play does not provide immediate benefits to the performer, it offers opportunities to learn skills necessary for later life, potentially enhancing survival and reproductive success in the long term, is still implicitly or explicitly supported by many contemporary play researchers. The beneficial effects of play that manifest later in life are referred to as 'delayed benefits' (Smith, 1982). Assuming such delayed benefits of play do exist, are they significant enough to influence an individual's survival and reproductive success? At present, few studies have directly examined the relationship between play and survival or reproductive success, and the evidence remains tenuous. Fagen & Fagen (2004, 2009) and Cameron *et al.* (2008) demonstrated that in brown bears (*Ursus arctos*) and horses (*Equus caballus*), respectively, juveniles that engaged in more play had higher survival rates. However, while Fagen & Fagen (2009) controlled for factors such as estimated juvenile health status, it remains possible that individuals with higher survival potential simply played more often and that play did not improve survival rates.

Regarding the relationship between play and reproductive success, similarities between play involving physical contact and pre-mating or mating behaviours have been noted in several species (Pellis, Pellis & Himmler, 2014; Ahloy Dallaire & Mason, 2017). However, studies directly investigating the impact of play on reproductive success are limited. One notable exception is Nunes (2014), who examined the impact of juvenile play experience on female reproductive success (i.e. whether subsequent pups were successfully reared to weaning) in Belding's ground squirrels (*Spermophilus beldingi*). The analysis revealed that females with higher frequencies of play during their juvenile periods had higher reproductive success. However, the study also showed that juveniles who played more frequently were more successful in establishing territories and exhibited more intense aggressive and vigilance behaviours. Therefore, it is possible that play itself did not directly enhance reproductive success but rather that behavioural tendencies correlated with play positively impacted reproductive success. Another recent study (Holmes *et al.*, 2024) analysed social play (i.e. play herding, which resembles adult male mating behaviour) in juvenile Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). They found that juvenile males who engaged more frequently in this type of social play achieved greater paternity success as adults, suggesting that play may function as a form of training for mating skills. Due to the limited number of existing studies, further research will be necessary to draw definitive conclusions about the relationship between play and survival or reproductive success.

Numerous empirical studies have investigated the relationship between play and specific skills. If play provides opportunities to practice specific skills, could this be considered the 'original function' that facilitated an evolutionary transition from 'serious' to playful animals, or was it a secondary utility acquired after the evolution of play? If the former is the case, this function should be consistently applicable to most, if not all, playful species. Conversely, if it is not, significant inconsistencies in the presence of this function should be observed. The following section addresses this issue by reviewing studies that have examined whether play contributes to the development of various skills (Table 1).

Table 1. Summary of hypotheses on the adaptive functions of play and supporting or contradicting evidence

Hypothesis	Evidence	Species	Reference	Details
Enhancing survival	For	Brown bears (<i>Ursus arctos</i>), horses (<i>Equus caballus</i>)	Fagen & Fagen (2004, 2009); Cameron <i>et al.</i> (2008)	Juveniles engaging in more play have higher survival rates.
Enhancing reproductive success	For	Belding's ground squirrels (<i>Spermophilus beldingi</i>)	Nunes (2014)	Females with frequent juvenile play achieve higher reproductive success.
	For	Indo-Pacific bottlenose dolphins (<i>Tursiops aduncus</i>)	Holmes <i>et al.</i> (2024)	Males with frequent juvenile play achieve higher reproductive success.
Learning motor, hunting, and fighting skills	For	Belding's ground squirrels (<i>Spermophilus beldingi</i>)	Nunes <i>et al.</i> (2004a,b)	Frequent social play predicts enhanced motor skills.
	For	Assamese macaques (<i>Macaca assamensis</i>)	Berghänel <i>et al.</i> (2015)	Intense social play predicts the rapid acquisition of motor skills.
	For	House mice (<i>Mus musculus domesticus</i>), rats (<i>Rattus norvegicus</i>), domestic cats (<i>Felis catus</i>)	Byers & Walker (1995)	The timing of increased play corresponds to neuromuscular development related to motor abilities.
	For	Pigs (<i>Sus scrofa</i>)	Weller <i>et al.</i> (2019)	Higher frequency of pre-weaning play observed among winners of aggressive encounters.
	Against	Meerkats (<i>Suricata suricatta</i>)	Sharpe (2005c)	No correlation found between play frequency and success in contests.
	Against	Domestic cats (<i>Felis catus</i>)	Caro (1980)	Opportunities for object play do not predict improvement in predation skills.
	Against	Coyotes (<i>Canis latrans</i>), northern grasshopper mice (<i>Onychomys leucogaster</i>)	Vincent & Bekoff (1978); Davies & Kemble (1983)	No correlation between social play and hunting success.
Learning tool-use skills	For	Chimpanzees (<i>Pan troglodytes</i>)	Hayashi & Takeshita (2022); Hayashi & Matsuzawa (2003)	Infant spontaneous object manipulation resembles adult tool use.
	For	Japanese macaques (<i>Macaca fuscata</i>)	Leca <i>et al.</i> (2008); Leca & Gunst (2023)	Stone-handling play is associated with stone-throwing displays.
	For	Long-tailed macaques (<i>Macaca fascicularis</i>)	Gumert <i>et al.</i> (2009); Luncz <i>et al.</i> (2017); Tan (2017)	Stone-handling play is associated with extractive foraging using stones.
	For	New Caledonian crows (<i>Corvus moneduloides</i>), palm cockatoos (<i>Probosciger aterrimus</i>)	Hunt (2000); Kenward <i>et al.</i> (2011); Lambert <i>et al.</i> (2017); Auersperg <i>et al.</i> (2014)	Both vigorous object play and habitual tool use observed in the wild.
	Against	Rooks (<i>Corvus frugilegus</i>), kea (<i>Nestor notabilis</i>), Goffin's cockatoos (<i>Cacatua goffiniana</i>), common ravens (<i>Corvus corax</i>)	Bird & Emery (2009); Gajdon <i>et al.</i> (2014); O'Hara <i>et al.</i> (2019); Heinrich & Smolker (1998); Auersperg <i>et al.</i> (2014)	Object play is observed, but habitual tool use in the wild is absent.

