Play Is All You Need

WR CJ MMZ

Attention Is All You Need

Ashish Vaswani* Google Brain avaswani@google.com Noam Shazeer* Google Brain noam@google.com Niki Parmar* Google Research nikip@google.com

Jakob Uszkoreit* Google Research usz@google.com

Llion Jones* Google Research llion@google.com Aidan N. Gomez* † University of Toronto aidan@cs.toronto.edu

Łukasz Kaiser* Google Brain lukaszkaiser@google.com

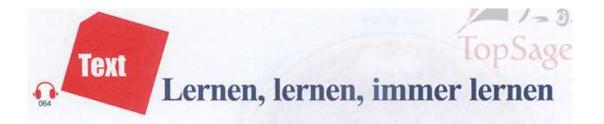
Illia Polosukhin* † illia.polosukhin@gmail.com

"Equal contribution. Listing order is random. Jakob proposed replacing RNNs with self-attention and started the effort to evaluate this idea. Ashish, with Illia, designed and implemented the first Transformer models and has been crucially involved in every aspect of this work. Noam proposed scaled dot-product attention, multi-head attention and the parameter-free position representation and became the other person involved in nearly every detail. Niki designed, implemented, tuned and evaluated countless model variants in our original codebase and tensor2tensor. Llion also experimented with novel model variants, was responsible for our initial codebase, and efficient inference and visualizations. Lukasz and Aidan spent countless long days designing various parts of and implementing tensor2tensor, replacing our earlier codebase, greatly improving results and massively accelerating our research.

Work performed while at Google Brain.

Work performed while at Google Research.

31st Conference on Neural Information Processing Systems (NIPS 2017), Long Beach, CA, USA.



25	Petra:	Und dann? Hast du am Freitag Zeit? Trinken wir
		zusammen Kaffee! TonC
	Wang Hongliang:	Nein, das geht auch nicht. Am Freitag gibt es immer
		Hausaufgaben.
	Petra:	Lernen, lernen, immer lernen. Du hast nie Zeit für das
30		Leben und für die Freunde. Du liest und liest.
		Schläfst du eigentlich noch? Isst du eigentlich noch?
	Wang Hongliang:	Oh, wie spät ist es jetzt? Was? Schon fünf vor elf? Der
		Unterricht beginnt.

Why do easterners and westerners have different attitudes toward learning and life?

Text 2 Wann studierst du eigentlich?

Wang Hongliang: Sag mal, hast du heute Nachmittag Zeit? Ich mache am Donnerstag eine Prüfung und habe noch Fragen. ←

Peter: Das geht leider nicht. Ich spiele Fußball. Vielleicht morgen Nachmittag?←

Wang Hongliang: Morgen? Dienstag? OK, aber erst nach halb fünf. Ich habe bis Viertel nach vier Vorlesung.←

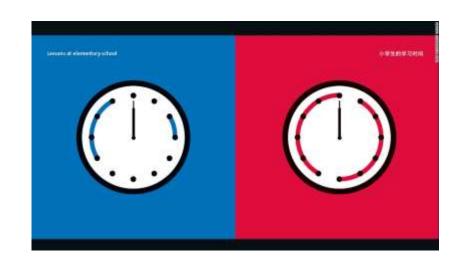
Peter: Erst nach halb fünf? Das geht leider wieder nicht. Julia gibt am Abend eine Party.←

Wang Hongliang: Dann am Mittwoch? Hast du da Zeit?←

Peter: Am Mittwoch Vormittag treibe ich sport. Und am Nachmittag, hm ... ja, da kommt Thomas. Und wir trinken zusammen Kaffee.←

Wang Hongliang: Ja ja, Kaffee trinken, Musik hören, Sport treiben, Fußball spielen. Sag mal, Peter, wann studierst du eigentlich?←

Stereotypes about eastern and western education







What are animals' natural instincts?

The diverse ways of playing in the animal kingdom













PART I: What is play behavior?

—WR

PART II: How do animals benefit from play behavior? —CJ

PART III: Why do adults play less than juveniles? — MMZ

PART I: What is play behavior?

(Definition and forms)

-WR

Can animals play?







An overview of playful behavior among animals

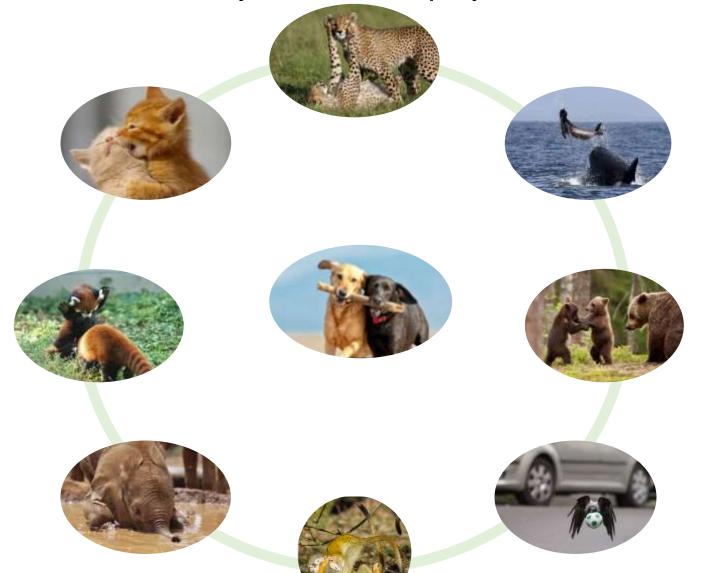
What is playful behavior?

Why do animals play? Is play an instinctive behavior?

Why are rats the best model for studying playful behavior?

- What is playful behavior?
- Why do animals play? Is play an instinctive behavior?
- Why are rats the best model for studying playful behavior?

Playful behavior plays a crucial role in the lives of animals





What is play behavior?

Play is a normative child behavior with defining characteristics. Specific subtypes of play are present from infancy throughout childhood, and include **sensorimotor or exploratory play**, **functional play**, **constructive play**, **pretend play**, and **rough-and-tumble play**. Play can also be categorized on the basis of the social aspects of the interaction, from solitary play to cooperative play with peers.

- (1) did not contribute to immediate survival strategies
- (2) was intrinsically rewarding (not lead to obvious, immediate and adaptive results)
- (3) differed from functional behaviour in form
- (4) was repeated but not stereotyped (exaggeration of movements, repetition of motor acts, and fragmentation or disordering of sequences of motor acts)
- (5) was initiated under stress-free conditions



(Paul martin and T. M. Caro . *Behaviour*. 1985.)
(H. S. Galpayage Dona et al . *Animal Behaviour*. 2022.)

Different classification of playful behavior

- Locomotor play refers to apparently spontaneous movements which carry the individual about its environment; include running, leaping, pirouetting, head shaking, heel kicking, and whirling around.
- □ **Object play** refers to play directed at inanimate objects; can be performed alone or with conspecifics.
- Social play (rough-and-tumble play) refers to play directed at conspecifics; involves vigorous interactions between two or more animals.

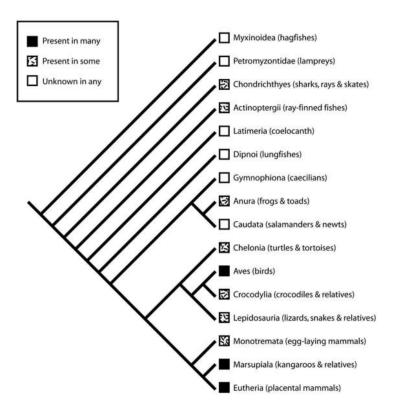






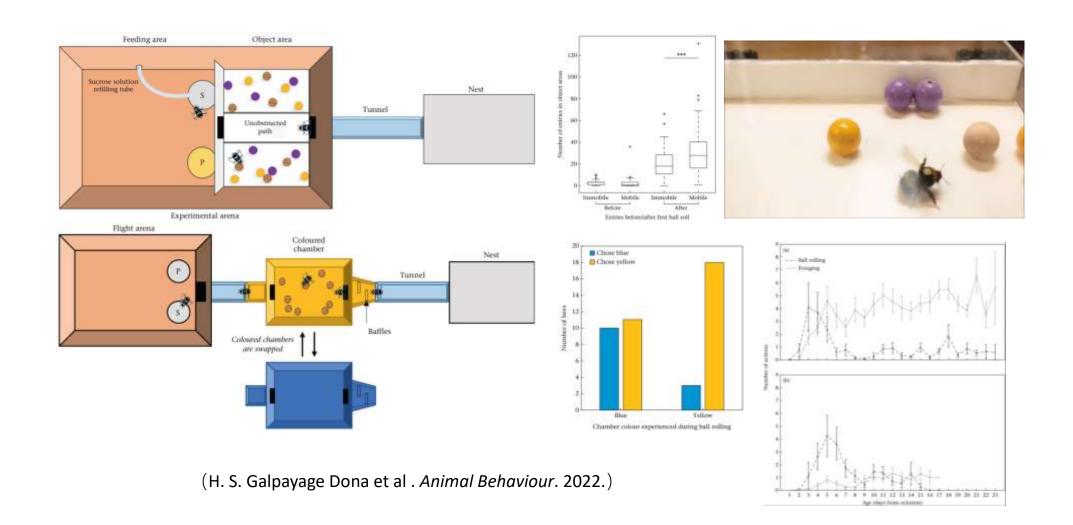
Playful behavior exists in various animals and varies greatly

What animals engage in play?

