

Play and the Evolution of Creative Societies

Erice, 14th-18th May 2023

Directors: Gordon M. Burghardt, Elisabetta Palagi, Sergio M. Pellis & Jeff Schank

Sunday 14th, May

Arrival in Erice and Registration

After dinner reception at the Marsala Room (San Rocco)

Informal introduction to the Conference by the Workshop Directors while drinking wine in the Marsala Room (San Rocco)!

Monday 15th, May

- 09:00-09:10 – Welcome by **Stefano Parmigiani**, the director of the International School of Ethology “Danilo Mainardi”

Session #1 – morning

- 09:10-10:00 – **Gordon M. Burghardt** (University of Tennessee Knoxville, Departments of Psychology and Ecology and Evolutionary Biology)

The enduring search for the nature of play

10:00-10:20 - coffee break

- 10:20-11:10 – **Marek Špinka** (Czech University of Life Sciences, faculty of Agrobiolology, Food and Natural Resources)
- Play and wellbeing**

- 11:10-12:00 – **Heather M. Hill** (St. Mary’s University, Department of Psychology)
- Having a whale of a time!**

- 12:00-12:50 – **Jamie Ahloy-Dallaire** (Laval University, Department of Animal Sciences)
- Commonalities and differences between types of play**

12:50-14:30 - Lunch

Session #2 – afternoon

- 14:30-15:20 – **Pichon Swann** (Geneva School of Health Science)
- Investigating the impact of video game play on affect and cognition**

Selected short presentations

15:20 – 15:35 – **Lindsay Mehrkram** - **Play, attention, and interspecific audience effects: how studying play extensions of the human-canine bond**

15:35 – 15:50 – **Megan L. Lambert** - **Does object play foster innovation? Investigations with kea parrots**

15:50 – 16:05 – **Sabrina Brando** - An investigation into the flexibility of enrichment objects and their possible afforded actions in belugas (*Delphinapterus leucas*) in managed care

16:05 – 16:20 – **Isabelle Laumer** - The development of object manipulations in wild and zoo-housed orangutans

16:20 – 16:35 – **Luca Pedruzzi** - The interconnection of hierarchy, affiliation, and play shapes social dynamics in cattle

16:35 – 16:50 – **Amanda Dettmer** - Social play buffers the effects of social instability in young rhesus monkeys

16:50-17:10 - coffee break

- 17:10-18:00 – General discussion
- 18:00-19:00 – Poster session

Tuesday 16th, May

Session #3 - morning

- 09:00-09:50 - **Sergio M. Pellis** (University of Lethbridge, Department of Neuroscience)
Play and the development of the social brain
- 09:50-10:40 – **Marijke E. J. Achterberg** (Universiteit Utrecht, Departement Dier in Wetenschap en Maatschappij)
Neural mechanisms of social play behaviour

10:40-11:00 - coffee break

- 11:00-11:50 – **Heidi M. B. Lesscher** (Universiteit Utrecht, Departement Dier in Wetenschap en Maatschappij)
Healthy play better coping: a perspective on play in health and disease
- 11:50-12:40 - **Tracy R. Gleason** (Wellesley College, Department of Psychology)
Play, imagination, and sociocognitive development

EXCURSION TO MOZIA ISLAND– 12.40 POCKET LUNCH

Wednesday 17th, May

Session #4 - morning

- 09:00-09:50 - **Elisabetta Palagi** (University of Pisa, Department of Biology)
Adult play and the evolution of tolerant and cooperative societies
- 09:50-10:40 - **Jean-Baptiste Leca** (University of Lethbridge, Department of Psychology)
Object play and tool use: an elusive connection

10:40-11:00 - coffee break

- 11:00-11:50 - **Martine Hausberger** (Université de Rennes)
Play, coping and welfare
- 11:50-12:40 - **Giada Cordoni** (University of Turin, Department of Life Sciences and System Biology)
Play as a tool to understand how domestication affected sociality

12:40-14:30 - Lunch break

Session #5 - afternoon

- 14:30-15:20 - **Michael J. Kuba** (Okinawa Institute of Science and Technology, Physics and Biology Unit)
Play in invertebrates
- 15:20-16:10 - **Masaki Shimada** (Teikyo University of Science, Department of Animal Science)
Social networks and social play

16:10-16:30 - coffee break

- 16:30-17:20 **Fausto Caruana** (Italian National Research Council, CNR, Institute of Neuroscience)
Exploring human laughter and its contagion using neuroscientific techniques

Selected short presentations

- 17:20 - 17:35 – **Jackson R. Ham** - **Social skills in adult male rats are reflected in prefrontal cortex neuroanatomy and juvenile play experiences**
- 17:35 - 17:50 – **Veronica Maglieri** - **Are you playing or fighting? Just look at the faces in wolves**
- 17:50 - 18:05 – **Sasha Winkler** - **Evidence of playful teasing in great apes**
- 18:05 - 18:20 – **Kris H. Sabbi** - **Trends in adult social play reveal a hidden cost of motherhood for chimpanzees**
- 18:20-19:00 - General Discussion and Closing Remarks

20:30-22:30 - Social Dinner

Thursday 18th, May

Departures

EXCURSION TO MOZIA ISLAND - Pocket lunch + Bus + Boat included in the workshop fee

Island ticket entrance not included: cost 10 €

BOOK ABSTRACT: TALKS

The enduring search for the nature of play

Gordon M. Burghardt

University of Tennessee

Our understanding of the evolution, phylogeny, mechanisms, development and functions of playfulness in both human and nonhuman animals is surprisingly minimal, as well as controversial, especially the issue of the adaptive function of play. Consequently, biologists have typically ignored play and social scientists have produced much descriptive data and theoretical formulations that have resolved little. **Brian Sutton-Smith's seven rhetorics of play** encapsulated both the dilemmas involved in studying play and the rich importance of truly understanding play. In recent years, however, much research has advanced our understanding of play, including innovative empirical studies. This includes identifying play and its diversity, the neuroscience of play, the ontogeny and functions of play, and theoretical and modeling contributions. This talk will explore some of this recent work in the context of the history of play research and set the stage for the exciting work to be presented at this meeting.

The unity and diversity of play: implications for animal welfare

Marek Špinka

Czech University of Life Sciences, Faculty of Agrobiolgy, Food and Natural Resources, Prague

Play behaviour exists in an exuberant diversity of forms and, as far as we know, varies widely in its function. Furthermore, play behaviour has a peculiar phylogenetic distribution. Play is almost universal among mammalian species (while still varying widely in amount and quality), scattered among other vertebrate taxa and, as far as we know, rare in other animals. These two aspects of play present a major challenge when using play behaviour as a welfare indicator, seemingly forcing us to refrain from any generalisation. Here I address the play-welfare relationship while focusing on the most numerous and archetypical category of play, namely the juvenile mammalian play (JMP). I start with reviewing the specific features of JMP. First, JMP contains self-handicapping elements that result in temporary relaxation of control of own body kinematics. Thus, JMP actions are by design inefficient in attaining their seeming proximate goals. Second, the affective mechanism of “fun” motivates JMP and is related to the alternation of loss and regaining of control. Third, JMP is repetitive, i.e. once a play sequence is performed, it tends to be repeated over and over. The three aspects are linked. Loss of control, which would be aversive in “serious” context and block the repetition of the behaviour, does the opposite in play: it contributes to the fun affect and promotes the repetition of current play elements. I propose that the repetitive performance of JMP serves to pre-map own locomotive and emotional skills vis-à-vis the unpredictable nature of the environment, including the conspecifics. I argue that recent, current and future welfare the young mammals could be related to this basis structure of JMP. First, there is empirical evidence that the better the animal has been coping with fitness threats till now, the more likely it is to engage in the risky repetitive loss-of-control performance of play. Second, the immediate welfare is enhanced through the presence of opioid-mediated pleasurable fun emotion. Finally, JMP may improve future welfare through the long-term benefits in physical and psychological fitness. I will outline some areas for future theoretical and empirical research that could enhance our understanding about the play – welfare relationships in developing mammals.

Having a whale of a time!

Heather M. Hill

St. Mary's University, Department of Psychology

Like many species, dolphins and whales are especially playful. Whether in managed care or in their natural habitat, numerous anecdotes of play-like and play behaviors have been reported. Systematic investigation of play by dolphins and belugas in managed care suggests that this activity is both a solitary and social activity that serves a number of functions, including developing motor and/or social skills, improving foraging skills, building and/or maintaining bonds, practice solving problems, and cognitive stimulation. Utilizing specific examples, case studies, and some experimental evidence, this talk will explore each of the proposed functions across several species of cetaceans, highlighting the gaps that continue to exist in the world of cetaceans about the role play has in behavioral adaptation and variability. Throughout the talk, proximate questions such as developmental milestones and learning processes will also be addressed.