	Against	Bumblebees (<i>Bombus terrestris</i>)	Galpayage Dona et al. (2022)	Object play does not improve object manipulation skills.
	Against	Woodpecker finches (<i>Camarhynchus pallidus</i>)	Kaplan (2020)	Habitual tool use in the wild is observed, but object play is absent.
Establishing social hierarchies and assessing resource-holding potential (RHP)	For	Yellow-bellied marmots (<i>Marmota flaviventris</i>)	Blumstein et al. (2013)	Juvenile play is correlated with adult dominance.
	For	Rats (<i>Rattus norvegicus</i>)	Panksepp (1981)	Stable dominance relationships are established through repeated play interactions.
	For	Chimpanzees (<i>Pan troglodytes</i>)	Paquette (1994)	Frequent social play precedes rank reversals.
	For	Pigs (<i>Sus scrofa</i>)	Weller et al. (2020)	High-frequency play influences decisions in contests based on RHP.
	For	Wolves (<i>Canis lupus</i>)	Cordoni (2009)	Frequent play occurs among pairs with close ranks.
	Against	Red-backed squirrel monkeys (<i>Saimiri oerstedii</i>)	Baldwin & Baldwin (1974)	Dominance hierarchies exist, but play is absent in a group.
Building social bonds	For	Geladas (<i>Theropithecus gelada</i>)	Mancini & Palagi (2009)	Frequent play among partners predicts agonistic support.
	For	Chimpanzees (<i>Pan troglodytes</i>), Japanese macaques (<i>Macaca fuscata</i>)	Shimada & Sueur (2014, 2018)	Positive correlation exists between play and affiliative social networks.
	For	Chimpanzees (<i>Pan troglodytes</i>)	Samuni et al. (2024)	Social play promotes cooperation.
	For	Chimpanzees (<i>Pan troglodytes</i>), Bonobos (<i>Pan paniscus</i>), common marmosets (<i>Callithrix jacchus</i>)	Palagi et al. (2004); Yamanashi et al. (2018); Palagi et al. (2006); Norscia & Palagi (2011)	Social play increases during, and possibly alleviates, social tension.
	Against	Meerkats (<i>Suricata suricatta</i>)	Sharpe (2005a,b); Sharpe & Cherry (2003)	Frequent social play does not predict dispersal partnerships or affiliative behaviours.
	Against	Capuchins (<i>Cebus apella</i>), hamadryas baboons (<i>Papio hamadryas</i>), diademed sifakas (<i>Propithecus diadema</i>)	Lutz et al. (2019)	Play occurs primarily among individuals with pre-existing strong affiliative relationships.
	Against	Orangutans (<i>Pongo pygmaeus</i>), brown bears (<i>Ursus arctos</i>)	Rijksen (1978), Fagen & Fagen (2004)	Solitary species engage in juvenile social play.

(a) Learning motor, hunting, and fighting skills

Various forms of play involving bodily movement may serve as physical training, enhancing hunting and fighting skills. However, the results of studies examining the existence of this function are inconsistent.

Nunes et al. (2004a,b) found that juvenile Belding's ground squirrels with higher frequencies

of social play scored higher on an assessment of balance ability. Similarly, Berghänel, Schülke & Ostner (2015) showed that in Assamese macaques (*Macaca assamensis*), the age at which various motor skills were first observed was earlier in individuals who engaged in prolonged and intense social play. Furthermore, Byers & Walker (1995) found that the peak frequency of play in house mice (*Mus musculus domesticus*), rats (*Rattus norvegicus*), and domestic cats (*Felis catus*) coincided with the period of cerebellar synaptogenesis and muscle fibre differentiation, indicating that juvenile play behaviour might aid neuromuscular development related to motor ability. Weller *et al.* (2019) examined the relationship between the frequency of pre-weaning play-fighting and the outcomes of aggressive encounters later in life in pigs (*Sus scrofa*). The analysis revealed that among females, the winners of aggressive encounters had a higher frequency of pre-weaning play than the losers, suggesting that play experience might influence fighting skills. However, among males, the losers had a higher frequency of pre-weaning play, indicating that play-fighting does not generally improve fighting skills across sexes.

Regarding the relationship between play and various motor skills, negative results have been reported as frequently as positive ones. Caro (1980) divided 4- to 12-week-old kittens into groups with and without opportunities for object play and tested their predation skills on live prey at 6 months of age, but found no significant group differences. Vincent & Bekoff (1978) examined the relationship between the frequency of social play in coyotes (*Canis latrans*) observed at 20–34 days of age and hunting success rates after 35 days of age, finding no significant correlation. Similarly, Davies & Kemble (1983) reported no correlation between social play and hunting success in northern grasshopper mice (*Onychomys leucogaster*). Regarding the hypothesis that juvenile play-fighting improves fighting skills, Sharpe (2005c) found no significant correlation in meerkats (*Suricata suricatta*) between the frequency of play-fighting during the first year of life and success in subsequent dominance contests.

(b) Learning object manipulation and tool-use skills

It has been hypothesised that object play provides an opportunity to learn complex and precise object manipulation skills, which can lead to the development of tool-use behaviours (Power, 2000). This hypothesis is based on the observation that animal species displaying vigorous and complex object play are often proficient tool users (Montgomery, 2014).

Early studies often did not distinguish between the types of actions involved in object manipulation (for a review, see Power, 2000). However, studies on humans and other great apes have meticulously traced the developmental process of object manipulation, suggesting a connection between object play and tool use. Rat-Fischer *et al.* (2024), in a study of human infants, found that infants who playfully combined objects while adult experimenters demonstrated combining objects performed better on subsequent tasks, including those involving tool use. Hayashi & Takeshita (2022) and Hayashi & Matsuzawa (2003) found that spontaneous (possibly at least partially playful) object manipulation behaviours in infant chimpanzees (*Pan troglodytes*), such as inserting objects into other objects, are similar to the use of sticks as tools observed in wild chimpanzees. Compared to chimpanzees, there are fewer reports of bonobos (*Pan paniscus*) using tools to obtain food (Furuichi *et al.*, 2015), and it is also reported that wild bonobos engage in object play less frequently than chimpanzees (Koops, Furuichi & Hashimoto, 2015).

A relationship between object play and tool use has also been observed in other species. In groups of Japanese macaques (*Macaca fuscata*) and long-tailed macaques (*Macaca fascicularis*) where stone-handling play is particularly frequent, behaviours such as stone-throwing displays (Leca *et al.*, 2008; Leca & Gunst, 2023) and extractive foraging using stones to break open shells (Gumert, Kluck & Malaivijitnond, 2009; Luncz *et al.*, 2017; Tan, 2017) are observed, suggesting these behaviours are associated with play. Some parrots and corvids, such as New Caledonian crows (*Corvus moneduloides*) and palm cockatoos (*Probosciger aterrimus*), also engage in vigorous object play and habitually use tools in the wild (Hunt, 2000; Rutz *et al.*, 2010; Kenward *et al.*, 2011; Auersperg *et al.*, 2014; O'Hara & Auersperg, 2017; Lambert *et al.*, 2017).