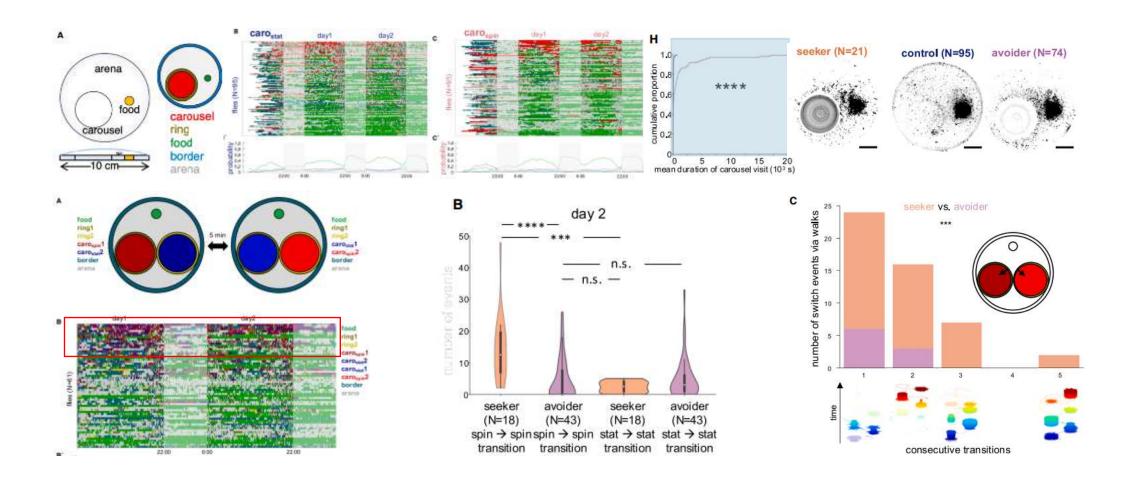


- Play is well-developed in primates, rodents, carnivorans, ungulates, elephants, and cetaceans.
- These playful orders contain numerous species that show great diversity in habitat, home range size, locomotor pattern, life history, body size, social organization, and diet.

Bumble Bees also have the behavior of playing games for fun, and male rolled individual balls for longer durations than females

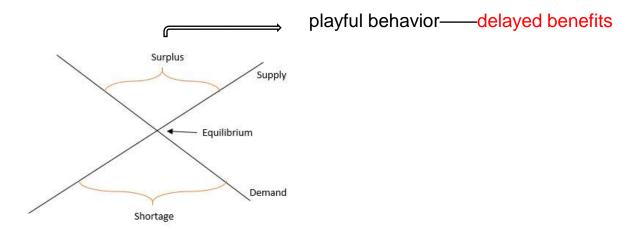


Play-like behavior exhibited by the vinegar fly Drosophila melanogaster



- What is playful behavior?
- Why do animals play? Is play an instinctive behavior?
- Why are rats the best model for studying playful behavior?

Why do animals play and what are the benefits of playing?

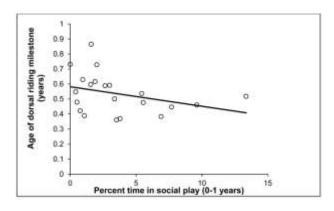


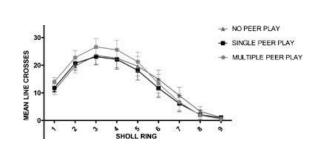
Surplus Resource

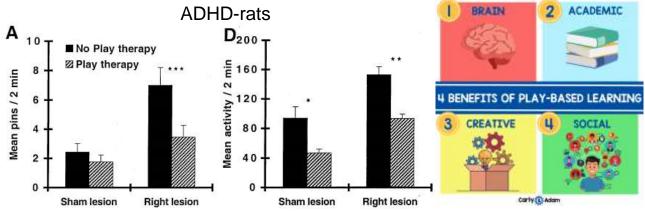
- The origins of play are found in animals with sufficient metabolic resources for sustained activity and complex behavior that needs to be deployed in varying ways. They also need the time and safety to engage in behavior that may not be immediately advantageous, but through which animals learn or perfect behavioral skills, social acumen, physiological or perceptual abilities, and other means that enhance survival compared to non-playing conspecifics.
- In its ancient and more primitive incarnations, playing may not have had any specific advantage over non-playing, but eventually the benefits outweighed the often serious costs of play in energy and risks of injury and predation.

(Gordon M. Burghardt. *Current Biology*. 2015.)

The significance and benefits of playing







Physiological aspect:

Develop motor skills . Train for the unexpected

Cognitive aspect:

Assess one's own physical and cognitive capabilities

Social aspect:

Assess the reliability and capabilities of potential social partners. Learn social norms. Foster social cohesion

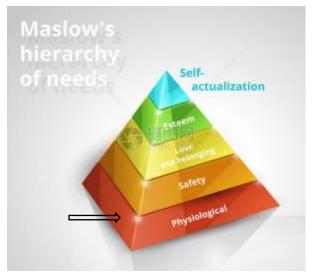
(Matthew R. Heintz et.al . Am J Primatol. 2017.)

(Heather C. Bell et.al . Behavioural Brain Research. 2010.)

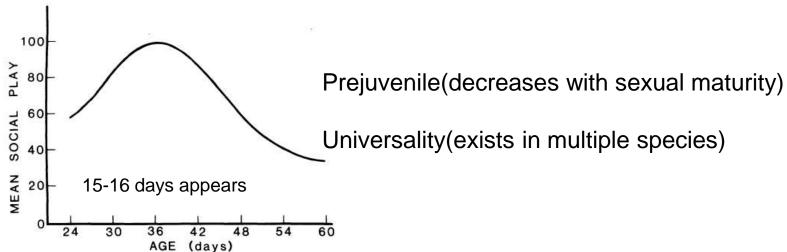
(Jaak Panksepp et.al . *Brain and Cognition* .2003.)

Playing is an instinctive behavior

Psychological aspect:

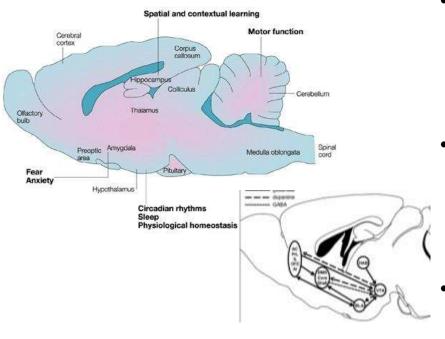


Evolutionary perspective:



- What is playful behavior?
- Why do animals play? Is play an instinctive behavior?
- Why are rats the best model for studying playful behavior?

The rat as an optimal animal model to study the neurobiology of play



- Play in the rat is easily quantified, tightly regulated, and can be modulated by genetic factors and postnatal experiences (rough-and-tumble play);
- Brain areas most likely to be involved in the modulation of play include regions within the prefrontal cortex, dorsal and ventral striatum, some regions of the amygdala, and habenula.
- It has a good foundation of neural modulators and neural circuits

Some types of playful behaviors are produced through learning

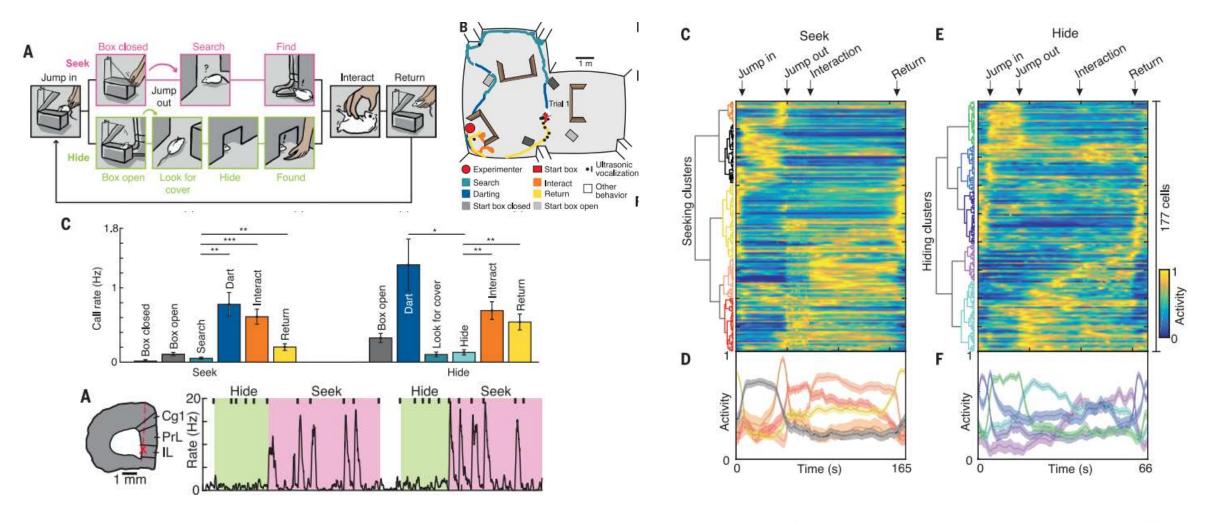
Learning-style play:







Neuronal correlates of hide-and-seek in rat medial prefrontal cortex



(Annika Stefanie Reinhold. et.al . *Science*. 2019.)

Take home message

- ➤ Criteria for play-like behavior require the activity to be (1) of no immediate relevance for survival; (2) voluntary, intentional, and rewarding; (3) non-ethotypical; (4) repeated, yet unstereotyped; and (5) free from stress.
- The role of play is most prevalent in juveniles, with many of the benefits of play being manifested through developmental processes, but play can also serve a function in adulthood.
- ➤ Play is a prevalent animal behavior that appears to be an adaptation to the challenges of a dynamic social and ecological environment.

PART II: How do animals benefit from play behavior?

(Influence and consequences)

—C.

土拨鼠"打架"



In wild populations, natural selection winnows out any behaviour that is more costly than beneficial

How do animals benefit from play behavior?