Commonalities and differences between types of play

Jamie Ahloy-Dallaire

Laval University, Department of Animal Sciences

Play encapsulates an extreme variety of different actions, such as children turning somersaults, young rats wrestling, adult dogs chasing each other, and monkeys gleefully destroying household objects. The diversity of play types within and between species is part of the reason why ethologists have long struggled to formulate a comprehensive definition of play. It also raises the more fundamental question of whether play can be viewed as a unified concept at all, or instead should be considered a collection of disparate phenomena among which we perceive superficial resemblance. In the latter view, there are no simple or single answers to the questions of how play evolved, what its functions are, how it affects development, how it is regulated in the brain, what motivates animals to play, or what relationships exist between play, emotions, and wellbeing. This presentation will address commonalities and differences between types of play at different levels of ethological explanation, within and across taxonomic groups.

Investigating the impact of video game play on affect and cognition

Pichon Swann

Geneva School of Health Science

The democratization of video games has led to increasing interests in understanding their potential impact on cognition and affect. Besides this, gamification and video game technologies also offer a growing field of motivating and adaptive solutions to facilitate learning and adherence in health interventions. Evidence suggests that acquiring expertise in video games which require high attentional control may have beneficial effects on some aspects of cognition and attention. Attention and executive control are key functions to deploy emotion regulation strategies effectively, and their impairment in mental health conditions like anxiety may impede effective regulation. The underlying assumption of cognitive models of anxiety is indeed that efficient attentional control – the ability to monitor and flexibly allocate resources to goal-relevant information while inhibiting goal-irrelevant information - is a key component for implementing cognitive regulation strategies and to filter out distracting emotional stimuli or undesired thoughts. Adolescence is a critical period for the onset of anxiety disorders, which further raises the importance of understanding whether video games with specific characteristics may have beneficial effects on anxiety or may be used to support the development of cognitive skills important for emotion regulation. We will introduce existing work probing this hypothesis, together with a randomized controlled trial that my collaborators and I are implementing to evaluate the effect of a 6-week video game intervention on adolescent anxiety and investigate whether reduction in anxiety may be due to improvements in attentional control abilities.

Play, attention, and interspecific audience effects: how studying play extensions of the human-canine bond

Mehrkam, L.R. *, Wynne, C.D.L. **

*Monmouth University (West Long Branch, New Jersey, USA), **Arizona State University (Tempe, Arizona, USA)

Domestic dogs are a highly playful species that are sensitive to the attentional state of conspecifics as well as humans. It is well-established that an animal's social environment can influence play, and audience effects may catalyze social play. Prior research has shown that dogs and humans engage in play signals, and that intraspecific attention maintains social play in dog–dog dyads. However, whether interspecific (specifically, human) attention maintains social play is not thoroughly investigated or understood. In this talk, we will present a series of experimental studies that examines the relationship between the availability of human attention and social play in domestic dogs. In the original experiment, familiar dog–dog dyads were exposed to conditions that differed in the degree of availability of owner attention. Observed levels of social play were significantly higher during conditions in which an attentive owner was present than during conditions in which an owner was either inattentive or absent. This is the first experimental evidence of an interspecific audience effect facilitating social play in domestic dogs. We will also present the results of three additional experiments that attempt to clarify the possible learning mechanisms contributing to this relationship. Collectively, these results suggest that the availability of caretaker attention may be a proximate explanation for social play in canids that have ontogenetically rich histories with humans and also retain neotenized behavior as adults, and may aid in a more comprehensive understanding of the evolution and development of play behavior.

Does object play foster innovation? Investigations with kea parrots

Megan L. Lambert

Messerli Research Institute, University of Veterinary Medicine, Vienna, Austria

Despite its apparent costliness, object play and exploration may function to provide opportunities to acquire information about the physical environment, including solutions to novel problems. For example, tool-using species typically show more frequent and complex object manipulation and play than their non-tool-using counterparts, either during ontogeny or adulthood. The kea parrot (*Nestor notabilis*), a highly explorative and playful species from New Zealand, is adept at solving novel physical problems, and has been known to spontaneously innovate tool use in captive settings. This study examined whether kea were more likely to innovate a solution to either of two novel tool-use tasks if they had previous experience exploring the tasks and combining them with nearby objects/potential tools in an unrewarded play context. Five of thirteen subjects spontaneously solved at least one tool-use test, typically in their first few sessions; however, birds were no more likely to solve the task if they had a prior opportunity to engage with the setup. Instead, the kea's general tendency to persist in repeated exploration and object-structure combinations eventually led them to the solution. We further describe differences in object play and exploration depending on age category, sex, and context (goal-directed vs. play). Our results broadly show that this species' persistent flexibility in approaching novel problems may reduce the need for applying information previously gathered during play.

An investigation into the flexibility of enrichment objects and their possible afforded actions in belugas (*Delphinapterus leucas*) in managed care

Sabrina Brando, Heather Manitzas Hill, Tiffany L. Garcia, Jackson R. Ham

AnimalConcepts, Teulada, Spain

Enrichment is an important pillar in contemporary animal care programs, in both zoos and aquariums. The presence of enrichment has been shown to encourage species-specific behaviours, reduce undesired behaviours, and increase engagement with the environment. The type and characteristics of enrichment does not only elicit various behaviours from the behavioural repertoire of an animal, but also provides different cognitive, social, and physical opportunities. The purpose of this study was to investigate the relationship between the degree of flexibility of an enrichment object and the number and types of actions elicited by different objects. Specific initial questions of the study include: 1) How many different behaviours can be performed with an object; 2) how many different behaviours can be performed in a sequence; and 3) can belugas incorporate other types of play (e.g., social play) in a sequence with object play, if so, what kind of play, and how much? Data collected from 22 belugas (*Delphinapterus leucas*), or white whales, in an aquarium in the USA, within a 15-year longitudinal behavioural study, were analysed for interactions with various enrichment devices. Objects that promote diversity in behavior, especially actions that are novel, can provide cognitive and physical stimulation that is critical for providing the best state of wellbeing for animals in human care. Across 14 years of data, over 6200 individual events and 699 sequences showed that belugas perform significantly more object play and different object play behaviours with 2 objects than 1 object, and perform significantly more behaviours with 2 objects than 1 object. It was found that belugas do sometimes incorporate other types of play (e.g., social play) in a sequence with object play. Differences in the number of behaviours in a sequence and duration of sequence were found across 3 different age groups, including some sex differences. In this study, no difference was found in the diversity of behaviours with regard to the flexibility of an object.

The development of object manipulations in wild and zoo-housed orangutans

Isabelle Laumer^{1*}, Shubhangi Kansal², Anais van Cauwenberghe¹, Marlen Fröhlich³, Tatang Mitra Setia⁴, Caroline Schuppli¹

1 Max Planck Institute of Animal Behaviour, Konstanz, Germany; 2 University of Leipzig, Leipzig, Germany; 3 Universität Tübingen, Tübingen, Germany; 4 Department of Biologi, Graduate Program, Universitas Nasional, Jakarta, Indonesia

In human infants, object manipulations are one of the main mechanisms to learn about objects and the physical principles connected to them. We looked at the development of exploratory object play and manipulations in captive and wild Sumatran orangutans (*Pongo abelli*). Our aim was to investigate similarities in object manipulations in orangutans and humans, as well as to look at the developmental plasticity of this behaviour. Our data included 3200 exploration events collected on 12 wild immatures between the ages of 0.5 and 14 years at Suaq Balimbing in Indonesia, and 2500 events collected on 12 immatures of the same age from various zoos. We found similar age trajectories of object manipulation rates at both sites, which closely resemble the ones found in humans. Exploration rates in wild orangutans increased steeply during the early dependency period, peaked at the age of around 2 years and subsequently decreased by the age of weaning. Zoo-housed immatures, however, showed the highest exploration rates later at the age of around 3 and continued to show higher exploration rates when getting older than their wild counterparts. Furthermore, exploration events in wild orangutans, just as in humans, became more variable with increasing age. Our results suggest that just as human infants, immature orangutans use object manipulations to learn about objects and that the conditions under which individuals grow up significantly affect object manipulations. Furthermore, whereas object manipulations in zoo orangutans proved not to be representative of the species' natural behaviour, they show the species' exploration potential.