Several negative findings regarding the relationship between object play and tool use or object manipulation skills have been reported. For example, some species of parrots and corvids, such as the rook (*Corvus frugilegus*; Bird & Emery, 2009), kea (*Nestor notabilis*; Gajdon, Lichtnegger & Huber, 2014), Goffin's cockatoo (*Cacatua goffiniana*; O'Hara *et al.*, 2019), and common raven (*Corvus corax*; Heinrich & Smolker, 1998), display active object play but do not habitually use tools in the wild, although they sometimes learn goal-directed tool use in captivity. Additionally, object play in the western bumblebee (*Bombus terrestris*) does not correlate with the improvement of object manipulation skills (Galpayage Dona *et al.*, 2022). Furthermore, the woodpecker finch (*Camarhynchus pallidus*), which habitually uses tools to extract insects from tree cavities, has not been reported to engage in object play (Kaplan, 2020).

(c) Establishing social hierarchies and assessing resource-holding potential

In group-living animals, social play may function to establish dominance relationships without resorting to intense aggressive conflicts. For example, Blumstein, Chung & Smith (2013) showed that in yellow-bellied marmots (*Marmota flaviventris*), the outcomes of juvenile play-fighting were significantly correlated with later dominance ranks in adulthood, suggesting that yellow-bellied marmots might use play to establish dominance relationships during their juvenile periods in a minimally costly way. Panksepp (1981) traced the temporal patterns of behaviours used during social play by pairs of rats from 18 to 64 days of age and found that one individual in the pair established stable dominance over the other through repeated play interactions with the same partner.

Group-living animals may use play to assess their own and others' fighting abilities, or resource-holding potential (RHP), facilitating the establishment of dominance hierarchies. Paquette (1994) found that in captive adolescent chimpanzees, pairs exhibiting rank reversals without intense fighting had engaged in frequent social play involving vigorous physical contact shortly before the reversals, implying that chimpanzees might use social play to gauge each other's abilities. Weller *et al.* (2020) showed that pigs with higher play frequencies seemed to decide the extent of escalation in fights (i.e. the costs they were willing to incur to continue the contest) based on their own RHP (i.e. body mass), whereas pigs with lower play frequencies did not exhibit this tendency. Based on this, the authors suggested that pigs might use play to assess their own RHP. Assessing rivals' fighting abilities may be particularly important among individuals with close ranks, where rank reversals are more likely to occur. Indeed, Cordoni (2009) showed that in wolves (*Canis lupus*), pairs with closer ranks played more frequently.

However, as with other proposed functions of play, negative findings have also been reported regarding the role of social play in establishing dominance hierarchies. Baldwin & Baldwin (1974) reported behavioural data from a rare group of red-backed squirrel monkeys (*Saimiri oerstedii*) in which social play was never observed during a 10-week observation period. This group's social structure did not differ significantly from other groups, suggesting that play is not essential for establishing dominance relationships. Additionally, in species with strict dominance hierarchies, such as Japanese macaques and spotted hyenas (*Crocuta crocuta*), where rank reversals are rare and rank is inherited from parent to offspring (Engh *et al.*, 2000; Kutsukake, 2000), it is unlikely that juvenile play significantly influences the establishment of dominance relationships.

(d) Building social bonds

Social play may provide opportunities to learn skills for building affiliative social relationships. However, as with other functions discussed earlier, the results have been inconsistent.

Mancini & Palagi (2009) found that in geladas (*Theropithecus gelada*), the frequency of support in agonistic conflict was higher among individuals who played together socially more frequently, indicating that playing together may help form alliances. Shimada & Sueur (2014), who analysed chimpanzee play networks using social network analysis, found a significant positive

correlation between the play networks of infants and juveniles and affiliative social networks calculated from the number of times they travelled in the same nomadic parties. In a similar study on Japanese macaques, Shimada & Sueur (2018) found that the social play network from the previous season significantly correlated with the affiliative social network based on proximity in the following season. Furthermore, social play in chimpanzees has been shown to promote cooperation among individuals in collective hunting and territorial defence (Samuni *et al.*, 2024).

Play may also have a proximate function in alleviating social tension within a group. Palagi, Cordoni & Borgognini Tarli (2004) and Yamanashi *et al.* (2018) found that social play among captive chimpanzees increased during the pre-feeding period when social tension was heightened, and argued that play may function to alleviate temporarily heightened social tension. The tension-alleviating function of play is also supported by studies on captive bonobos (Palagi, Paoli & Tarli, 2006) and captive common marmosets (*Callithrix jacchus*) (Norscia & Palagi, 2011).

Animals have evolved signals specific to the context of play, employing diverse modalities such as facial expressions (Bertini *et al.*, 2022; Maglieri *et al.*, 2024a,b; Cordoni *et al.*, 2024), vocalisations (Biben & Symmes, 1986; Burke *et al.*, 2017), gestures (Fröhlich, Wittig & Pika, 2016; Heesen *et al.*, 2019), face-to-face configuration and eye contact (Iki & Hasegawa, 2020, 2021; Heesen *et al.*, 2021), and body posture and movement (Bekoff, 1995; Yanagi & Berman, 2014) (for a review, see Palagi *et al.*, 2016; Heesen *et al.*, 2017). These signals have been suggested to serve several functions, including soliciting play (Fröhlich *et al.*, 2016), establishing joint engagement in play (Iki & Hasegawa, 2020, 2021), displaying motivation to play (Iki & Kutsukake, 2023), maintaining ongoing play (Bekoff, 1995; Mancini, Ferrari & Palagi, 2013; Cordoni *et al.*, 2024; Facondini *et al.*, 2024), resuming interrupted play (Warneken, Chen & Tomasello, 2006; Facondini *et al.*, 2024), signalling readiness to end the interaction (Heesen *et al.*, 2021), and preventing play from escalating into conflict (Burke *et al.*, 2017; Pellis & Pellis, 1996). These functions, likely contributing to the coordination of play, may ultimately foster the development of social bonds within groups.

There are also negative findings regarding a function of play in social bonding. For instance, meerkats do not tend to disperse with the group members they played with most during their juvenile period (Sharpe, 2005a). Similarly, in meerkats, there is no significant correlation between the frequency of social play and other affiliative behaviours like grooming (Sharpe, 2005b), nor is there a tendency for frequent playmates to engage in fewer aggressive interactions (Sharpe & Cherry 2003). Lutz, Ratsimbazafy & Judge (2019) used social network analysis to study play partner selection in tufted capuchins (*Cebus apella*), hamadryas baboons (*Papio hamadryas*), and diademed sifakas (*Propithecus diadema*), finding that play occurred primarily among individuals with already strong affiliative relationships, suggesting that play is not used to form new affiliative relationships. Additionally, solitary species like orangutans (*Pongo pygmaeus*) (Rijksen, 1978) and brown bears (Fagen & Fagen, 2004) engage in social play, particularly during their juvenile periods. Moreover, in species where individuals leave their natal groups upon reaching sexual maturity, such as male Japanese macaques (Iki & Hasegawa, 2020, 2021; Iki & Kutsukake, 2023), vigorous social play occurs during juvenile periods in the natal group. Even if social play in these species has the effect of building affiliative relationships during juvenile periods, it is doubtful whether it is a function that confers natural selection benefits determining subsequent survival and reproduction (Smith, 1982).