Evolutionary and Developmental Benefits

Motor Skills Social bonding

Reduction of Aggression Cooperation

Sexual behaviour Life span

Brain development and cognitive flexibility

Neurobiological Mechanisms

Opioids Prefrontal cortex (PFC)

Cannabinoids Striatum

Dopamine Nucleus accumbens (NAc)

Noradrenaline

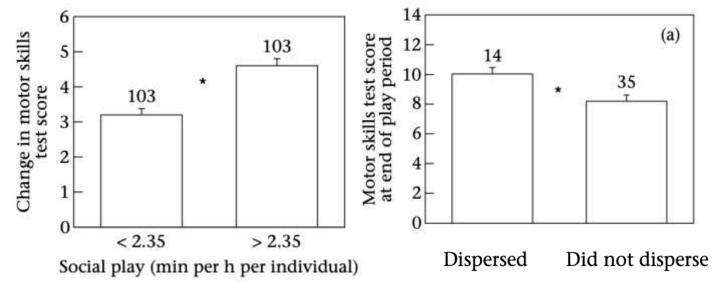
Motor Skills







- (a) hanging(b) perching
- (c) balancing skills

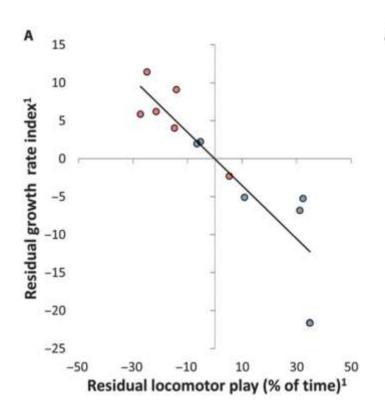


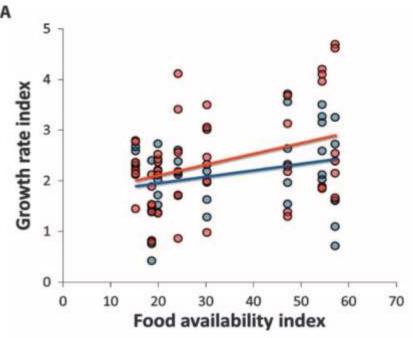
Motor Skills

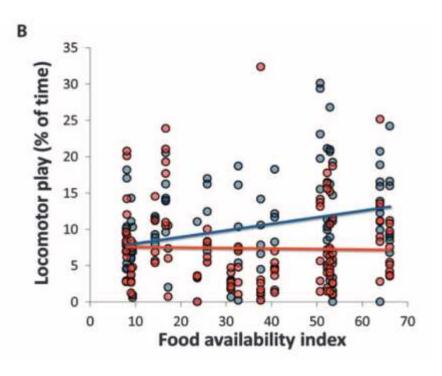


Locomotor play drives motor skill acquisition at the expense of growth: A life history trade-off

<u>Andreas Berghänel</u> ^{1,*}, <u>Oliver Schülke</u> ^{1,†}, <u>Julia Ostner</u> ^{1,2,†}







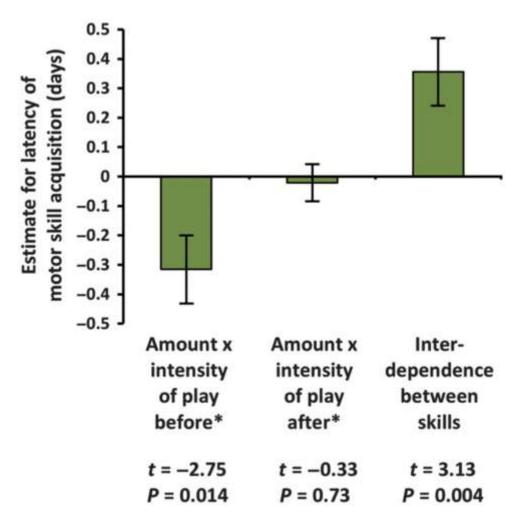
Andreas Berghänel et al. Sci. Adv. 2015

Motor Skills



Locomotor play drives motor skill acquisition at the expense of growth: A life history trade-off

Andreas Berghänel 1,*, Oliver Schülke 1,†, Julia Ostner 1,2,†



Andreas Berghänel et al. Sci. Adv. 2015

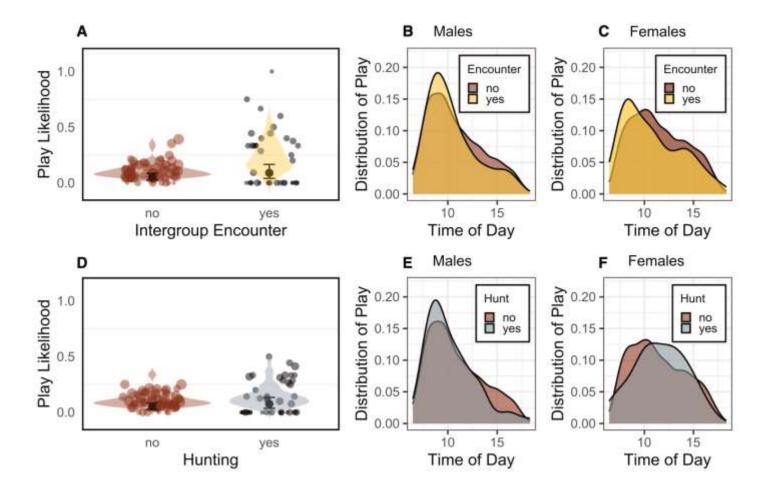
Cooperation

Current Biology

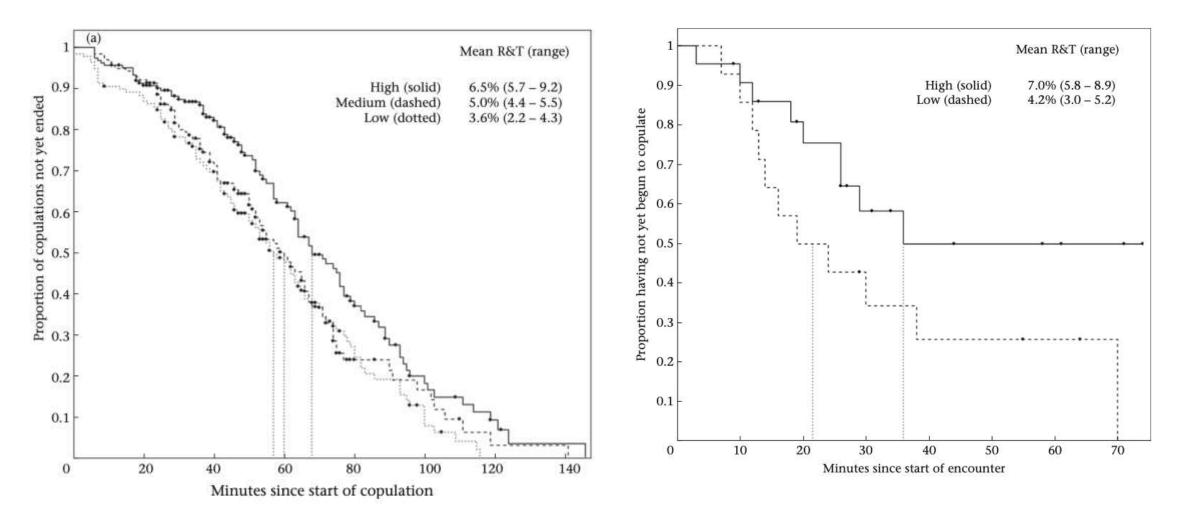
Report

Social play fosters cooperation in wild adult chimpanzees

Liran Samuni, 1,2,5,8,* Alexander Mielke, 3,6 Catherine Crockford, 2,4,7 and Roman M. Wittig2,4,7



Sexual behaviour



Frequent juvenile R&T (rough-and-tumble play) predicted long-lasting copulations in adult males and longer latencies to copulate in adult females.

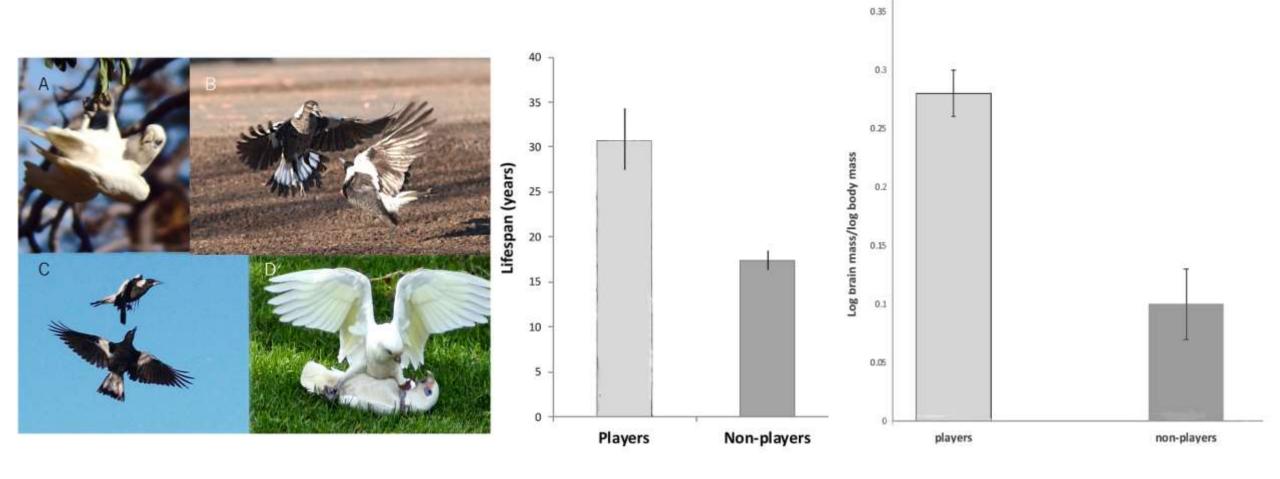
Jamie Ahloy Dallaire et al. Animal Behaviour. 2017