The interconnection of hierarchy, affiliation, and play shapes social dynamics in cattle

Luca Pedruzzi^{1,*}, Samuel Bagnato^{1,*}, Jacopo Goracci², Elisabetta Palagi¹

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* = equal contribution

The modalities group living animals play with each other and show affiliation can be affected by the dominance relationships arising between them. Here, we carried out a naturalistic study to investigate the possible interconnection between the playful domain and the affiliative and agonistic one in a group of Maremmana beef cattle living in an extensive breeding system. The group showed a clear linear hierarchy, with the dominant animals being the oldest and receiving affiliative behaviours with the highest frequency. Social play mainly consisted of play fighting and the dominant subjects of the group were also those playing with the highest frequency. The longest sessions were those slightly unbalanced, where the patterns were unreciprocated and one subject tended to prevail over the other. However, playful modality was independent from the playmates' relative rank position. This indicates that play fighting here has a slightly competitive rather than cooperative nature and that it may be used as physical training to develop competitive skills in all groupmates, independently from their rank. The longest play fighting sessions lasted longer when playmates exchanged affiliative behaviours while playing, suggesting that such behaviours are used to convey benign intents and downgrade competition during play fighting. In conclusion, under naturalistic conditions, agonistic, affiliative, and playful behaviours are strongly interconnected in shaping social dynamics and our study further suggests how extensive farming conditions are ideal to study the behavioural strategies domestic ungulates enact to form cohesive social groups.

Social play buffers the effects of social instability in young rhesus monkeys

Amanda M. Dettmer*, Wooddell LJ#, Kaburu SSK^

*Yale Child Study Center, Yale School of Medicine, New Haven, Connecticut, USA #Neuroscience and Behavior, California National Primate Research Center, Davis, California, USA ^Department of Biomedical Science and Physiology, Faculty of Science & Engineering, University of Wolverhampton, WV1 1LY, UK

Social play is a necessary component of healthy development in young primates. While several functions of play have been studied, its role in buffering responses to stressful events is poorly understood. Social instability (SI) is a stressful event that occurs when there is contested competition over social status. Many animal studies have shown that SI increases animals' physiological stress and decreases individuals' social status certainty. Adults take proactive coping mechanisms to buffer the effects of SI, like increasing affiliative behaviors or focusing on preferred social partners. However, very little is known about how juveniles cope with SI, although they too experience it. We hypothesized that social play may be related to chronic stress profiles in a group of rhesus macaque yearlings (*Macaca mulatta*, N=18) after group relocation, which resulted in SI. We used social network analysis to measure individuals' dominance certainty and their position in affiliative networks, and analyzed hair cortisol concentrations (HCCs) as a measure of chronic stress across the study. Dominance certainty decreased during SI, and monkeys increased their rates of social grooming while decreasing rates of social play during SI, reflecting potential coping mechanisms. While social play did not predict HCCs during SI, monkeys that were more connected in the social play network exhibited smaller increases in HCCs during SI, revealing a potential buffering effect of social play. Our results indicate a novel role for social play in young primates, and underscore the need for further research on the potential roles for social play during ontogeny.

Play fighting, the cortex and the development of the social brain

Sergio M. Pellis

Dept of Neuroscience, University of Lethbridge, Lethbridge, Canada

Rough-and-tumble play or play fighting has been intensively studied in rats and some other rodents, revealing much about the neural mechanisms involved. Denying juveniles the opportunity to engage in play fighting with peers, leads to a range of cognitive and emotional deficits that diminish social skills. Many of these deficits are associated with altered development of areas of the prefrontal cortex (PFC). While play fighting involves competition, which for rats is to access and nuzzle the nape of the neck, it is moderated by cooperation. In this way, such play involves reciprocal role reversals. By selectively rearing juveniles with peers that allow for frequent play, but reduced reciprocity, the development of the PFC is altered and they have impoverished social skills as adults. This suggests that the socio-cognitive skills recruited to negotiate playful interactions so as to ensure that they remain reciprocal provides the experiences that, in turn, refine those skills and the PFC circuits upon which they depend.

Neural mechanisms of social play behaviour

E.J.M. Achterberg¹, A.M. Baars¹, J.C.J.M. Hendriks¹, J.G. van 't Klooster¹, M.C.M. Luijendijk², L.J.M.J. Vanderschuren¹

1. Department of Population Health Sciences, Unit Animals in Science and Society, Division of Behavioural Neuroscience, Faculty of Veterinary Medicine, Utrecht University, The Netherlands. 2. Department of Translational Neuroscience, University Medical Centre Utrecht, The Netherlands.

Social play behaviour is rewarding and known to facilitate the development of brain and behaviour. Disruptions of social play behaviour in rats are associated with deficits in social behaviour and cognition but also altered development of the prefrontal cortex (PFC). Several neurotransmitters, including opioids, dopamine (DA) and noradrenaline (NA) have been implicated in social play, but the precise neural circuitry through which these neurotransmitters modulate social play behavior is incompletely understood. Previous work showed the nucleus accumbens to be an important site of action for enhancing social play by mu-opioid receptor activation. Here we show that also regions in the PFC are involved in the modulation of social play expression by opioids. Earlier work from our lab demonstrated a differential involvement of DA and NA in two distinct aspects of social play behavior, i.e. the expression of play and the motivation to play. The motivation for social play was found to be modulated by DA, whereas play itself was mediated by NA. With the use of designer receptors exclusively activated by designer drugs (DREADD) to specifically target the DA and NA innervation of the limbic forebrain in adolescent rats, we aimed to identify the catecholaminergic mechanisms that modulate social play behavior in rats. The amount of social play was unaffected whereas operant responding for social play was markedly enhanced by activating VTA-DA neurons in adolescent rats. The present data adds to our increasing understanding about the neural mechanisms of social play behaviour.

Healthy play better coping: a perspective on play in health and disease

Heidi Lesscher

Department of Animals in Science and Society, Division of Behavioural Neuroscience, Faculty of Veterinary Medicine, Utrecht University, The Netherlands.

Play is considered essential for the healthy social, emotional and cognitive development of individuals. Rats that were isolated during the stage of their lives in which they play most, essentially depriving them of social play behaviour, develop reduced and dysfunctional social behaviour, enhanced anxiety-like behaviour and impaired cognitive control. In humans, reduced risky/outdoor play has been associated with lower fitness, self-esteem, pro-social behaviour and academic achievements. The consortium Healthy Play Better Coping aims to understand the impact of play (restrictions) on the development of brain and behaviour, using an interdisciplinary approach. Our studies on social play in rats have shown for example that individual variations in social play in rats predict the resilience to loss of control over substance. What about children? A particular group that may be hampered in their play behaviour are children with a chronic or life-threatening disease. Being hospitalized, experiencing pain, fatigue or social isolation and the 'other-than-normal' treatment of diseased children may cause physical and social isolation and likely compromise participation in social play. Data from the ongoing PROactive cohort study, revealed the impact of childhood chronic disease on young adults, achieving significantly fewer developmental milestones, or at older age than their peers, with significant consequences for their wellbeing and functioning later in life. To understand the potential role of play in the development of these children, we have developed a Lego-based instrument to objectively measure play in children. In addition, we have developed an applied game that is aimed at reducing loneliness in children with a chronic disease. Another important factor that hampers play is the gradual reduction in outdoor space for children, combined with the gradual increase in risk aversiveness in our society. Therefore, in collaboration with geoscientists, we studied the factors that determine risky play behavior, from the perspective of both the children and the parents. Moreover, we have developed a model to study the impact of risky play in rats, and found that opportunities to engage in risky play results in long-lasting changes in cognitive control and contributes to the development of inhibition in the prefrontal cortex. Taken together, these studies highlight the importance and potential of play for the healthy development of young mammals.

Play, imagination, and socio-cognitive development

Tracy R. Gleason

Wellesley College, Department of Psychology

Although research on the influence of play—pretend play specifically—on child outcomes has recently come under scrutiny, when taken as a whole, the plethora of studies in this area suggests a role for pretend play in children’s socio-cognitive development. In particular, the use of imagination in play offers opportunities for children to construct scenarios and situations that include elements that they themselves wish to explore. Just as play with objects helps children learn and understand the physical world, imaginative play offers a forum for exploration of aspects of the social, emotional, and mental worlds that children seek to understand. One avenue children use for investigating abstractions such as relationships and their associated emotions is the creation of imaginary companions (ICs). By thinking about the behaviors, cognitions, and emotions of an IC, and discussing them with real others, children explore the content of social relationships as well as reveal their nascent thinking about the nature of human social interaction. Play with ICs also relates to the development of sophisticated relationship concepts, such as the distinctions between caregivers and friends. Moreover, such play might facilitate the normative use of fantasy in managing and fostering social relationships later in life.

Adult play and the evolution of tolerant and cooperative societies

Elisabetta Palagi

Department of Biology, Unit of Ethology, University of Pisa, Via Alessandro Volta 6, 56126, Pisa, Italy

Due to its dual nature involving competition and cooperation, social play is a powerful tool to acquire information on others at any stages of life. Such information can be used to obtain social power, improve reproductive success and increase survival probability. In this view, the emergence and consistency of social play during the entire life span appear particularly fruitful in those species characterized by enlarged social spheres, a large variety of affiliative behaviors and fluidity in social bonds. In this talk, I focus on adult social play as a trait favored by natural selection especially when species live in groups characterized by high level of social tolerance and cooperation. Due to their variability in social tolerance and cooperative tendency, primates and social carnivores are excellent models to test such assumption. I will discuss the potential correlation between social tolerant styles and the occurrence of adult play. Finally, I will investigate the relationship between cooperation and adult play by providing data on the role of this activity in synchronizing groups and favoring collective decision making.