Various other functions have been proposed, such as play providing cognitive training for coping with unexpected situations (Spinka, Newberry & Bekoff, 2001) and emotion regulation (Pellis *et al.*, 2014). Similar to the hypotheses mentioned above, these proposed functions have received support in some cases but not in others. Therefore, based on the results of existing research, it seems unlikely that there is one function of play that is robustly applicable to each playful species (Burghardt, 2005). Moreover, even if a certain type of play in a particular species has some current utility, this does not necessarily mean it is identical to the original function that enabled the

evolution from ‘serious’ animals to playful animals. It is implausible that incipient play in the early stages of evolution already exhibited diverse behavioural variations and complex cognitive control, as seen in extant primates and corvids. Presumably, the earliest play consisted of only rudimentary physical movements or monotonous, crude interactions with objects or other individuals. Given that adaptive benefits are unclear even for the well-established forms of play in extant animals, it is difficult to imagine that incipient play in the early stages of evolution conferred a decisive selective advantage (Bernstein, 1982; Burghardt, 1998; Pellis *et al.*, 2015; Auerbach *et al.*, 2015). If incipient play indeed lacked decisive functions, how could play have evolved?

The question of the origin of play ultimately circles back to the opposition between Spencer and Groos. Spencer's non-selectionist theory and Groos's selectionist theory can be understood in terms of the distinction between proximate and ultimate explanations (Burghardt, 1984, 2005). Proximate and ultimate explanations are not mutually exclusive but rather complement each other in elucidating complex biological phenomena. By combining Spencer's non-selectionist explanation with Groos's selectionist explanation, Burghardt (1984, 2005) addressed why play evolved despite lacking clear adaptive value while also explaining why certain types of play in specific animal species exhibit clear functions.

III. SURPLUS RESOURCE THEORY: A SYNTHESIS OF SELECTIONISM AND NON-SELECTIONISM

Burghardt's *The Genesis of Animal Play: Testing the Limits*, published in 2005, sets out in detail his Surplus Resource Theory. The originality of this theory lies in its division of the evolution of play into three progressive stages: the initial evolutionary stage, or the ‘primary process’ is the evolution of incipient play, wherein ‘serious’ animals evolved into playful animals; this is followed by the subsequent ‘secondary process’ and ‘tertiary process’, wherein play behaviour acquires roles that enhance fitness by maintaining or improving specific behavioural and psychological capacities (Burghardt, 1998, 2005, 2010). According to Burghardt, the primary process can be understood in terms of Spencer's non-selectionist perspective, whereas the secondary and tertiary processes are explained from Groos's selectionist perspective.

According to the Surplus Resource Theory, natural selection did not play a role in the initial evolution of incipient play (i.e. the primary process). At this stage, play evolved as a by-product of several proximate factors (Burghardt, 2005, p. 119). It is only during the secondary and tertiary processes that variations in play within populations are subject to natural selection, leading to the evolution of play with adaptive functions. Notably, Burghardt (2005) did not posit that all forms of play in extant animals have necessarily reached the tertiary process. Different species, occupying distinct ecological niches, experience varying types and intensities of selection pressures. Consequently, some species have evolved play behaviours with clear adaptive functions, while others have not, accounting for the inconsistencies observed in studies on the functions of play.

What conditions facilitated the evolution of play as a by-product in the primary process? Burghardt (2005) categorised these conditions into four groups and hypothesised that play has evolved independently multiple times in lineages meeting these conditions: (i) energetics; (ii) ontogeny; (iii) ecology; and (iv) psychology and sociality. The first three of these conditions made possible the evolution of incipient play: animals with excess energy reserves (the first condition), periods in their life history with a reduced need to engage in ‘serious’ behaviour (the second condition), and living under relaxed selection pressures (the third condition) were likely to have the surplus resources necessary for the evolution of play (Burghardt, 1984, 2005).

Once these conditions were satisfied, the fourth condition could serve as a facilitating factor for play. However, understanding this fourth condition requires careful consideration. Although Burghardt (2005) labels this ‘psychology and sociality,’ the relative importance of social and psychological factors in the primary process of play evolution varies greatly. Regarding social factors, Burghardt (2005, p. 161) states, ‘while the complexity of social organization may have

some influence on the secondary features of play, it appears to have little to do with the occurrence of play itself'. Thus, Burghardt actually seems to believe that social factors are primarily related to later (secondary and tertiary) processes where play acquires functions according to the characteristics of species-specific social structure.

By contrast, psychological factors play a crucial role in facilitating the occurrence of incipient play in the Surplus Resource Theory. Under relaxed selection, animals exempt from engaging in 'serious' behaviours find themselves in a state of prolonged disuse of their instinctive adaptive behavioural repertoire, even though they have ample energy reserves. This situation is equivalent to stimulus deprivation, where the releaser stimulus that triggers a behaviour is absent for an extended period, leading to the emergence of 'boredom' – a psychological factor facilitating play. The Surplus Resource Theory thus suggests that incipient play served as self-stimulation to relieve boredom and achieve an optimal arousal level (Burghardt, 1984, 1988, 2005, 2010).

This explanation is similar to Berlyne's (1960) classical optimal arousal theory. According to this theory, an animal's arousal state is influenced by environmental novelty and complexity, and animals act to maintain their arousal state at an optimal level (Berlyne, 1960). Extremely novel and complex situations can overstimulate animals and cause surprise or fear, motivating behaviours to reduce arousal (e.g. avoidance behaviours). Conversely, situations with little novelty or complexity can understimulate animals and cause boredom, motivating behaviours to increase arousal. The optimal arousal theory posits that in such situations, exploratory behaviour – defined as behaviour that enables 'access to previously unattainable environmental information' (Berlyne, 1960, p. 79) through 'responses that alter the stimulus field' (p. 78) – is likely to emerge.

While it is not entirely clear from Burghardt (2005) whether there is inherent adaptive significance in relieving boredom, Pellis & Burghardt (2017) acknowledge that maintaining an optimal level of arousal can provide immediate benefits, such as improved attention to threats from predators and resources like food. By contrast, Burghardt consistently uses the term 'by-product' to describe the evolution of incipient play [e.g. Burghardt (2005, pp. 121, 132); Burghardt (2012, p. 2652)]. The term 'by-product' typically refers to traits that do not confer fitness benefits themselves and arise without undergoing natural selection by association with some other adaptive feature that is developmentally closely linked to them (Buss *et al.*, 1998; Leca, 2021; Tripoli & Fux, 2021). This implies that Burghardt holds a non-selectionist stance regarding the primary process of play evolution, akin to Spencer's theory. Burghardt's insight that incipient non-functional play evolved as a by-product of other traits and later acquired adaptive functions through natural selection in some taxa seems to align well with the observation that some play behaviours in extant animals have identifiable adaptive functions, while others do not. The idea that incipient play can evolve even without direct adaptive benefits, provided that ample resources are available, has also been supported by mathematical modelling (Auerbach *et al.*, 2015).