Life span

scientific reports

OPEN Play behaviour, not tool using, relates to brain mass in a sample of birds

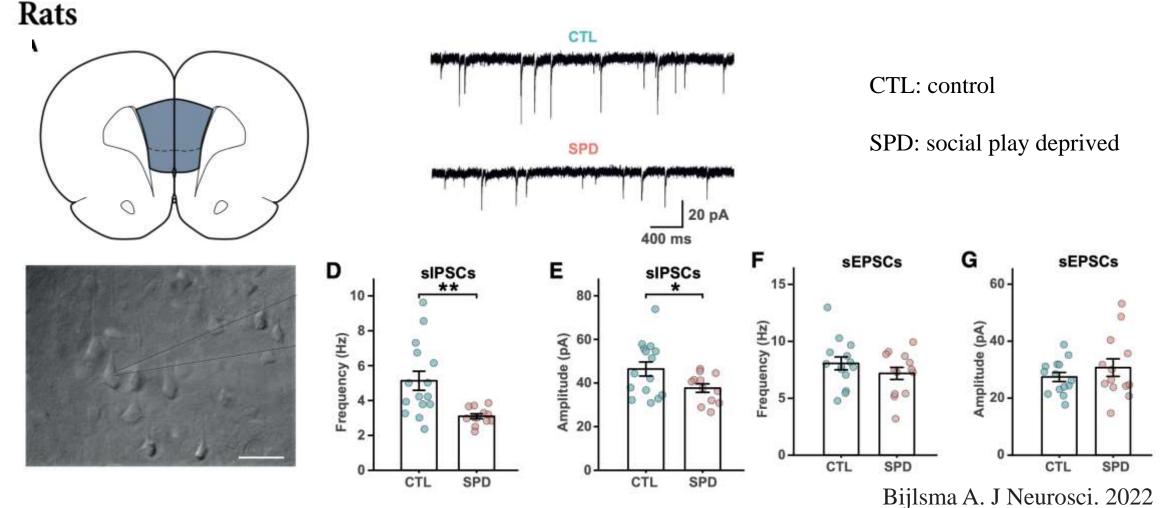
Gisela Kaplan



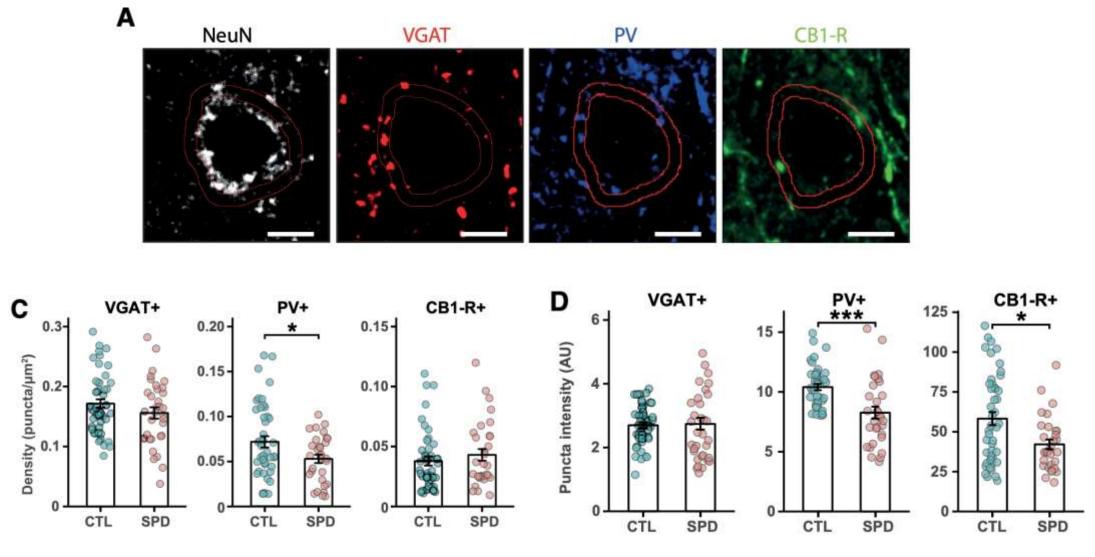
Behavioral/Cognitive



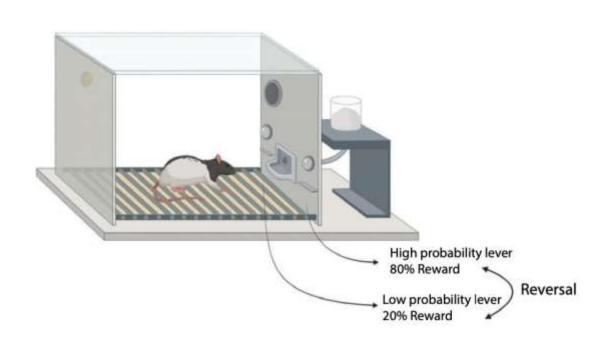
Social Play Behavior Is Critical for the Development of Prefrontal Inhibitory Synapses and Cognitive Flexibility in

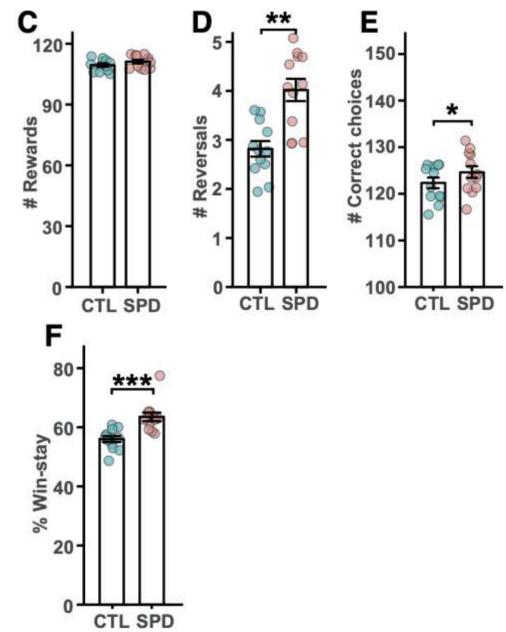


Reduction in perisomatic inhibitory synapses after SPD

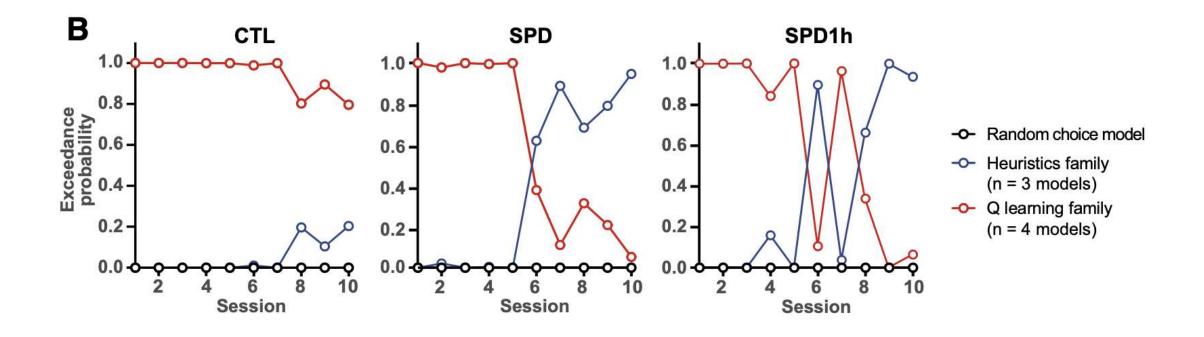


Bijlsma A. J Neurosci. 2022





Bijlsma A. J Neurosci. 2022



Heuristics Family (启发式策略): 依赖简单规则而非复杂计算的决策方式,依赖基底神经节习惯系统类似策略简化见于:精神分裂症。 ADHD,前额叶损伤患者。

Q learning family:整合多试次历史信息,需要前额叶工作记忆和估值系统。

How do animals benefit from play behavior?

Evolutionary and Developmental Benefits

Motor Skills Social bonding

Reduction of AggressionCooperation

Sexual behaviour Life span

Brain development and cognitive flexibility

Neurobiological Mechanisms

Opioids Prefrontal cortex (PFC)

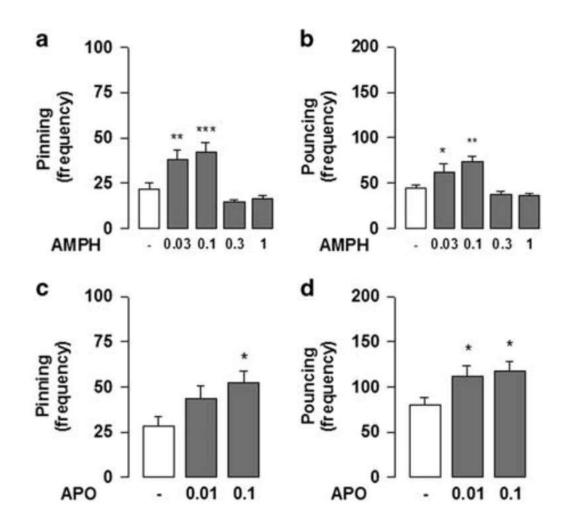
Cannabinoids Striatum

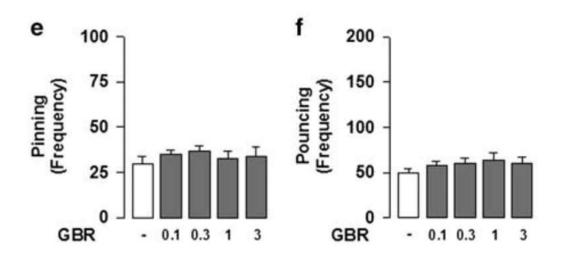
Dopamine Nucleus accumbens (NAc)

Noradrenaline

Dopamine

Manipulation of NAc dopaminergic neurotransmission affects social play behavior

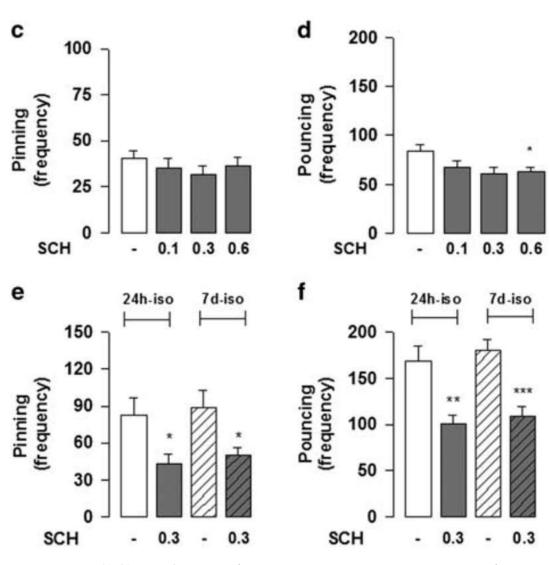




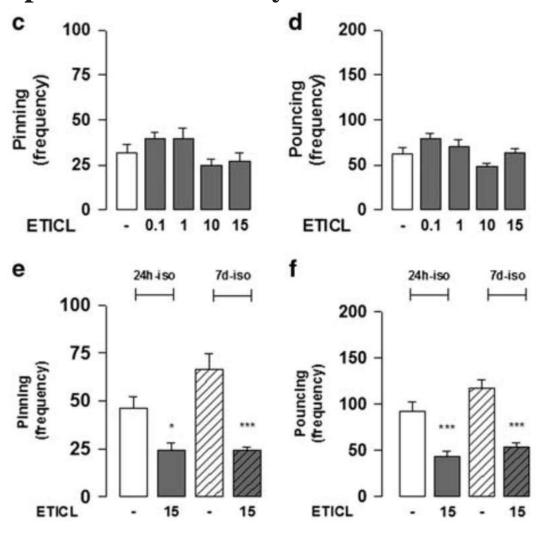
AMPH: amphetamine, dopamine releaser/ reuptake inhibitor APO: apomorphine, the nonselective dopamine receptor agonist GBR: the selective dopamine reuptake inhibitor