Object play and tool use: an elusive connection

Jean-Baptiste Leca

Department of Psychology, University of Lethbridge, Lethbridge, Canada

Behavioral scientists, theorists, educators, and therapists have often argued that the expression of object play behavior promotes the acquisition of knowledge and skills applied to the physical domain, such as tool use. In Psychology, the “Affordance Learning” theory holds that the combination of visual and tactile perception of an object’s physical and action-relevant properties, together with pressure-free opportunities for exploratory activity, such as those enabled by object play, contribute to determining this object’s potential use for the goal-oriented actions required for tool use. However, longitudinal, experimental, and phylogenetic studies do not currently provide a consensual answer on whether – and if so, to what extent – the expression of object play behavior actually facilitates the development and evolution of tool use. I will review major research findings on the structural and functional links between different forms of seemingly playful and potentially beneficial object manipulation in various animal taxa. I will argue that, under relaxed selective pressures (e.g., food provisioning) and if proximately enhanced (e.g., pleasurable feedback, cultural processes), motor play practice may serve the function of maintaining in some populations a set of behavioral variants that could be exapted to new uses. Indeed, like other traits lacking specialized design for a particular function, play has versatility and thus evolvability.

Play, coping and welfare in animals

M. Hausberger^{1,2,3}, A. Lemasson^{1,4}, S. Henry¹

1Université de Rennes, Université de Caen-Normandie, UMR 6552, Laboratoire d’Ethologie animale et humaine, France; 2 Université de Paris Cité, UMR 8002, Integrative Center for Neuroscience and Cognition, France; 3 Honorary Professor, Rhodes University, Department of Zoology and Entomology, South Africa; 4 Institut Universitaire de France, Paris

There is no consensus regarding the functions of play. As play behavior is a characteristic of young stages of development in most species, it has been suggested that the higher prevalence of adult play observed in domestic animals, as compared to their wild counterparts, could be the result of their “neotenic retardation.” Functional hypotheses have dealt with long term benefits, such as “rehearsal,” “motor training” for future adult competencies or “training for the unexpected.” However, there is little consistent experimental evidence favoring a particular hypothesis, especially at the adult stage. Because play is associated with positive emotions, it has been largely assumed that it could constitute an indicator of good welfare. However, regular observations of adult play in captive/domestic animals living in suboptimal conditions lead to question this assumption, especially as welfare is a chronic state whereas emotions are transient states. We will here, through examples in targeted species (horses, cercopithecids), test the functional significance of adult play as a potential reliable indicator of good welfare, a by-product of domestication and/or a tool for social cohesion. We will see that the significance of play, especially in adults, may be ambiguous, acting as a potential coping mechanism in adverse conditions, hence as a useful way to evacuate stress, but not as a reliable welfare indicator.

Play as a tool to understand how domestication affected sociality

Giada Cordini

University of Torino, Department of Life Sciences and System Biology

The domestication syndrome is a set of physical and behavioural traits that can apply to either self-domestication or domestication processes, which involve similar traits (e.g. increased tolerance) but differ in a key element. Self-domestication favoured intra-species cooperation over competition, as the result of an evolutionary process that has lasted millions of years. Domestication - driven by humans over a much shorter period of time - has possibly maintained - or even enhanced - intra-species competition to promote inter-species cooperation (with domesticated individuals forming a social unit with humans rather than with other conspecifics). Playfulness is a neotenic behavioural feature that is consistently found in self-domesticated and domesticated species, where it is over-expressed and persists in adulthood. Play is a polyfunctional behavioural system that blends cooperative and competitive elements. In the light of the Polyvagal Theory, play can be viewed as a neural exercise as it requires the capacity to swing between a fight/flight competitive response and a cooperative social interaction. For these reasons, play may be a good candidate to understand to what extent self-domestication or domestication processes have moulded the valence of relationships between conspecifics (cooperation/competition). Here, I draw from an extensive dataset and analyses on measurable play features (e.g. frequency, signals, and structural indexes of repetition, asymmetry, variability and evenness) and I compare social play in domesticated (Caninae, Felinae, Suinae) and (allegedly) self-domesticated (Homininae, Elephantinae) taxa. Results indicate that the way individuals play reflects whether the processes of self-domestication/domestication were more or less intrusive in influencing the levels of intra-species cooperation or competition. A better understanding of the domestication syndrome can have a broader anthropological interest, as humans are considered a playful, self-domesticated species. Hence, play can be used as a tool to shed light on the socio-cognitive convergences between humans and other self-domesticated species (at the ultimate level) and domesticated species (at a more proximate level).

Play in invertebrates: are cephalopods a perfect animal to study?

Michael J. Kuba

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Invertebrates have been perfect models to uncover basic principles in biology. From plathelminths to annelids to arthropods there are several important/model organisms for studying brain and behaviors. There is one group of mollusks which could be essential for uncovering the evolution of brains, sensory perception, and behavior – Cephalopods. Based on the “Bauplan” of cephalopods, one can focus on exploration, learning and play behavior to establish a key to discover general principles in cognitive behaviors. An interdisciplinary approach to the study of sensory perception and motor control in the soft bodied, flexible muscular hydrostat bodies gives us new insights what the invertebrate cephalopod does with the huge central (CNS) and peripheral nervous system (PNS). Additionally, as some cephalopods are social animals more efforts need to be made to study the development and complexity of their social behaviours. So why study cephalopods? Study of behavior seeks to reveal how underlying brain organization and physiology permit an animal to adapt to its environment. In this regard, there are several areas where a cephalopod study can benefit a wider scientific community. They process the sensory world in a way that is very different from that of the vertebrate and arthropod species with whom they share an environment. This makes them an important subject for comparative studies in psychophysiology, perception, eco-morphology and learning. Recently, researchers have begun to re-examine how diverse organisms solve similar tasks in similar or different ways. These unique animals show many advanced behaviors, although their nervous systems are organized along a relatively simple molluscan scheme. Yet, their brains are remarkably complex. Moreover, various cephalopods have evolved very unique morphological characteristics (multiple, flexible arms, elaborate camouflage, etc) which lead to unique strategies for coping with the marine environment. Indeed, all work on cephalopods in general and octopuses in particular must consider the multi-arm manipulation capabilities of these animals. Recently researchers developed experimental mazes which allow to probe the role of the octopus brain in controlling octopus arms (Gutnick et. al., 2011, 2020, 2022). They used a specific mazes to demonstrate and study if the octopus can direct its arm at a visually identified target, thus dispelling the old myth that the behavior of the arm is entirely independent of the CNS. Still, it is important to recognize that 60% of the octopus’s nervous system and thousands of sensory cells are located on the arms. An international group of experts, we have developed a novel technique to overcome the impediments to studying the electrical brain activities that underlie freely moving, awake behaviors in octopuses (Gutnick et al 2023) and cuttlefish. Using a combination of data loggers and high definition video recording, we are able, for the first time, to combine electrophysiology and learned behavior in “smart” marine invertebrates. At last, we are in a position to directly confront the central question of my research: “how does neural circuitry lead to complex behavior, and are the principles of neural organization the same for invertebrates as for vertebrate species?” In 2001, when I embarked on my PhD research in the Konrad Lorenz Institute, I was interested in exploring the behavioral repertoire of “the smartest” of the invertebrates – the octopus. Supervised by Jennifer Mather, I studied a variety of vertebrate-like behaviors, such as exploration. I was able to characterize a specific pattern of behavior, generally considered to be a feature of the brain of higher vertebrates, that can only be described as “play” (Kuba et al. 2003, 2006, 2014). Now about 20 years later we know more about cephalopods than we ever did before and using multidisciplinary approaches we will be able to investigate all three different types of play behavior in an invertebrate.

Social network and social play

Masaki Shimada

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A hypothesis that participants of social play can strengthen their social ties was tested by analyzing the long-termed field data of wild Japanese macaques (*Macaca fuscata*) and chimpanzees (*Pan troglodytes*) using techniques of social network analysis (SNA). The pairs of juvenile Japanese macaques that played socially frequently in the previous season tended to stay close in non-playful contexts in the next season. Even though both social grooming and social grooming may function to strengthen the affiliative relationship between participants, for juvenile macaques, social play, rather than grooming, functions as an important social mechanism to strengthen affiliative relationships. In addition, the frequency of participation in social play positively contributed to the development of affiliative social relationships within the chimpanzee group during the infant or juvenile period, but did not have the same effect during the adolescent and adult period. The social play network may allow individuals to develop the social techniques necessary to acquire a central position in a society and enable them to develop affiliative relationships during the infant or juvenile period. In the talk, I discuss the insight of the importance of play behavior for the human evolution.