IV. EVOLUTION FROM 'SERIOUS' ANIMALS TO PLAYFUL ANIMALS: THE CURIOSITY HYPOTHESIS

Burghardt (1984, p. 36) humorously remarked, '[p]lay originated from boredom and deteriorated behaviour, an outrageous speculation that may, after all, also be true of the writer and his thesis'. However, what he actually endorses is a more nuanced view, where boredom is not the definitive evolutionary trigger for the emergence of incipient play but rather one of several facilitating factors for its occurrence (Burghardt, 1984, 2005).

So when the facilitating conditions specified by the Surplus Resource Theory are met, from what traits can incipient play originate? In this section, I argue that play originally evolved as a by-product of curiosity-motivated intrinsic exploration. As will be further elaborated below, this claim builds upon prior views, such as that of Burghardt (2005, p. 59), who stated, '[s]ome types of exploration, curiosity, and stimulation seeking could be both developmental and phyletic precursors to play', as well as earlier seminal works by Berlyne (1960), Welker (1971), and Hutt

(1966), among others. Pellis & Burghardt (2017, p. 712) also noted that ‘it seems that, for animals that have evolved play, especially in its most complex forms, exploration is intimately integrated with that play’. Thus, they acknowledge that, at least in some extant species, play and exploration are connected. However, they also stated, ‘exploration and play do not have a privileged association’ (p. 702), indicating that play and exploration should be viewed as distinct behavioural systems.

Here, building upon Burghardt (2005, 2012) and Pellis & Burghardt (2017), I argue that relying on the widely accepted classification that divides exploration into intrinsic and extrinsic types can advance our understanding of the evolutionary relationship between play and exploration. As will be discussed in detail below, extrinsic exploration and play should be considered distinct behavioural systems in many respects. However, the boundary between intrinsic exploration and play is less clearly defined, suggesting an evolutionary continuum linking these behaviours.

The hypothesis proposed in this section posits the following two evolutionary steps (Fig. 1): (i) from ancestral animals that perform extrinsic exploration triggered by conventional drives such as hunger and thirst, animals evolve that perform intrinsic exploration triggered by curiosity; and (ii) play behaviour evolves as a by-product of intrinsic exploration triggered by curiosity.

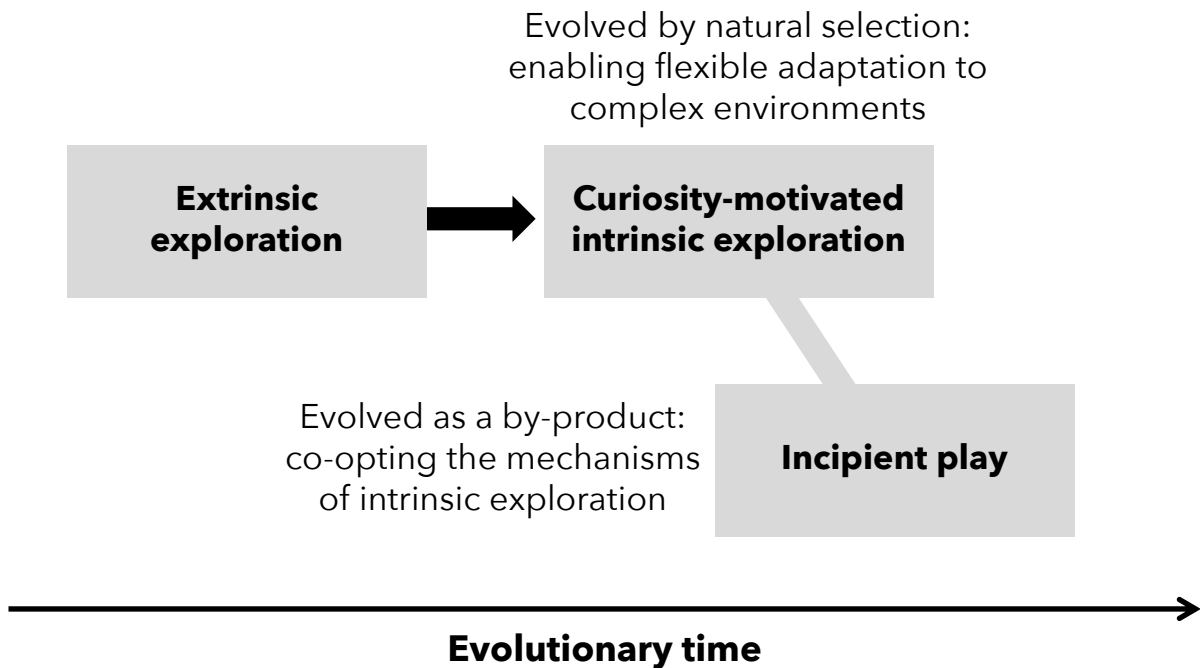


Fig. 1 The curiosity hypothesis of incipient play evolution. Incipient play evolved as a by-product through co-opting the neural, behavioural, and cognitive mechanisms of curiosity-motivated intrinsic exploration. The arrow from extrinsic to intrinsic exploration indicates that the latter evolved by natural selection. The edge connecting intrinsic exploration and incipient play signifies that these two behaviours are correlated traits, with the latter having evolved as a by-product of the former.

(1) Evolution of intrinsic exploration

To discuss the evolution of intrinsic exploration from extrinsic exploration, it is first necessary to articulate in greater detail the difference between them (Reader, 2015). There is no significant difference between these two types of exploration in terms of the actions performed. Both types of exploration can be categorised into three actions (Berlyne, 1960): (i) orienting responses, which alter the orientation or posture of sensory organs; (ii) locomotor exploration, which changes the

organism's position in the environment; and *(iii)* investigatory responses, which involve interacting with external objects. The primary difference between extrinsic and intrinsic exploratory behaviour lies in their goals and motivational structures. Extrinsic exploration aims at acquiring information necessary for achieving specific predetermined goals (Reader, 2015). Typically, the information sought during extrinsic exploration relates to reinforcers essential for survival and reproduction, such as food, mating partners, and shelter from predators (Wood-Gush & Vestergaard, 1991). By contrast, intrinsic exploration is not aimed at acquiring information to achieve specific predetermined goals but is driven by the exploration itself, seeking out and creating novel and complex sensory input (Wood-Gush & Vestergaard, 1991). For extrinsic exploration triggered by traditional drives like hunger or sex, exploration ceases once the necessary information about a target (e.g. food, mating partner) is obtained, leading to consummatory behaviour (foraging, mating). However, intrinsic exploration, which lacks specific predetermined external goals, is usually not followed by consummatory behaviour. The mechanism driving intrinsic exploration, which is not triggered by deficiency or rewards but is inherently reinforcing, is termed curiosity (Silvia, 2012).