Dopamine

Role of NAc D1 and D2 Dopamine Receptors in Social Play Behavior



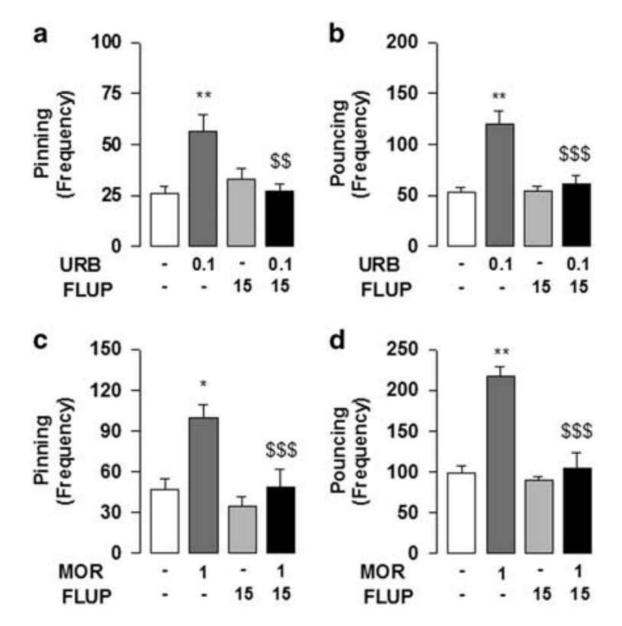
SCH: dopamine D1 receptor antagonist ETICL: dopamine D2 receptor antagonist



Manduca A. Neuropsychopharmacology. 2016

Dopamine

Activation of dopamine receptors in the NAc is necessary for endocannabinoid and opioid modulation of social play behavior



FLUP: nonselective dopamine receptor antagonist

URB: anandamide hydrolysis inhibitor

MOR: morphine

Endocannabinoids

Article

Neuron

Microglial Phagocytosis of Newborn Cells Is Induced by Endocannabinoids and Sculpts Sex Differences in Juvenile Rat Social Play

Highlights

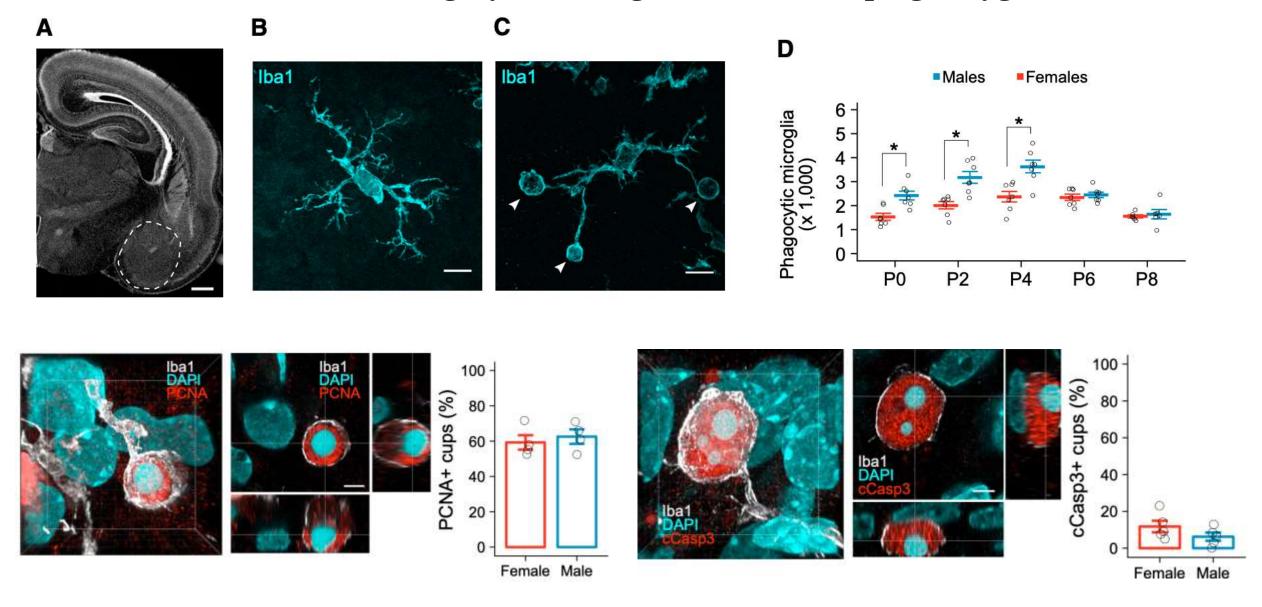
- Microglia are more phagocytic in the male amygdala during neonatal development
- Androgen-induced endocannabinoids increase phagocytosis in males

Authors

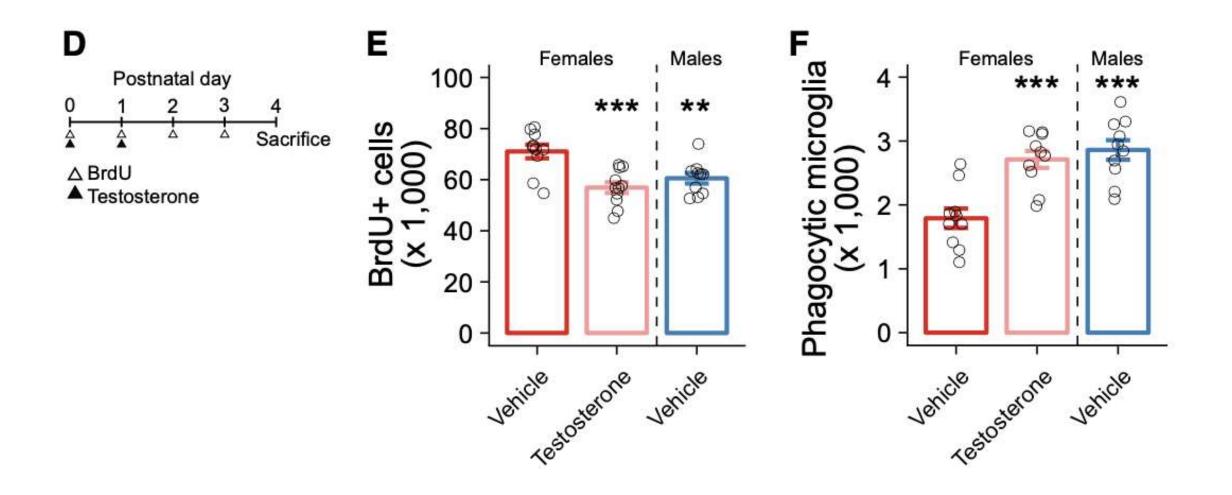
Jonathan W. VanRyzin,
Ashley E. Marquardt,
Kathryn J. Argue, ...,
Sheryl E. Arambula, Matthew N. Hill,
Margaret M. McCarthy

Why do males typically show higher levels of juvenile play behavior compared to females?

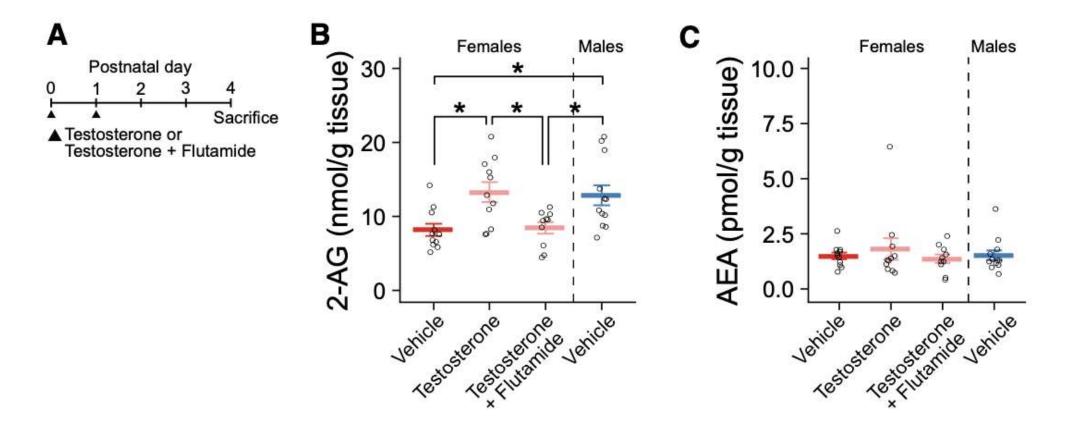
Males Have More Phagocytic Microglia in the Developing Amygdala



Testosterone Masculinizes Newborn Cell Number and Phagocytic Microglia Number in the Developing Amygdala