Exploring human laughter and its contagion using neuroscientific techniques

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Classic theories of laughter suggested that laughter can be explained as the outcome of a feeling of dominance (Superiority Theory), the appreciation of something that violates our expectations (Incongruity Theory), or the release of nervous energy (Relief Theory). Capitalizing on recent electrical stimulation studies in humans, I will bring grist to the mill of an alternative, naturalistic, hypothesis, suggesting that laughter is, first and foremost, a social behavior contributing to the reinforcement of ongoing interactions and affiliation. Besides providing neuroscientific evidence in support of this hypothesis, I will sketch a mechanistic explanation of the affiliative nature of laughter and the role of its contagion in boosting social bonding.

Social skills in adult male rats are reflected in prefrontal cortex neuroanatomy and juvenile play experiences

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Juvenile social play has been associated with the development of socio-cognitive skills and the neural mechanisms that control those skills. Experimental manipulation of play experience, such as social isolation or altered-peer associations, during the juvenile period in rats has been shown to lead to adults, especially males, that have difficulty in inhibiting escalating to aggression when interacting with strangers. Along with these behavioral deficits, these rats have altered cytoarchitecture of pyramidal neurons of the medial prefrontal cortex (mPFC). However, it is not known whether natural variation in social skills amongst adults reflects variation in the social play animals experience as juveniles. In the present study, the social skills of 54 adult male rats, reared in groups of six, was assessed. When paired with an unfamiliar male in a neutral arena, 11 of the 54 rats escalated to aggression, suggesting poor socio-cognitive skills. Compared to matched group mates two predictions were tested. (1) The mPFC pyramidal neurons of the rats with poor social skills should have less dendritic pruning of the mPFC neurons than the rats that did not escalate to aggression. (2) The play experience of the rats with poor socio-cognitive skills should have been less or atypical play as juveniles. Using virtual microscopy to digitally reconstruct neuron morphology and highly refined measures of play (e.g., assessing asymmetry in the play of pairs of rats), this study will test if natural variation in juvenile play experience alters the development of behavior and the brain.

Are you playing or fighting? Just look at the faces in wolves

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Play fighting often involves patterns recruited from real aggression thus making signals essential to modulate the behavioural patterns of the two spheres. This appears particularly evident in social carnivores that show high level of aggressive propensity. Here, we focussed on facial expressions to understand if they are specific of the playful and the aggressive domains in two groups of wolves (*Canis lupus lupus*, N=10, BelPark, Spormaggiore, Italy; *C. l. arctos*, N=24, Planete Sauvage, Nantes, France). A priori we defined the two contexts (play vs aggression). By using an integrated approach of different techniques (Dog Facial Acting Coding System, an unsupervised cluster analysis and the Levenshtein Distance), we empirically demonstrated i) the existence of highly context-dependant facial expressions, ii) the presence of two playful facial expressions (full-Relaxed Open Mouth, ROMfull and half ROM, ROMhalf) and iii) the presence of three different facial expressions during the aggressive context (light, medium and heavy THREAT). As a whole, our data indicate a strong consistence of the facial expressions according to the different domains and, at the same time, a huge variability in the performance of facial expressions within each domain. The next step will be trying to unveil the role of such variability in managing the interactions of these social spheres in wolves.

Evidence of playful teasing in great apes

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Playful teasing is a highly ambiguous behavior containing elements of both aggression and play. A phenomenon observed in preverbal infants, it can be considered a form of proto-humor that exhibits cognitive complexity without linguistic sophistication. Because playful teasing requires careful prediction and monitoring of the partner's expectations to avoid negative outcomes, it provides researchers with a rich domain to investigate inferences about others' behavior and mental states. While studies of animal behavior have often viewed teasing as aggressive, we conducted a systematic literature review revealing forms of playful teasing that have been observed in non-human primates and possibly other animals. Great apes, in particular, have been described performing three types of playful teasing seen in preverbal infants: *offer and withdrawal*, *provocative non-compliance*, and *disrupting others' activities*. Inspired by these findings, we developed and applied an extensive behavioral coding system to define and measure playful teasing behavior, using 75 hours of focal follow video of zoo-housed great apes. Chimpanzees, bonobos, gorillas, and orangutans all engaged in interactions that met our definition of playful teasing. These interactions involved "provocative" (attention-getting) behaviors, which were frequently one-sided, and often accompanied by play signals and markers of intentionality. Playful teasing had some similarities across species, including being more often initiated by juveniles than adults. However, the specific behaviors used to tease others varied between individuals and age classes. Together, this evidence of playful teasing in all four great apes suggests that a key cognitive building block of humor was present in our last common ancestor.

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Trends in adult social play reveal a hidden cost of motherhood for chimpanzees

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Though social play is considered essential to the development of many species, including ourselves and other social mammals, this behavior decreases with age and disappears by adulthood in most species. This change is often explained as a shift in trade-offs with the costs of social play outweighing its benefits as animals age. However, benefits like reducing tension and reinforcing bonds also stand to effect adults and, further, adults may represent important competent partners for younger players. Here, we use 10 years of behavioral and ecological data to test the hypothesis that adult participation in social play is constrained among wild chimpanzees (*Pan troglodytes schweinfurthii*) in Kibale National Park, Uganda. We analyzed nearly 4000 social play bouts involving at least one adult player, revealing that adults participated in more social play when fruit availability was high. While this relationship was similar for both adult males and females, adult females played more than males overall, which was surprising given that adult male chimpanzees are generally considered more gregarious than females. A large portion of adult female play comprised bouts between mothers and offspring, which persisted even during times of very low high-quality fruit availability. Together, our results suggest that easing food availability constraints promote social play in adult chimpanzees, arguing against the hypothesis that social play disappears in adulthood simply because it has no value. Further, the persistence of mothers' play presents strong evidence that, like humans but not other primates, social play serves critical functions for mother chimpanzees, especially as play partners for their offspring.

BOOK ABSTRACT: POSTERS

Prenatal stress and individual differences in play behavior in immature Assamese macaques

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Animals express behavioral differences among individuals that persist through time and contexts which are mostly referred to as personality. Individuals also differ in their degree of behavioral variation across environments, i.e., behavioral plasticity. Prenatal exposure to maternal stress has been associated with lasting effects on personality and plasticity. Within a larger project on maternal effects on infant development, we here present preliminary results on the repeatability of play behavior and the effects of prenatal maternal physiological stress (measured as immunoreactive fecal glucocorticoid levels during gestation) on individual differences in play behavior in wild immature Assamese macaques (*Macaca assamensis*) at Phu Khieo Wildlife Sanctuary, Thailand. Three cohorts of infants (N = 57) were followed from birth to one year of age using focal animal sampling of social, object and locomotor play. Data were aggregated in 2-month blocks for each focal animal, which resulted in six data points per immature. Calculating the reaction norm intercept repeatability including age as a fixed variable, we found high repeatability values for proportion time in solitary play ($r > 0.5$) and moderate repeatability values for proportion time in social play ($r > 0.3$). Results of the effects of prenatal physiological stress on play behavior are currently being conducted and will be included in the presentation.

Do free-flying ravens use objects to initiate social interactions?

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Social play has been shown to facilitate the formation and development of social relationships between individuals. Social play may also involve objects. However, not much is known about why and how individuals may use objects in those interactions. Ravens (*Corvus corax*) have been shown to engage in playful caching of objects and thereby learn about the intentions and competitive strategies of others. Here we hypothesize that common ravens engage in object-handling behaviours to attract the attention of, and initiate interactions with, other ravens. Similar to object caching, mediating social interactions via objects may be less costly as compared to interactions involving food or potentially harmful aggressive interactions. To examine our hypothesis, we have conducted behavioural observations and experiments on object-handling in a free-flying non-breeder group since October 2021. Here we focus on the observational part, involving around 120 focal protocols on 20 individually marked ravens. Our preliminary analysis shows a trend that object-handling behaviour elicits approaches from other ravens and, indeed, may lead to social interactions. The potential implications of these results and further steps in the analysis will be discussed.

The seed slide: a test of children's innovative creativity

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Based on their playfulness, human children are typically characterised as imaginative and creative. However, a recent body of work shows that when this creativity needs to be directed to real world problems, young children can struggle to identify innovative solutions. In this study children were presented with a physical puzzle box where they needed to use two tools concurrently to retrieve a reward: a short sturdy stick could hold a gate open and a long flimsy stick could knock the reward off a plinth and into reach. The likelihood of successfully retrieving the reward increased between 4 and 9 years of age (N = 105), with just under half of the oldest children solving the task. In contrast, children were more likely to succeed when the tools could be used sequentially. In discussing this work, we make links to Fraga's tooling theory and theories of innovation and social learning and the implications for our understanding of creativity in different contexts.