As Hughes (1997) noted, boredom aligns with the classical drive reduction theory (Hull, 1943), where an unpleasant psychological state drives specific behaviours, and the behaviour ceases when the drive is satisfied and reduced. By contrast, curiosity often does not diminish through reinforcement; it may even intensify, and the curiosity-motivated behaviour itself can become the animal's primary goal even in the absence of external rewards (Harlow, 1950; Butler, 1965). This distinctive motivational structure of curiosity, which resists explanation by drive reduction theory or extrinsic motivation, aligns with the intrinsic and autotelic nature of play (Burghardt, 2005), as discussed further below.

On an evolutionary timescale, it is almost certain that extrinsic exploration existed first, and that intrinsic exploration emerged from the former. Presumably, the evolution of intrinsic exploration occurred as an extension of the scope and context of information-seeking behaviours rooted in extrinsic exploration. Extrinsic exploration for information necessary for survival and reproduction is not limited to vertebrates but is also performed by many motile invertebrates (Bell, 1990). By contrast, intrinsic exploration driven by curiosity is considered to be limited to species with more developed sensory, information-processing, and learning abilities (Byrne, 2013). Among invertebrates, strong curiosity is observed in only a few species, such as octopuses (Mather & Anderson, 1999). Unfortunately, no systematic comparative analysis of the phylogenetic distribution of extrinsic and intrinsic exploration has been conducted. Nonetheless, the presence of intrinsic exploration in species phylogenetically distant from vertebrates, such as the octopus, suggests that it has evolved independently multiple times.

What differentiates animals that evolved intrinsic exploration from those that did not? This difference may be articulated in terms of the expandability of the sensory-motor repertoire. For example, when a tick perceives butyric acid from the skin of a mammal, it drops from a branch toward the odour source (Uexküll, 1934/1992). If it lands successfully on the animal's body, it searches for a hairless skin surface to bite and suck blood. This exploration, driven by a clear goal of blood-sucking, is a good example of extrinsic exploration: exploration performed solely to discover the appropriate key stimulus (hairless warm skin) that triggers the existing consummatory behaviour (blood-sucking). As illustrated by this example, the stimulus–response system of an animal that performs only extrinsic exploration consists of pre-existing, fixed pairs of key stimuli and behavioural responses, with no capacity to incorporate novel responses to previously unknown stimuli into its repertoire.

By contrast, intrinsic exploration motivated by curiosity pursues novel and complex sensory inputs, even if they are unrelated to patterns of stimuli embedded in the animal's pre-existing sensory-motor functions. Although such novel and complex stimuli may not always lead to direct survival or reproductive benefits, some random responses to a novel stimulus may occasionally yield rewards for the organism. In such cases, a response to that novel stimulus can be incorporated

into the individual's sensory-motor repertoire. Thus, animals engaging in curiosity-motivated intrinsic exploration can expand their repertoires by acquiring new sensory-motor functions.

Highly receptive animals that plastically expand their sensory-motor repertoires therefore could have a selective advantage under certain ecological conditions. For example, in species inhabiting complex environments with high spatial and temporal heterogeneity, or in environments where the rate of environmental change is relatively rapid compared to the generation time, the strategy of responding immediately to environmental changes through *ad hoc* intrinsic exploration may be more adaptive than evolving new sensory-motor functions tailored to new environments over a long period. There is some evidence to support this: a study comparing responses to novel objects in 76 species of parrots found that species inhabiting highly heterogeneous and complex environments, such as forest edges, have shorter latencies for novel object exploration than those in relatively homogeneous or simple environments, such as savannas (Mettke-Hofmann, Winkler & Leisler, 2002). Furthermore, it is expected that species with high levels of curiosity are more likely to succeed in novel environments as invasive species. To test this hypothesis, Augustyniak *et al.* (2024) compared the reactions of two invasive goby species (racer goby, *Babka gymnotrachelus* and monkey goby, *Neogobius fluviatilis*) with those of two native counterparts (European bullhead, *Cottus gobio* and gudgeon, *Gobio gobio*) to novel environments, demonstrating that more exploratory behaviour was observed in the invasive species. Additionally, generalist species with opportunistic foraging strategies are expected to benefit more from curiosity-motivated intrinsic exploration than species with specialised diets. Bergman & Kitchen (2009) compared responses to novel objects between a generalist forager (chacma baboon, *Papio ursinus*) and a herbivorous specialist (gelada baboon) and found that the former exhibited more exploratory behaviour towards novel objects. Such selective advantages may have formed the basis for the evolution of curiosity and intrinsic exploration.

(2) Evolution of incipient play as a by-product of curiosity-motivated intrinsic exploration

(a) Information seeking through intrinsic exploration and play

As many researchers have pointed out, intrinsic exploration and play share commonalities, such as a lack of clear external goals and the absence of consummatory behaviours (Hutt, 1966; Welker, 1971; Weisler & McCall, 1976; Baldwin & Baldwin, 1977; West, 1977; Hughes, 1978, 1979; Wood-Gush, Vestergaard & Petersen, 1990; Pellegrini, Dupuis & Smith, 2007; Weisfeld & Cronin Weisfeld, 2016). One researcher with a particularly significant influence on discussions about the relationship between exploration and play is Corinne Hutt. Her analysis of the behaviour of human children showed that the types and nature of information gathered through exploration and play differ (Hutt, 1966). According to her, when children encounter a novel object, they first engage in exploratory behaviour to gather information, asking, 'What does this object do?' Through this exploratory behaviour, they gradually uncover the object's basic properties. Once a basic understanding is achieved, children begin to play with the object, shifting their focus to, 'What can I do with this object?' This transition from exploration to play is a common pattern observed across species [red-backed squirrel monkeys (Baldwin & Baldwin, 1974); domestic cats (West, 1977); common octopuses, *Octopus vulgaris* (Kuba, Gutnick & Burghardt, 2014)] (Fig. 2). Thus, using Hutt's (1966) functional distinction, the development from intrinsic exploration to play can be understood as a progression from passive information gathering about the 'stimuli' derived from a particular object to more active information gathering about the 'responses' of the object elicited by the animal's interactions with it. Through this active information gathering, animals can encounter unexpected patterns that are not included in their pre-existing sensory-motor repertoire. Although Hutt's (1966) description primarily focuses on object play, a similar transition from passive to active information gathering can be observed in different types of play. For example, in the early ontogeny of common squirrel monkeys (*Saimiri sciureus*), social play begins with brief exploratory interactions, such as gently

touching partners with their hands or mouth, and gradually develops into more coordinated and competitive forms (Baldwin, 1969; Baldwin & Baldwin, 1974). A comparable pattern is observed for locomotor play involving movements in various environments (e.g. underwater, on slopes, in trees). For example, calves (*Bos taurus*) introduced to a novel environment first explore it by licking or sniffing, and such exploration functions to mediate subsequent locomotor play, such as running or jumping (Rushen & de Passillé, 2014). In any type of play, the initial occurrence is typically preceded by exploration, but once animals have become sufficiently familiar with a specific object, partner, or environment, subsequent play bouts can occur without the need for further exploration (Brownlee, 1954; Hutt, 1966).