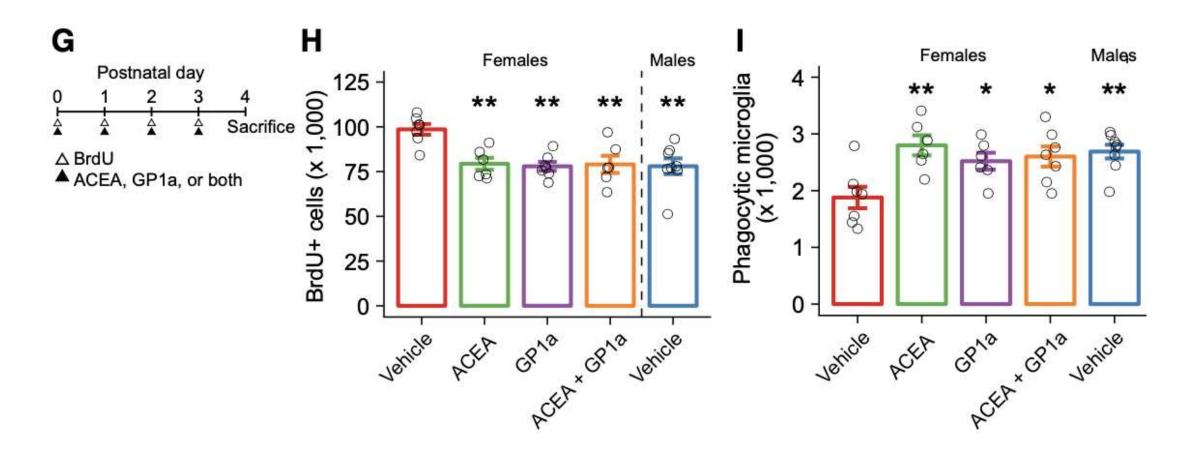


Testosterone Masculinizes Female 2-AG Content



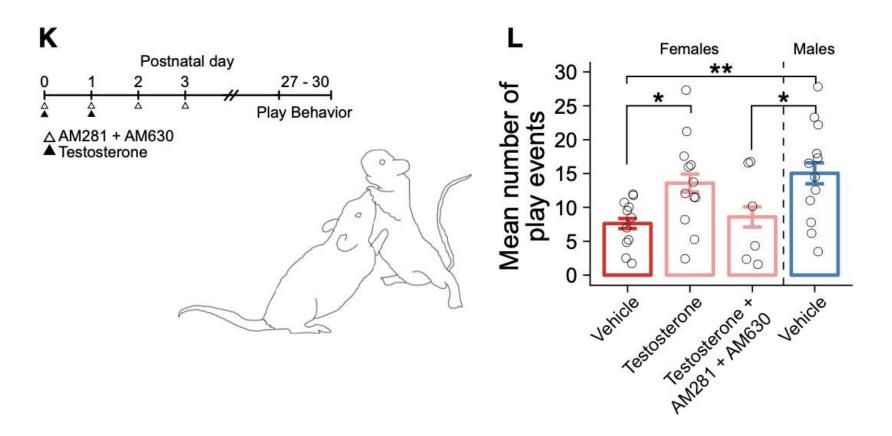
Endocannabinoid: 2-AG, AEA

CB1R/CB2R Agonists Mimic Testosterone's Effects



ACEA: agonist of CB1R GP1a: agonist of CB2R

Androgen-mediated masculinization of play occurs via increasing endocannabinoids



AM281: antagonist of CB1R AM630: antagonist of CB2R

How do animals benefit from play behavior?

Evolutionary and Developmental Benefits

Motor Skills Social bonding

Reduction of Aggression Cooperation

Sexual behaviour Life span

Brain development and cognitive flexibility

Neurobiological Mechanisms

Opioids Prefrontal cortex (PFC)

Cannabinoids Striatum

Dopamine Nucleus accumbens (NAcc)

Noradrenaline

References

- 1. S. Nunes *et al.*, Functions and consequences of play behaviour in juvenile Belding's ground squirrels. *Animal behaviour* **68**, 27-37 (2004).
- 2. B. M. Cooke, D. Shukla, Double helix: reciprocity between juvenile play and brain development. *Dev Cogn Neurosci* 1, 459-470 (2011).
- 3. J. Ahloy Dallaire, G. J. Mason, Juvenile rough-and-tumble play predicts adult sexual behaviour in American mink. *Animal behaviour* **123**, 81-89 (2017).
- 4. A. M. Kopec, C. J. Smith, N. R. Ayre, S. C. Sweat, S. D. Bilbo, Microglial dopamine receptor elimination defines sex-specific nucleus accumbens development and social behavior in adolescent rats. *Nat Commun* **9**, 3769 (2018).
- 5. E. J. M. Achterberg, M. M. H. van Swieten, D. J. Houwing, V. Trezza, L. Vanderschuren, Opioid modulation of social play reward in juvenile rats. *Neuropharmacology* **159**, 107332 (2019).
- 6. J. W. VanRyzin *et al.*, Microglial Phagocytosis of Newborn Cells Is Induced by Endocannabinoids and Sculpts Sex Differences in Juvenile Rat Social Play. *Neuron* **102**, 435-449 e436 (2019).
- 7. G. Kaplan, Play behaviour, not tool using, relates to brain mass in a sample of birds. *Sci Rep* **10**, 20437 (2020).
- 8. M. K. Loth, Z. R. Donaldson, Oxytocin, Dopamine, and Opioid Interactions Underlying Pair Bonding: Highlighting a Potential Role for Microglia. *Endocrinology* **162** (2021).
- 9. A. Bijlsma *et al.*, Social Play Behavior Is Critical for the Development of Prefrontal Inhibitory Synapses and Cognitive Flexibility in Rats. *J Neurosci* **42**, 8716-8728 (2022).
- 10. L. Samuni, A. Mielke, C. Crockford, R. M. Wittig, Social play fosters cooperation in wild adult chimpanzees. *Curr Biol* **34**, 5839-5845 e5833 (2024).
- 11. K. M. Witt, D. N. Harper, B. A. Ellenbroek, The role of the dopamine D1 receptor in anticipatory pleasure and social play. *Neuropharmacology* **264**, 110225 (2025).

PART III: Why do adults play less than juveniles?

(Regulation and modulation)

-MMZ

Juvenile individuals exhibited higher levels of play behavior









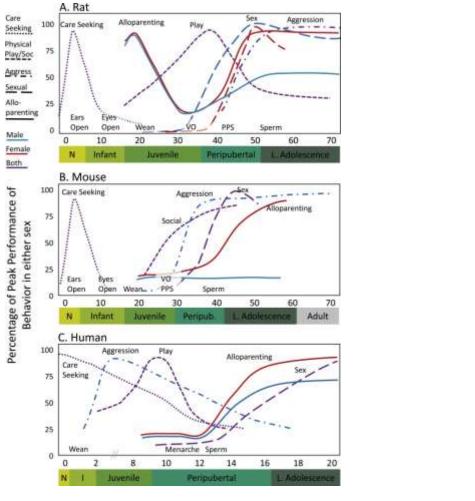


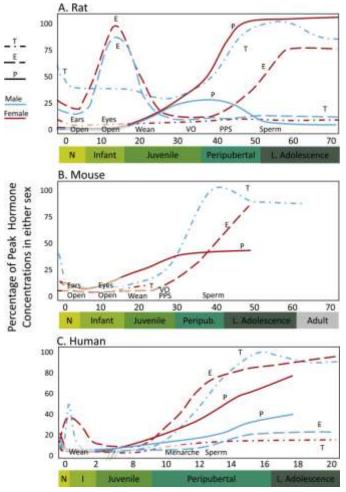






Play behavior peaks during juvenility in both rats and humans





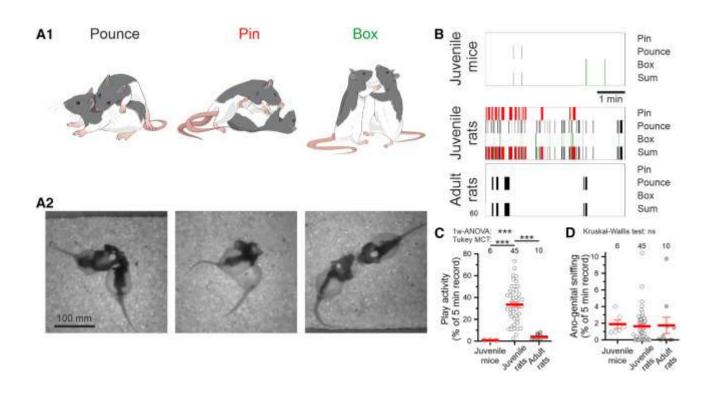
• Why do adults play less than juveniles?

• What additional factors influence play behavior?

• Why do adults play less than juveniles?

• What additional factors influence play behavior?

Rough and tumble play in juvenile rats









Social play behavior is driven by glycine-dependent mechanisms

Anton Dvorzhak 1 · Michael Brecht 2,3 · Dietmar Schmitz $\overset{\circ}{\sim}$ 1,2,3,4,5,6,7 \boxtimes

Affiliations & Notes ✓ Article Info ✓

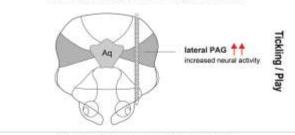


Highlights

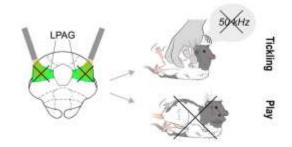
- · Activity of periaqueductal gray (PAG) neurons is required for social play
- · Neuronal activity and glycinergic neurotransmission in PAG decline with age
- Glycine stimulates social play through potentiation of NMDA receptors in PAG
- · Age-related social play decrease is partially dependent on glycine decline in PAG

PAG is required for play behavior

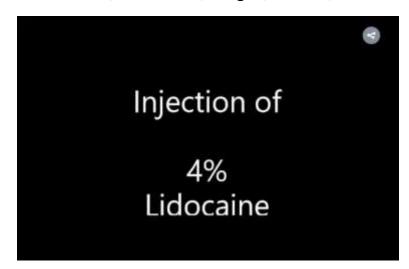
Electrophysiological recordings in the PAG

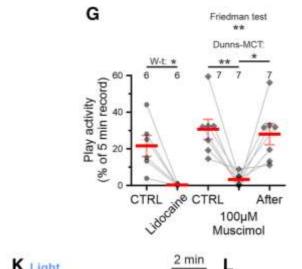


Optogenetic inactivation of the lateral PAG



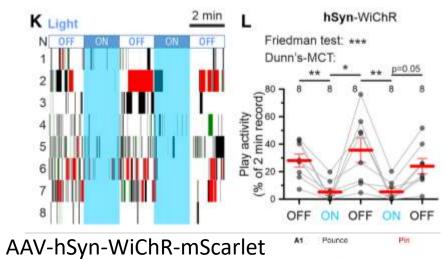
Gloveli N, Simonnet J, Tang W, Neuron, 2023.