Sex-specific involvement of paraventricular nucleus oxytocin neurons in juvenile rat social play behavior

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Social play is a highly motivated and rewarding behavior primarily displayed by juveniles of many mammalian species. While exposure to social play aids in the development of social competence, deficits in social play, as seen in autistic children, may contribute to life-long social impairments. Oxytocin (OXT) is considered a potential therapeutic to improve social interaction in autistic individuals, however, little is known about the role of OXT in social play. Given this, we first determined the involvement of OXT cell populations in the paraventricular nucleus of the hypothalamus (PVN) in the regulation of social play behavior in juvenile rats. Briefly, an excitatory DREADD construct under the control of the OXT promoter was infused into the PVN of 26-day-old rats. Social play testing took place over two days, with clozapine-N-oxide or saline administered 30-minutes prior. A significant sex x drug interaction was found, in which chemogenetic stimulation of PVN-OXT cells decreased social play duration in males and increased social play duration in females. Currently, we are examining the involvement of PVN-OXT projections to the nucleus accumbens (NAc). Using the excitatory DREADD described above in combination with cannulation of the NAc, we can specifically stimulate PVNOXT terminals within the NAc to determine the role of this pathway in juvenile social play. These findings provide first evidence for a sex-specific role of OXT in the regulation of social play behavior, which may have implications for the potential need for sex-specific use of OXT-based therapeutics to improve social play engagement in autistic children.

Studying play in zoos and aquariums

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Zoos and aquariums (hereafter zoos) are excellent places to study many aspects of behaviour but are especially appropriate for studying play. Zoo research on play may provide insights into many aspects of this little understood – indeed often misunderstood – but ubiquitous behaviour. It has long been recognized that play behavior is seen in well-kept, captive wild animals more often than in the wild. Zoos therefore provide an opportunity to gain important knowledge about play's short-term and long-term effects on animals, proximate factors such as the motivation to play, individual differences in playfulness, enclosure and social conditions that facilitate or inhibit play, and the role of play in assessing animal welfare. Play behavior research in zoos can also address comparative and theoretical issues in play research, as well as illustrating the role of critical anthropomorphism and controlled deprivation in studying and interpreting the behavior of captive animals. In addition, we will provide some suggestions on how exhibit-based institutions may use play as a means to both enhance the visitor experience and the lives of captive animals, including the role of play in animal training. This poster will discuss how to recognize play, the types of play, a variety of observations of play in exhibit facilities, some examples of published research on play that took place in zoos, and the potential for play research in zoological settings to help advance both basic and applied understandings of play.

Object combinations and the origins of tool use

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Tool use in nonhuman animals takes a wide variety of forms, from digger wasps using pebbles to pound their nests closed to the complex tool sets of cockatoos and chimpanzees engaged in resource extraction. The desire to separate stereotyped, hard-wired tool use from so-called “intelligent” tool use has led to an oversimplified dichotomy in the tool research literature. We suggest that all forms of tool use fall on a continuum originating from a propensity for object combination. This propensity may be very narrowly specialized or more generalized, and is mediated by a species’ cognitive abilities, which results in varying degrees of tool use flexibility along this continuum. Thus, a species like the New Caledonian crow may have an in-born ability to use basic twig tools for extraction, likely derived from ancestral caching combinatory behaviour, but can also learn to manufacture complex tool types like pandanus stepped tools, and innovate in novel situations.

Without *OPTI-MUM* support: effect of maternal early deprivation on play in chimpanzees (*Pan troglodytes*)

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In chimpanzees (*Pan troglodytes*), the acquisition of species-typical complex behavioral repertoire is facilitated by the maternal presence. The consequences of precocial maternal deprivation include growth and fitness reduction and limited abilities to interact with conspecifics. Social play goes far beyond just having fun, needing sophisticated communicative skills, contributing to adjust social relationships, and thus constituting an interesting field to evaluate social competence. Here, we investigated the effect of the maternal role by comparing play frequency and modality of immature subjects belonging to three groups ($N_{1\text{mother-reared}}=10$; $N_{2\text{mother-reared}}=3$; $N_{\text{hand-reared}}=10$) hosted at Chimfunshi Wildlife Orphanage (Zambia). We found that orphans engaged in play fighting less often than their counterparts. Moreover, they also showed shorter play fighting sessions. Shortening the sessions is probably a tactic to reduce the risk of aggressive escalation as supported by the finding that orphans' sessions rarely turned into in real fighting. Facial mimicry, the capacity to automatically, unconsciously, and rapidly mirroring a facial expression, did not differ across the four groups. This result can indicate that this peculiar facial resonance phenomenon is probably well-rooted in the ontogeny of play behaviour and not sensitive to an early perturbation of the social sphere. It is also possible that this capacity can be easily restored if the infant received a proper stimulation. The support provided by surrogate mothers, together with the prompt integration into a group of peers, could be enough to maintain the ability to mirroring others' play faces.

Do bumblebees play?

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A variety of animals have been found to interact with and manipulate inanimate objects ‘just for fun’, that is, to play. Most clear examples of object play come from mammals and birds. However, whether insects interact with inanimate objects as a form of play has never been systematically examined. Here, we show that rolling of wooden balls by bumble bees, *Bombus terrestris*, fulfils behavioural criteria for animal play and is akin to play in other animals. We found that ball rolling (1) did not contribute to immediate survival strategies, (2) was intrinsically rewarding, (3) differed from functional behaviour in form, (4) was repeated but not stereotyped, and (5) was initiated under stress-free conditions. Through the design of the experiment and with the support of behavioural observations, we excluded the possibilities that ball rolling was driven by exploration for food, clutter clearing or mating. Similar to vertebrate play, we also found age and sex differences for ball rolling by bumble bees: younger bees rolled more balls than older bees and male bees rolled individual balls for longer durations than females. We explicitly show that ball rolling is itself a rewarding activity. After being trained to find freely movable balls in one of two differently coloured chambers, bees showed a preference for the colour of the chamber where they had rolled balls. Our results contribute to the question of sentience in insects and lend further support for the existence of positive affective states in these animals.

Play and tickling responses map to the lateral column of the rat periaqueductal gray

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Although play behaviour is known to be critical for development, its behavioural implications and underlying neuronal circuits have yet to be fully understood. Thus, we aimed to identify neural drivers of play behaviour encoded in the rodent brain. Combining a behavioural and electrophysiological approach, we investigated the involvement of the periaqueductal gray (PAG) in play. To this end we performed extracellular recordings using Neuropixels probes in freely moving rats during tickling and play. We found that the neurons in the PAG respond to tickling and play in a column specific manner, with the lateral column of the PAG being particularly activated during play. In addition, we performed column specific optogenetic inhibition during tickling and social play behaviour. Our results show that the inhibition of the lateral column of the PAG interferes with play behaviour and reduces 50 kHz vocalizations during tickling. Collectively, our results indicate that the lateral columns of the PAG are critically involved in ticklishness and play.

Alleviating anxiety through video game play: the effectiveness of a video game mixing action mechanics and cognitive training compared to a commercialized casual video game on adolescent anxiety - a randomized controlled trial

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Adolescence is a critical period for the onset and the maintenance of anxiety disorders, which raises the importance of designing effective intervention for this population. On the one hand, previous research attempted to alleviate anxiety by using video games as a relaxing distraction tool through their immersive features. On the other hand, literature highlighted a bidirectional link between attentional control and anxiety. This led to design interventions aiming at improving attentional control such as working memory training studies, which showed improvement in attentional control and reduction in anxiety. In the same extent, a growing body of literature has shown that playing action video games leads to better attentional control. However, little to no study have ever used action video games to reduce anxiety by both targeting attentional control and using it as a positive distraction tool. We present a randomized control trial where we will investigate how training with an action-based video game (AVG) we developed can impact mental health among anxious adolescents. This training will be contrasted with training on a commercialized casual video game (CVG) and a no-contact group. Participants will play at home four sessions of thirty minutes per week during six weeks for a total of twelve hours of training. 150 adolescents (12-14 years old) will be randomly assigned to one of the three groups. Participants will be assessed on a set of cognitive tasks and questionnaires before the training (Pre-test), one week after ending the training (Post-test) and four months after Post-test (Follow-up).