A



B



Fig. 2 Development from intrinsic exploration to play. (A) Juvenile and infant Japanese macaques (*Macaca fuscata*) approach and explore an unfamiliar wheelbarrow. (B) After a period of exploration, the monkeys begin to play with the water in the wheelbarrow's bucket.

The distinction between exploration as passive information gathering about ‘stimuli’ and play as active information gathering about ‘responses’ is not always clear-cut. Indeed, recalling Berlyne's (1960) classification of exploration, orienting responses, locomotor exploration, and investigatory responses are all forms of information gathering that involve, to varying degrees, the animal's active physical movements. In early evolutionary stages, incipient play probably did not differ clearly from intrinsic exploration in terms of body movements or the purposes of information gathering and may have emerged by co-opting at least some of the mechanisms of intrinsic exploration. More specifically, based on the supporting evidence discussed below, it is likely that intrinsic exploration and incipient play were correlated traits sharing common mechanisms. Even if incipient play did not have independent adaptive benefits as a behavioural system distinct from exploration, it could have evolved as a by-product if intrinsic exploration was selected for its adaptive benefits in allowing flexible and rapid adaptation to complex environments. In the following sections, I will focus on two pieces of supporting evidence for the curiosity hypothesis: (i) the commonality between stimuli that elicit curiosity and those that elicit play, and (ii) the shared neural basis of curiosity and play.

(b) Commonality between stimuli that elicit curiosity and those that elicit play

Until recently, it was often argued that curiosity and play are triggered by different types of stimuli. For instance, Burghardt (1984, 2005) claimed that curiosity and exploration are evoked by novel environments, whereas play occurs in familiar environments, suggesting that they should be considered distinct behaviours. However, recent findings suggest that there are commonalities between stimuli that evoke curiosity and those that elicit play. Studies analysing gaze behaviour in situations unrelated to reward acquisition (i.e. intrinsic exploration) in human infants (Kidd, Piantadosi & Aslin, 2012; Wu *et al.*, 2022) and rhesus macaques (*Macaca mulatta*; Wu *et al.*, 2022) have shown that the relationship between the novelty and complexity of stimuli and the frequency and intensity of exploration follows an inverted U-shape. Thus, intrinsic exploration is more strongly evoked by stimuli of moderate novelty and complexity compared to stimuli that are too novel and complex or too familiar and simple. Similarly, it has been shown that human infants engage in more play when exposed to stimuli of moderate complexity and novelty. Stahl & Feigenson (2015) found that 11-month-old infants exhibited more object play when presented with objects that behaved in unexpected ways, defying physical laws, compared to objects behaving in familiar, predictable ways. Studies by Schulz & Bonawitz (2007) with preschool children averaging 57 months old, Schulz, Standing & Bonawitz (2008) with preschool children averaging 48 months old, and Bonawitz *et al.* (2012) with children aged 4–7 years also demonstrated that play increased when objects behaved unexpectedly or when there was uncertainty about the behaviour of the objects. In these experiments, the objects that elicited more play did not behave in ways that were so novel and complex as to evoke fear. Thus, human children's play was evoked more strongly by moderately novel and complex stimuli (Singer & Singer, 1990; Andersen *et al.*, 2022). Pelz & Kidd (2020) presented findings that contrast with the conventional view that humans become less curious with age, showing that children become increasingly exploratory from toddlerhood to adolescence. Their results are consistent with the fact that humans are one of several species that remain highly playful even into adulthood (Huizinga, 1949; for examples of adult play in other species, see Burghardt, Ward & Rosscoe, 1996; Cordoni *et al.*, 2022; Palagi, 2023; Samuni *et al.*, 2024), corroborating the hypothesis proposed herein that curiosity underpins play.

There are few studies on non-human animals that examine whether play increases under moderate conditions, i.e. where stimuli are neither too novel nor too familiar. Nonetheless, some observational data suggest that non-human animal play is more strongly evoked by situations that are partially novel and partially familiar. Rushen & de Passillé (2014) measured exploratory behaviour and locomotor play in calves introduced to a novel arena at 9 and 19 weeks old, finding that individuals with greater increases in exploratory behaviour also showed greater increases in

locomotor play. This result suggests that individuals who gathered enough information through exploration and became moderately familiar with the novel arena were more likely to engage in play (similar observations can be found in Brownlee, 1954). Kuczaj *et al.* (2006) observed object play in captive common bottlenose dolphins (*Tursiops truncatus*) and suggested that dolphins create partially novel and partially familiar situations by using new action patterns with familiar objects. Ham & Pellis (2023) focused on social play in rats, analysing their responses to partners with varying levels of novelty. The experiment presented the subjects with three types of partners: cage-mates they frequently played with, individuals housed on the opposite side of a cage divided by a transparent partition (familiar but never played with), and completely unfamiliar individuals from other cages. Their analysis showed that the subjects preferred to play with partners who were familiar but with whom they had not previously played (i.e. partners that were moderately novel and familiar). Together, these findings suggest that, in non-human animals, play is also elicited by moderately novel and moderately familiar stimuli.

(c) Shared neural basis of curiosity and play

Recent neuroscientific findings indicate that both curiosity (intrinsic exploration) and play involve brain regions associated with the reward system and executive control. Below, I provide an overview of the existing research on the relationship between these neural systems and curiosity/play.

(i) Reward system

The motivational structures of intrinsic exploration and play, where the behaviour itself is rewarding even in the absence of external rewards, are deeply linked to the reward system. Knowledge about the connection between the reward system and curiosity comes primarily from experiments with humans and macaques. Studies on humans have shown that curiosity is associated with activation in the striatum, particularly the nucleus accumbens (NAcc) (Kang *et al.*, 2009; Gruber, Gelman & Ranganath, 2014; Charpentier, Bromberg-Martin & Sharot, 2018; Lau *et al.*, 2020), and the midbrain ventral tegmental area (VTA) (Gruber *et al.*, 2014; Charpentier *et al.*, 2018). Additionally, the frequency of information-seeking behaviour is positively correlated with the strength of functional connectivity between the VTA and NAcc (Eschmann *et al.*, 2023). Activity of the striatum and midbrain dopamine neurons during information exploration has also been demonstrated in studies on rhesus macaques (Bromberg-Martin & Hikosaka, 2009; White *et al.*, 2019), suggesting that the link between the reward system and curiosity is common to primate species. Moreover, the amygdala, which has close neural connections with the striatum and the anterior cingulate cortex (ACC) and is involved in the emotional evaluation of stimuli, has also been implicated in curiosity (Jellestad, Follesø & Ursin, 1994). Studies on humans have reported increased amygdala activity when ambiguous information is presented (Hsu *et al.*, 2005) and abnormal increases in curiosity and exploration in individuals with bilateral amygdala damage (Feinstein *et al.*, 2011).