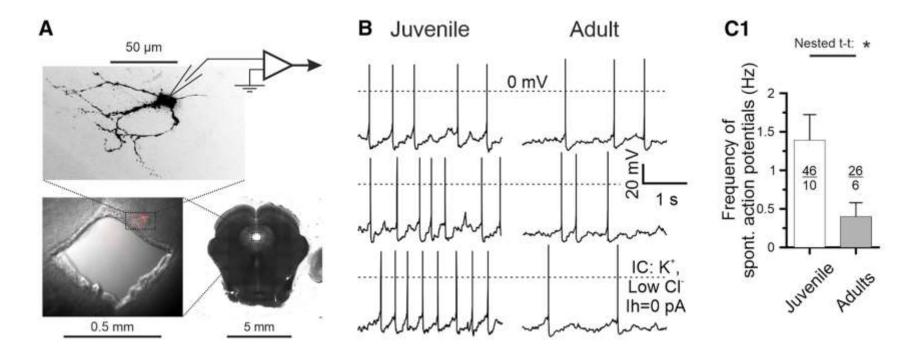
Lidocaine: Na⁺ channel bloker

Muscimol: agonist of the GABA receptor



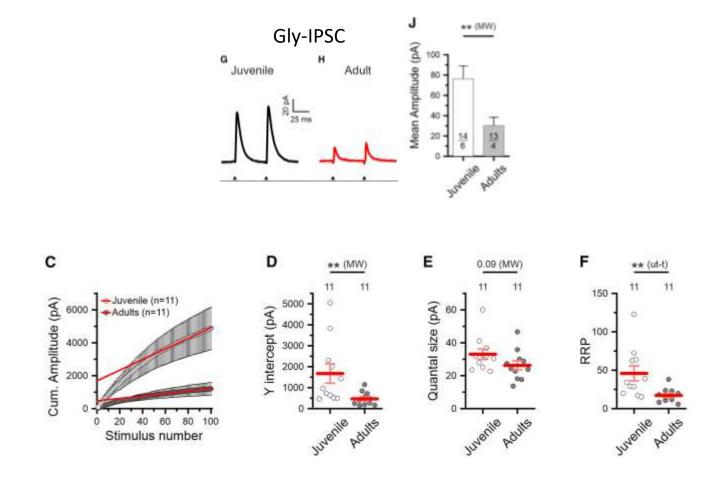
Dvorzhak A, Brecht M, Schmitz D., Curr Biol. 2024.

A striking difference in firing properties of neurons of juvenile and adult animals

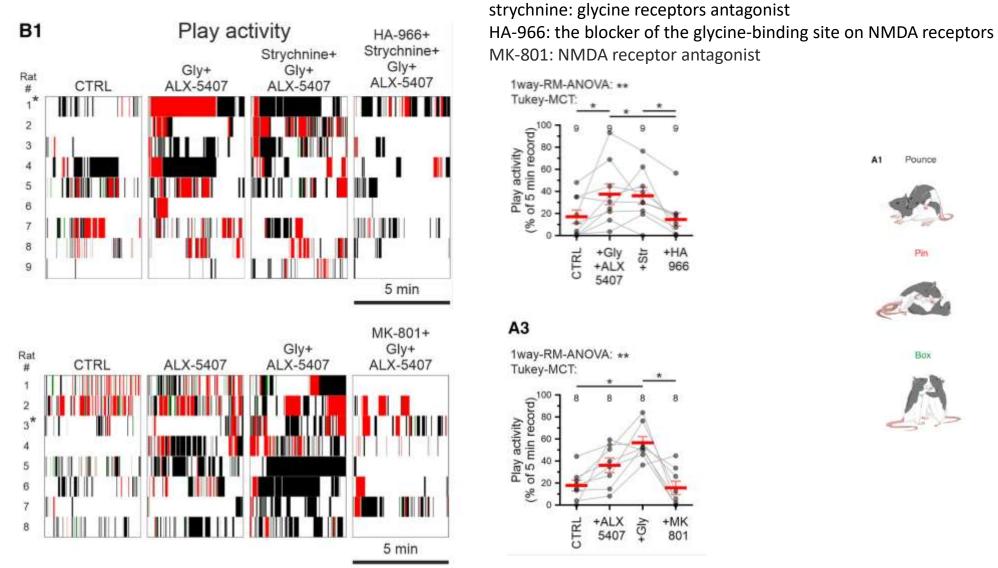


Dvorzhak A, Brecht M, Schmitz D., Curr Biol. 2024.

Adult rats exhibit a smaller glycine RRP (readily releasable pool) in PAG

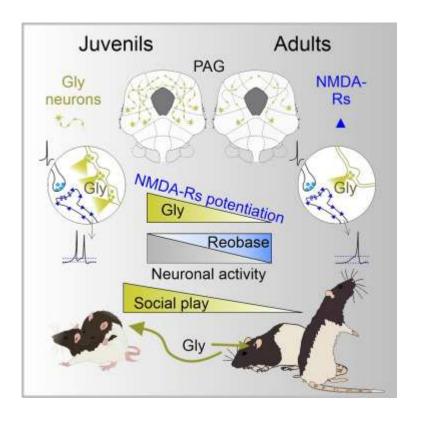


High Gly levels enhance NMDA receptor activity in the PAG of juvenile rats



ALX-5407: glycine transporter 1 (GlyT1) inhibitor

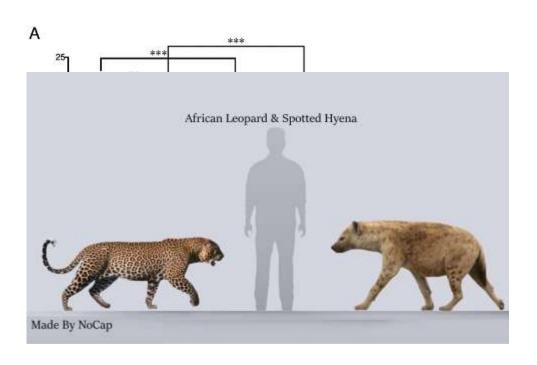
Elevated Gly concentrations in PAG of juvenile mice drive high-intensity play behavior

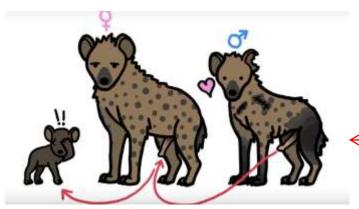


• Why do adults play less than juveniles?

• What additional factors influence play behavior?

Sex difference of play fighting

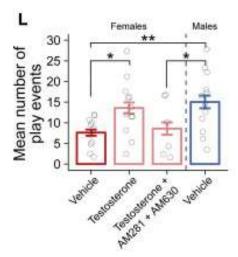




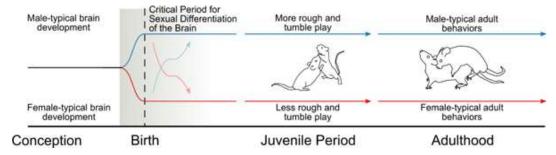
Species Studied Sex with Higher Play Frequency		References	Additional Notes	
Humans	Males	Whiting & Edwards, 1973; DiPietro, 1981; Humphreys & Smith, 1987		
Rats	Males	Poole & Fish, 1976; Olioff & Stewart, 1978; Meaney & Stewart, 1981b	The sex difference is most robust in same-sex dyads and least robust when highly motivated, i.e. preceded by a period of social isolation	
Cats (domestic)	Males	Caro, 1981	Males from all-male groups play at higher frequency than females from all-female groups; male play frequency was not influenced by the number of opposite-sex playmates while female play is affected by the number of male playmates	
Dogs (domestic)	Males	Pal, 2008; Ward et al., 2008	In mixed-sex dyads, males also engaged in offensive behaviors and self-handicapped more than females (Ward et al., 2008)	
Horses (domestic)	Males	Crowell-Davis et al., 1987		
Pigs (domestic)	Males	Dobao et al., 1987; Brown et al., 2018; Weller et al., 2019		
Cattle (domestic)	Males	Reinhardt et al., 1978	Additionally, both sexes prefer to direct play behavior toward male calves	
Sheep (domestic)	Males	Sachs & Harris, 1978		
Sheep (wild)	Males	Hass & Jenni, 1993	Male lambs also exhibit a larger repertoire of play behaviors than females	
Siberian ibex	Males	Byers, 1980		
Sea lions	Males	Gentry, 1974	Male pups also exhibit a larger repertoire of play behaviors that females	
Yellow-bellied marmots	Males	Jamieson & Armitage, 1987; Monclús et al, 2011	Females with larger anogenital distances (i.e. masculinized females) engaged in play more frequently than females with smaller anogenital distances (Monclús et al., 2011)	
Belding squirrels	Males	Holekamp et al., 1984		
Rhesus monkeys	Males	Goy & Deputte, 1996	Sex difference in frequency is based on a sex difference in play initiations (males > females)	
Squirrel monkeys	Males	Biben, 2010	Male play bouts are also longer than female play bouts	
Lowland gorillas	Males	Meder, 1990		
Baboons	Males	Owens, 1975		
Spotted hyenas	Females	Pedersen et al., 1990	Females of this species are dominant to males, are larger than males, and have external genitalia. Speaking to these observations, adult females also have higher levels of circulating testosterone relative to males than is typically seen in female mammals.	

The perinatal critical period for sexual differentiation of the brain

Testosterone: main androgen (male sex hormone) AM281+AM630: antagonists of testosterone

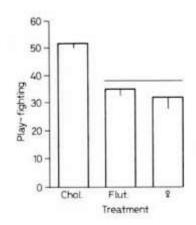


VanRyzin JW, et al., Neuron. 2019.



VanRyzin JW, Marquardt AE, McCarthy MM. Int J Play, 2020.

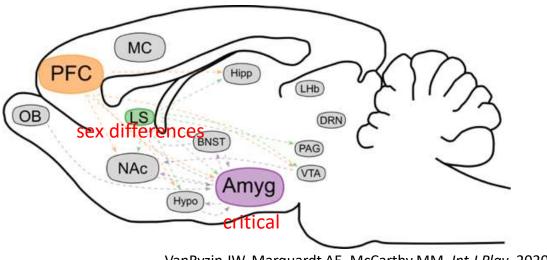
Flutamide treatment



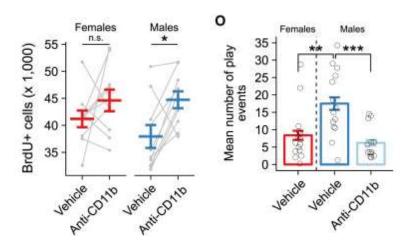
Flutamide: blocker of androgens (male hormones)

Meaney, et al., Neuroendocrinology, 1983.