Partner preference during social play in immature Assamese macaques

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Social play as a social affiliative interaction in immatures, might occur to maximize social cognition learning. Different hypotheses are discussed regarding its functional significance. The “social bonding hypothesis” states that play can strengthen the bond of play partners by building trust, reducing aggression and promoting cohesion. The “social skills hypothesis” mentions that play can be used as a strategy to further develop social skills by learning rules of fair behaviour and how to solve conflicts. The study aims to test these hypotheses looking into play partner preference of wild immature Assamese macaques (*Macaca assamensis*) from Phu Khieo Wildlife Sanctuary, Thailand. Play behaviour was registered during 40-min. focal sampling in infants (0-11 m) and juveniles (1-4y) using continuous and instantaneous recordings. Data collection took place during three observation periods in which focal subjects were followed between 6 to 18 months. Each individual was only followed during one observation period. We expect individuals to shift their play partner selection based on their potential social requirements according to their age: infants will seek to develop their social skills while juveniles to strengthen their social bonds. We predict that the relative amount of play devoted to kinship versus other group members will be lower for infants than juveniles, to increase their interactions with others and become better integrated in the group. We predict that the relative amount of play devoted to same sex play partners versus different sex partners will be higher for juveniles than infants to aid them in forming advantageous social bonds.

Curiosity in context: costs and limitations of neophilia

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An interest in novel stimuli is the basis for behaviours like play, exploration, and innovation. These novel stimuli usually elicit opposing tendencies, which are governed by independent motivations: avoidance (neophobia) and approach (neophilia). While these concepts are often attributed on a species level (e.g., the island dwelling kea parrot), individual differences of neotic responses (i.e., responses to novelty) highlight the range of neophilic expressions within a species. This study aims to investigate the costs and limitations of neophilia in kea and North Island robins (toutouwai), as well as possible fitness consequences. Subjects will be presented with three separate tests, during which they will get to choose between a) a novel object vs. a familiar object, b) novel object vs. familiar food, and c) novel food vs. familiar food. Different availabilities of resources will be simulated by presenting the tests in two conditions each: ephemeral (subjects only get to interact with the item they first chose) and stable (both items will remain available throughout the trial). Individuals willing to incur a cost are expected to choose the novel objects or the novel food instead of consuming the familiar food. Limitations to neophilia will be determined by the trial on which subjects stop choosing the novel option and are expected to vary between individuals. Subjects' choices are also expected to differ between the conditions (i.e., depending on the availability). Possible fitness consequences of individuals' neotic responses will be investigated by testing wild toutouwai and track the number of their offspring.

Object play in a wild falcon

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Animal play behavior has received increasing attention for its relationship to cognition and as a possible precursor to physical problem-solving abilities across taxa. In bird species, captive studies of play reveal that exploring and combining novel objects, possibly to learn their affordances, correlates with advanced problem-solving abilities. However, we lack systematic investigations into play in the wild, thus limiting our understanding of how play is structured, when it occurs, and who is likely to engage in a natural context. Striated caracara (*Phalcoboenus australis*), walking falcons endemic to the Falkland Islands, show striking behavioral similarities to the cognitively well-studied parrots and corvids, in that they are generalist opportunists, extractive foragers, gregarious, and long-lived with a prolonged adolescence. They readily and repeatedly interact with novelty and use their long legs and large talons to engage with their environment. Here we present preliminary results of the first ever field experiments on play with striated caracara, in which free-ranging caracara voluntarily show prolonged interest, particularly in social contexts, in manipulating arrays of objects that vary either in color, complexity, or internal properties. Our research supports the feasibility of further studies into the contexts of curiosity, exploration, and play in a falcon species, which as the closest related group to the parrots and corvids, would expand our empirically driven knowledge of the socio-ecological contexts that give rise to play behavior, and fill an important gap in our knowledge of avian play by systematically examining different types of play propensities in a wild population.

Involvement of vasopressinergic inputs to the ventral pallidum in the sex-specific regulating of social play behavior in juvenile rats

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The ventral pallidum (VP) regulates adult social behaviors such as pair-bonding and sociosexual motivation but its role in regulating juvenile social behavior is unknown. Social play behavior is one of the earliest peer-directed social behavior that juveniles engage in. Therefore, we first determined whether social play exposure altered VP activation in juvenile rats and found increased VP activation in males, but not females, following social play exposure. We then investigated neuronal inputs to the VP and whether these are also sex-specifically activated in response to social play. We demonstrated that in both sexes, social play exposure increased activation of VP-projecting neurons in the posterior bed nucleus of the stria terminalis (BNSTp) and the posterodorsal medial amygdala (MePD). We next focused on vasopressin (AVP) as a potential mediator of the BNSTp/MePD→VP pathways. We found that the proportion of VP-projecting BNSTp/MePD neurons was similar between sexes. However, males had denser AVP-immunoreactive fibers in the VP than females. This suggests that males have more axonal collaterals per BNSTp/MePD AVP neuron which may provide a basis for sex-specific modulation of VP activity by AVP in response to social play. In support, social play exposure increased activation of AVP 1a receptor (V1aR)-expressing cells in the VP in males only. Moreover, administration of a V1aR antagonist into the VP increased social play duration in males while it in females. Together, these findings provide evidence of the sex-specific involvement of the VP, modulated by BNST/MePD AVP inputs, in the regulation of social play behavior in juvenile rats.

Visual communication during play in cetaceans: the case of bottlenose dolphins

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Play is a social activity requiring sophisticated forms of communication to be enacted. Complex communicative abilities during play have been largely studied in several terrestrial mammal species with marine mammals that remain largely neglected. Within this taxon, the bottlenose dolphin (*Tursiops truncatus*) is an ideal model species for investigating play and its modalities. Bottlenose dolphins are extremely playful at any stage of life, and regardless of their age, they often engage in locomotor/acrobatic, object, and social play. Considering the playful propensity of the species, it is plausible that they evolved different communicative strategies to manage their playful contacts. Here, we focus on visual communication during play. We found that animals produce the Open Mouth display (OM) more during social compared to solitary play and when the sender was in visual contact with the receiver thus suggesting that animals are attentive to the playmate's attentional state. Perceiving an OM rapidly evoked (< 1 second) the same facial expression in the receiver. Play sessions were more reciprocal and long-lasting when they contained at least one event of rapid facial mimicry. Although our results need to be taken with caution, they strongly overlap with those obtained on social primates and carnivores. Although it is difficult to know whether such similarities derive from shared evolutionary pathways (homology) or from evolutionary convergence phenomena (homoplasy), the pervasive presence of OM and rapid facial mimicry in the mammal phylogenetic tree suggests the relevance of visual signals in shaping complex communication.

The practicality of the practice hypothesis: some models

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Although there is a large number of hypotheses regarding the functional benefits of play, few of these have been formally modelled. Perhaps the most popular class of accounts is that play offers some kind of practice for serious behaviour. Despite this, little has been done to show the ecological circumstances where this theory could hold true. In our approach, we model an individual who, over the juvenile and subadult ontogenetic periods has a choice between three behaviours: foraging, playing and rest, where playing improves an individual's ability in antipredatory, foraging (e.g., hunting) or reproductive behaviour. Using stochastic dynamic programming, we show that even when play is more energetically costly and an inferior form of practice than foraging itself, it is still optimal to play under a large range of circumstances. We present three models that differ in what ability is trained during play and foraging: (1) antipredatory ability that leads to a reduced mortality rate whilst foraging; (2) "hunting" ability that leads to an improved foraging success rate; and (3) "social" ability that improves reproductive success when the individual reaches sexual maturity. The three models predict different occurrence of play in ontogeny. This is a first step in showing the ecological feasibility of the practice hypothesis of play and raises further questions about why playful activity is more beneficial than more deliberate directed practice.

Comparative analyses of sex and gender differences in rough and tumble play

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Proposed functions of RTP include physical, cognitive, and social development, all of which may enhance reproductive fitness to varying extents according to sex and age differences. We explored the variation in sex differences across non-human mammals, using systematic review and phylogenetic comparative methods. RTP was predicted to be male biased for species with high levels of male competition. We found that although a male bias in RTP is common, it was not as consistent as predicted, and many studies found a lack of, or inconsistent, sex differences. We also consider cross-cultural variation in gender differences in human RTP, as similar expectations of a male bias are present in the literature. We consider gender variation through the lens of cultural evolution, as humans have much more complex systems of sex and gender compared to non-human mammals, due to factors including self-identification and social roles. We explored cultural factors in relation to gender differences in RTP using ethnographic data and phylogenetic comparative methods, considering mechanisms of social learning, and horizontal and vertical cultural transmission. According to phylogenetically informed regression models, we found that cultural and social factors were limited in their contributions to gender differences in RTP, but explored this further through qualitative analysis of cross-cultural ethnographic material. Overall, we draw attention to the role of RTP in male and female skill acquisition and life history, considering both biological and social contributions to the behaviour.