Recent research has also revealed that neural activity in the same reward system is related to play behaviour. In studies on rats, expression of the *c-Fos* gene, an indicator of neuronal activity, has been observed in the VTA, NAcc, and amygdala of individuals immediately after engaging in social play (Northcutt & Nguyen, 2014; van Kerkhof *et al.*, 2014). Comparative studies across primate species have shown that species with greater relative size of the amygdala (Lewis & Barton, 2006) and striatum (Graham, 2011) tend to engage in more social play. These findings suggest that the motivational structures of play, where the behaviour itself becomes the goal even in the absence of external objectives, may be based on the same reward mechanisms that underlie curiosity. However, it is important to note that these studies are mainly based on social play. While the intrinsically pleasurable nature of other types of play is also likely dependent on the aforementioned reward systems, further research is needed to confirm this.

(ii) Executive control system

The occurrence of intrinsic exploration and play, which do not necessarily lead to immediate benefits, is thought to be heavily influenced by brain regions involved in executive control, which weaken the demand for immediate rewards and prioritise information from stimuli not directly linked to rewards (Cervera, Wang & Hayden, 2020). Results supporting the connection between the executive control system and curiosity again come mainly from studies on humans and macaques. Studies on humans have shown activity in areas involved in executive and motivational control, such as the ACC and the orbitofrontal cortex (OFC), when curiosity is triggered or when ambiguous information is presented (Hsu *et al.*, 2005; Brydevall *et al.*, 2018; Charpentier *et al.*, 2018). These areas have connections with the striatum, suggesting that the executive control system regulates the process of information exploration in coordination with the reward system. Studies on rhesus macaques have shown that neurons in the OFC encode the value of information (Blanchard, Hayden & Bromberg-Martin, 2015) and that activity in the ACC is related to information prediction (White *et al.*, 2019). Furthermore, activity in the cortico-basal ganglia circuit has been causally linked to the occurrence of visual information-seeking behaviour to resolve uncertainty (White *et al.*, 2019).

Evidence linking the executive control system to play comes primarily from experiments with rodents. Inactivating areas of the prefrontal cortex, such as the prelimbic cortex (PL), infralimbic cortex (IL), and medial and ventral OFC, reduces the frequency and duration of social play in rats (van Kerkhof *et al.*, 2013). Studies using *c-Fos* expression as a marker of neuronal activity have shown that *c-Fos*-positive cells are detected in the ACC, PL, IL, and OFC of golden hamsters (*Mesocricetus auratus*) and rats immediately after social play (Cheng, Taravosh-Lahn & Delville, 2008; van Kerkhof *et al.*, 2013). Moreover, levels of *c-Fos* expression in the medial prefrontal cortex correlate with levels in the striatal projection areas (Van Kerkhof *et al.*, 2013), suggesting that the cortex–striatum projections are involved in social play. These findings indicate that the brain regions involved in executive control related to play may also be based on the neural mechanisms of curiosity and intrinsic exploration, as for the reward system.

V. CONCLUSIONS

- (1) Based on existing research, there does not appear to be a clear function common to all forms of play observed in extant animals. Given the inconsistencies found in previous research, even if a particular type of play in a certain species serves a specific function, it is not plausible to assume that the ‘current utility’ is identical to the ‘original function’ that drove the evolution from ‘serious’ to playful animals. Burghardt (2005) proposed that incipient play did not evolve as an adaptive trait through natural selection but rather as a by-product of energetic, ontogenetic, ecological, and psychological facilitating factors.
- (2) Building upon previous empirical and theoretical studies, this review discusses the evolutionary relationship between exploration and play. More specifically, I argue that by clearly distinguishing between extrinsic and intrinsic exploration, we can better articulate the continuity and discontinuity between play and exploration. This paper proposes the hypothesis that play originally evolved as a by-product of curiosity-motivated intrinsic exploration. I highlight two pieces of evidence supporting this hypothesis: (i) the commonality between stimuli that elicit curiosity and those that elicit play, and (ii) the shared neural basis of curiosity and play.
- (3) The above evidence suggests that intrinsic exploration and incipient play were correlated traits

sharing common mechanisms. In the early stages of evolution, these behaviours may have been even less distinguishable than they are now, forming a continuum of behaviours contributing to information gathering rather than separate behavioural systems. Therefore, even if incipient play did not confer independent adaptive benefits, it could have evolved as a by-product if intrinsic exploration was selected for its adaptive benefits in allowing flexible adaptation to complex environments. Presumably, incipient play in the earliest stage of evolution emerged as an active information-gathering behaviour involving greater physical activity, occurring after a certain amount of passive exploration. The establishment of play as a distinct behavioural system in some species, acquiring specific functions (see Section II.2), likely occurred during the later secondary and tertiary evolutionary processes proposed by the Surplus Resource Theory. Investigating how the possible foundations of incipient play in the earliest stages of evolution relate to the more sophisticated and unique forms of play in some extant species, such as mental play, pretence play, and sociodramatic play in humans, presents an intriguing avenue for future research.

- (4) There are several potential future research directions to test this hypothesis. Comparative studies on the phylogenetic distribution of curiosity and play could provide critical insights. If play evolved as a by-product of curiosity, we would expect to find play behaviours only in lineages where curiosity exists and an absence of play in lineages without it. Additionally, eco-sociological studies comparing the types of stimuli that strongly evoke curiosity in certain animals and the types of play they frequently engage in, considering their habitats and social structures, would be valuable. For instance, opportunistic omnivores relying on various types of food items or extractive foragers that engage in complex object manipulation are likely to exhibit greater curiosity towards objects and engage in more object play compared to other species. Conversely, species that form alliances even among non-kin or have complex social structures may show stronger curiosity towards conspecifics and engage in more social play. Psycho-behavioural studies with human infants have shown that stimuli with moderate novelty and complexity are more likely to induce play than those with too high or too low novelty or complexity. However, there are few studies on non-human animals that experimentally manipulate stimulus novelty and complexity to compare play frequency across conditions. Future research on non-human animals examining the characteristics of stimuli that induce play more strongly could provide crucial evidence for the evolutionary continuity between curiosity and play.
- (5) The evolutionary origins of play remain largely underexplored, and it is crucial to propose and test alternative hypotheses, including but not limited to the boredom-based hypothesis and the curiosity hypothesis articulated herein. I hope this review will encourage the proposal and testing of hypotheses on the origins of play.

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