Distinct Nodes in the Neural Circuitry of Play



VanRyzin JW, Marquardt AE, McCarthy MM. Int J Play, 2020.



VanRyzin JW, et al., Neuron. 2019.

The deviation of win-loss ratios from 50:50 triggers the transition from play to aggression









Playing versus Fighting

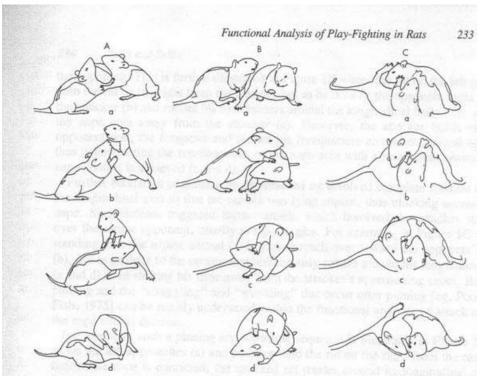


Fig. 1. Play-fights are initiated by an attack to the nape, which occurs both from the front (A) and from the rear (B). Even after the defender has adopted a supine position, the attacker continues to direct his attack to the nape, which in turn continues to be defended by the supine rat (C). Drawn from 16-mm movie film taken at 48 frames/sec. The rats represented in A and B are 31 days, and the rats in C are 56 days. Lower case letters signify frames of the sequence and are placed in a fixed location relative to the animals. The same procedure is used for subsequent figures.

Pellis & Pellis. 1987, Agg. Beh. 13: 227-242

Functional Analysis of Play-Fighting in Rats 237

Fig. 4. Offensive use of lateral movement of the pelvis toward the opponent (ie, lateral display) to gain access to a flank bite by an adult resident against an intruder. Drawn from 16-mm movie film taken at 24 frames/sec. See text for further explanation.

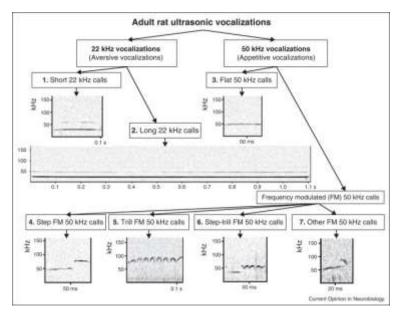
Pellis & Pellis, 1987, Agg. Beh, 13: 227-242.

Rats express emotions through ultrasonic vocalizations (USVs)

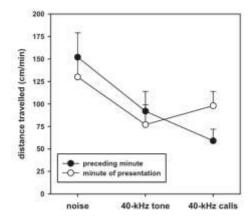
Call Subtype	Mating (Chases)	Play (DC)	Aggression (DC)
22-kHz	30°	12	31*
Flat 50-kHz	22	14	+.13
FM 50-kHz	+.63**	+.59**	+.35*
Call Subtype	Mating (PEI)	Play(Pin Duration)	Aggression (Freezing)
22-kHz	+.53**	+.41"	+.69**
Flat 50-kHz	19	+.35	70**
FM 50-kHz	57**	68**	69**

Note. Spearman's correlations were used for all comparisons involving 22-kHz calls and PEI during mating, and Pearson's correlations were used for all other comparisons. USVs = ultrasonic vocalizations; DC = dorsal contacts; FM = frequency modulated; PEI = postejaculatory interval. * p < .05. ** p < .005.</p>

Burgdorf J, et al., J Comp Psychol., 2008.

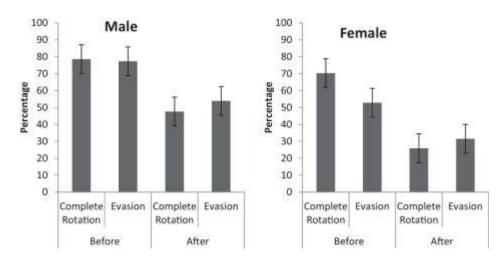


Brudzynski SM., Curr Opin Neurobiol. 2013.

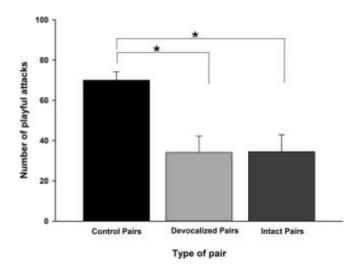


Wöhr, M., & Schwarting, R. K. W., Behavioral Neuroscience, 2008.

50-kHz USVs mean "I want to play with you"

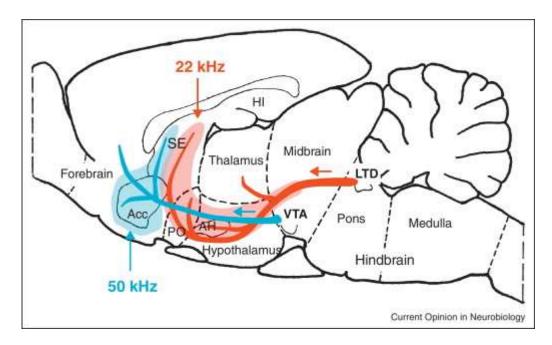


Kisko TM, Euston DR, Pellis SM., Behav Processes. 2015



Kisko TM., et al., Curr Top Behav Neurosci., 2017

The emotional valence affects behavior



Brudzynski SM., Curr Opin Neurobiol. 2013.

Take home messages

- Play is instinctive in animals.
- Play in childhood promotes healthy development and shapes adult behavior.
- Play behavior is modulated by age, gender, and emotion.

References

VanRyzin JW, Marquardt AE, McCarthy MM. Developmental origins of sex differences in the neural circuitry of play. Int J Play. 2020;9(1):58-75. doi: 10.1080/21594937.2020.1723370. Epub 2020 Feb 18. PMID: 33717644; PMCID: PMC7954123.

Bell MR. Comparing Postnatal Development of Gonadal Hormones and Associated Social Behaviors in Rats, Mice, and Humans. Endocrinology. 2018 Jul 1;159(7):2596-2613. doi: 10.1210/en.2018-00220. PMID: 29767714; PMCID: PMC6692888.

Pellis SM, Pellis VC. Play fighting of rats in comparative perspective: a schema for neurobehavioral analyses. Neurosci Biobehav Rev. 1998;23(1):87-101. doi: 10.1016/s0149-7634(97)00071-7. PMID: 9861614.

Dvorzhak A, Brecht M, Schmitz D. Social play behavior is driven by glycine-dependent mechanisms. Curr Biol. 2024 Aug 19;34(16):3654-3664.e6. doi: 10.1016/j.cub.2024.06.073. Epub 2024 Jul 24. PMID: 39053464.

Argue KJ, McCarthy MM. Characterization of juvenile play in rats: importance of sex of self and sex of partner. Biol Sex Differ. 2015 Sep 10;6:16. doi: 10.1186/s13293-015-0034-x. PMID: 26361539; PMCID: PMC4564956.

Dessì-Fulgheri F, Porrini S, Farabollini F. Effects of perinatal exposure to bisphenol A on play behavior of female and male juvenile rats. Environ Health Perspect. 2002 Jun;110 Suppl 3(Suppl 3):403-7. doi: 10.1289/ehp.110-1241190. PMID: 12060836; PMCID: PMC1241190.

Dean SL, Knutson JF, Krebs-Kraft DL, McCarthy MM. Prostaglandin E2 is an endogenous modulator of cerebellar development and complex behavior during a sensitive postnatal period. Eur J Neurosci. 2012 Apr;35(8):1218-29. doi: 10.1111/j.1460-9568.2012.08032.x. PMID: 22512254; PMCID: PMC3534986.

VanRyzin JW, Marquardt AE, Argue KJ, Vecchiarelli HA, Ashton SE, Arambula SE, Hill MN, McCarthy MM. Microglial Phagocytosis of Newborn Cells Is Induced by Endocannabinoids and Sculpts Sex Differences in Juvenile Rat Social Play. Neuron. 2019 Apr 17;102(2):435-449.e6. doi: 10.1016/j.neuron.2019.02.006. Epub 2019 Feb 28. Erratum in: Neuron. 2022 Apr 6;110(7):1271. doi: 10.1016/j.neuron.2022.03.013. PMID: 30827729; PMCID: PMC8046232.

Kisko TM, Wöhr M, Pellis VC, Pellis SM. From Play to Aggression: High-Frequency 50-kHz Ultrasonic Vocalizations as Play and Appearement Signals in Rats. Curr Top Behav Neurosci. 2017;30:91-108. doi: 10.1007/7854_2015_432. PMID: 26728173.

Burgdorf J, Kroes RA, Moskal JR, Pfaus JG, Brudzynski SM, Panksepp J. Ultrasonic vocalizations of rats (Rattus norvegicus) during mating, play, and aggression: Behavioral concomitants, relationship to reward, and self-administration of playback. J Comp Psychol. 2008 Nov;122(4):357-67. doi: 10.1037/a0012889. PMID: 19014259.

Brudzynski SM. Ethotransmission: communication of emotional states through ultrasonic vocalization in rats. Curr Opin Neurobiol. 2013 Jun;23(3):310-7. doi: 10.1016/j.conb.2013.01.014. Epub 2013 Jan 31. PMID: 23375168.

Wöhr, M., & Schwarting, R. K. W. (2008). Maternal care, isolation-induced infant ultrasonic calling, and their relations to adult anxiety-related behavior in the rat. Behavioral Neuroscience, 122(2), 310–330. doi:10.1037/0735-7044.122.2.310

Dvorzhak A, Brecht M, Schmitz D. Social play behavior is driven by glycine-dependent mechanisms. Curr Biol. 2024 Aug 19;34(16):3654-3664.e6. doi: 10.1016/j.cub.2024.06.073. Epub 2024 Jul 24. PMID: 39053464.