Exploring the neural bases of flow: modulation of brain responses to task-irrelevant stimuli while playing action-shooter video games

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The present work aims at characterizing, using EEG, the neural bases of the state of flow, defined by Csikszentmihalyi & Larson (2014) as a state of full immersion and optimal performance in the ongoing activity. We use video game play to induce either a high or a low flow state in each participant. As in Castellar et al. (2019), an auditory oddball paradigm requires participants to respond to rare auditory oddball stimuli while playing a video game either in a high or a low flow play state. We predict that the target oddball sounds will elicit slower RTs and reduced P300 amplitudes in the high flow state than in the low flow state, in accordance with the hypothesis that events irrelevant to the video game play receive fewer processing resources in a high flow state than in a low flow state. If confirmed, this approach opens the possibility of using the oddball task as an implicit and online neural marker of flow state in an activity as complex as video game play. Here we demonstrate the feasibility of EEG recording during video game play by showing that ERP markers of the auditory oddball, in particular the N100 and P300 components, can be recovered at the individual subject level. We discuss how data collection has been adapted to limit artifacts (head motion, jaw tension during game play), and how artifact correction has been optimized, in particular with respect to numerous eye movements. Finally, we present our planned design to further characterize the neural bases of flow.

Play ontogeny in young chickens is affected by domestication

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It is known that young chickens display different play behaviours, however, the ontogenetic pattern of these has previously not been described. Furthermore, play is believed to have increased in frequency during domestication, as part of the domestication syndrome. Therefore, the aim of the present study was to investigate the effects of domestication on play ontogeny in young chickens, by comparing its occurrence in ancestral Red Junglefowl (RJF) and domesticated White Leghorn (WL) from a commercial hybrid. Forty chicks from each strain were hatched in the same incubator and then housed in breed-separated groups of 20 each. Groups of four chicks from each breed were moved to enriched play arenas twice per week, from day 8 until day 53 post hatch. The frequency of 14 different play behaviours, categorized as locomotor play, social play and object play were recorded during 30 min. Play behaviour peaked between 30-40 days of age and no qualitative differences were found between the breeds. Total play and object play (the dominant category) were significantly more common in WL (total play: $F_{1, 252} = 106.1$, $P < 0.001$; object play: $F_{1, 252} = 5.9$, $P < 0.05$), whilst locomotor and social play were significantly more frequent in RJF, (locomotor play: $F_{1, 252} = 8.9$, $P < 0.001$; social play: $F_{1, 252} = 25.4$, $P < 0.001$). Hence, domestication has affected the occurrence of play in young chickens, in the sense that domesticated chicks play more and that this higher occurrence of play is mainly directed towards objects.

Affiliation and social play as tactics to cope with anxiety in Maremmana beef cattle

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The capacity to express internal affective states and share them with conspecifics can shape social group dynamics. Recently, allogrooming, social play, and agonistic behaviours have been demonstrated to have a role in assessing and improve farm animals' welfare and management. Periodic health checks are fundamental in breeding systems, but they can induce high stress when the animals are not used to human handling as it occurs in semi-extensive breeding systems. Here we tested if the routinary check of health status and performance can distress the animal and affect the expression of social behaviours of Maremmana cattle farmed in a semi-extensively condition (n=39, Tenuta di Paganico, Grosseto). We found that, compared to days far from the health check (Control), the time individuals spent socially playing and affiliating with each other drastically reduced the day after human handling (Post1), then spurt at the highest level in the following day (Post2). This rebound effect might allow the animals to compensate the lack of social interactions in the previous day and thus to restore the social homeostasis. On the contrary, aggression did not vary across the three phases. These findings suggest that behaviours such as social play and allogrooming might be used as effective coping strategies to mitigate anxiety evoked by handling procedures. Finally, we highlight how the study of social interactions can be informative about animals' internal states and how important it is to include such behaviours in a more comprehensive concept of animal welfare.

Insights into the neurobiology of play through the study of the inbred f344 rat

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Rats are an incredibly social and playful species. Play in the rat is a highly motivated behavior and critical for proper social, emotional, and cognitive development so it came as quite a surprise when my lab stumbled on an inbred strain of rat (the F344 strain) that did not play like other rats. A playful phenotype reflects a dynamic interplay between genetic framework and experiences that operate on hard-wired brain systems and this presentation provides a snapshot of how my lab has recently used the F344 rat to better understand the neurobiological underpinnings of play in the rat. We found that F344 rats are relatively insensitive to the pre-weaning effects of maternal care on both behavior and on hypothalamic oxytocin neurons. On the other hand, housing F344 rats with more playful rats after weaning increases the likelihood of F344 rats responding to playful nape contacts with a response that can prolong a play bout while not affecting play solicitation. These data suggest that early social experiences have strain-dependent effects that are sensitive to the type of experience, when in development they occur and what component of play is assessed. We have also recently found that F344 rats are particularly sensitive to the play-enhancing effect of alpha-2 noradrenergic antagonists suggesting that enhanced noradrenergic tone may contribute to the lower levels of play in this strain. Taken together, we suggest that the F344 rat, when compared to more playful strains, may be particularly useful for furthering our understanding of mammalian playfulness.

Susceptibility and bio-behavioral reactions to cognitive illusions in kea (*Nestor notabilis*) and Goffin's cockatoos (*Cacatua goffiniana*)

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Cognitive illusions—tricks that violate one's expectations of the physical world—offer a fascinating lens into animal behavior and cognition. Kea (*Nestor notabilis*) and Goffin's cockatoos (*Cacatua goffiniana*) are optimal animal models to examine susceptibility to cognitive illusions due to their extensive problem-solving and physical cognition skills, as well as playful and exploratory tendencies. It is their marked differences, however, namely the presence/absence of a movable crest and neotoc styles, that offer a fascinating perspective into how specific behavioral responses have evolved to manifest overtly or covertly. This study thus aims to perform a bait-and-switch cognitive illusion (i.e. magic trick) of food items varying in desirability to examine not only illusion susceptibility, but also potential species differences in overt (e.g., crest-raising; feather-fluffing) and covert (e.g., surface temperature change produced by arousal) bodily responses. Following the trick, subjects will also experience an information-seeking phase with the option to choose between the "magic" apparatus and a similar apparatus affiliated with food, the choice of the former indicating the prioritization of surprising information. We predict both species to exhibit prolonged investigation of where the demonstrated food items were expected to appear following a surreptitious swap, as well as covert surface temperature changes in response to the trick and in the information-seeking phase. We will further explore overt surprise behaviors and potential differences between species. Implications for this research include novel perspectives into species differences in overt versus covert behaviors in response to violated expectations, as well as expressions of information-seeking in non-human species.

Play with words and stories to create the life of the mind

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Children learn their native language without formal lessons or teachers. This amazing power of acquisition is still available to adult learners. In fact, how you learn words and stories creates an interior life, the life of the mind that informs and directs the way you live your life. The study of language acquisition involves a complex examination of the components of language, such as phonology, semantics, syntax, and pragmatics, and includes applying skills of morphology and prosody. Children use language creatively and systematically to analyze these component pieces. Analysis of our own adult language production affects the cultivation of the life of the mind. The language use of caregivers, family, siblings, and friends highlights the interdependency of all in the social, linguistic environment in early language acquisition. The child sorts all this out, using powers that neuro linguist Patricia Kuhl, University of Washington, describes as the “linguistic genius of babies.” The child takes statistical measures of language use, accounting for all variables and factors, and comes up, creates on her own, a way of speaking that works, using language to do things. Judith Wells Lindfors, University of Texas, aptly states:

Virtually every child, without special training, exposed to surface structures of language in many interaction contexts, builds for himself – in a short period of time and at an early stage in his cognitive development – a deep-level, abstract, and highly complex system of linguistic structure and use. (1987, p. 90)

This is the stuff of genius, and this power to play with words and stories continues to create the life of the mind, even still.

The sound of play: laughter and other animal signals

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Play in animals is highly ambiguous because the types of behaviors used during play tend to overlap with those used in more serious contexts such as aggression. Many animals have evolved specialized play signals that help reduce uncertainty by marking their behaviors as distinctly playful, thus reducing the risk they will be misinterpreted. Acoustic play signals are especially interesting because human laughter likely evolved from a play-specific, pant-like vocalization in a primate ancestor. We conducted an extensive comparative review of acoustic play signals that revealed a wide diversity of sounds used during play in at least 65 mammal and bird species. Many of the play vocalizations in primates and social carnivores shared features akin to panting (e.g., short, rhythmic, low-frequency, noisy calls linked to breathing), supporting the theory that human laughter and its ancestral play call both originated from a cue of heavy breathing during play. Meanwhile, human laughter appears to have evolved several unique functions for language and social group signaling outside of the original play context. Future research on the psychological and physiological mechanisms that underpin human laughter would benefit from a comparative perspective, and more research across diverse animal taxa will help illuminate the conditions under which signals like laughter are likely to evolve.