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Marsupial Cognition

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Introduction

Marsupials are all the members of the infraclass Marsupialia which diverged from the main radiation of placental mammals around 130–160 mya. They exhibit a myriad of adaptations to different habitats, wide array of diet, locomotor modes, and social and mating systems. Even though their point of origin is contested, the earliest metatherian fossil record (comprising marsupials and their closest fossil relatives) has been discovered in Asia and dated to the Early Cretaceous (stretching from 146 Ma and 100 Ma). The earliest common ancestor of eutherians (modern placentals) and metatherians is thought to be *Juramaia sinensis*. Dated back to the Jurassic (160 Ma) and discovered in China, it exhibits scansorial (adapted for climbing) forelimb anatomy, weights around 15–17 g, and based on tooth morphology, was an insectivore. It is more closely related to most modern day placentals than all metatherians including the earliest known *Sinodelphys* and *Deltatheridium*.

All extant marsupials are native to Australia, New Guinea, and the Americas, but the fossil record shows that they have been present on all continents at different points in time. Over 330 extant species of marsupials had been described, with around 100 in the Americas and the rest in Australia and New Guinea.

The main difference between placentals and marsupials regarding cognition can be expected due to difference in their developmental mode (the specific type of developmental stages and conditions that an organism undergoes). Despite their name and designation, the marsupial infraclass does undergo placentation but it is relatively short, and some marsupials do not even have a pouch (marsupium), like the short-tailed opossum (*Monodelphis domestica*). Besides the confusing naming nomenclature, most marsupials do have a very different developmental mode to placentals. They have very short gestation periods (typically between 2 and 5 weeks) and most of the fetal development takes place in the marsupium. This exposes both the developing offspring and the mother to an array of very different developmental/parental conditions as compared to placentals. This also predisposes differences in cognitive and behavioral development.

The striking difference in developmental mode and early phylogenetic divergence, and the subsequent morphological convergence between the two infraclasses of mammals presents a wonderful opportunity for studies on comparative/convergent cognitive evolution. Despite that marsupials are remarkably understudied from psychological perspective. There are only a handful of studies

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assessing the cognitive abilities of the infraclass, either purely descriptive or in comparative perspective.

What follows is a summary of the current state of understanding of marsupial cognition, starting off by defining cognition and its neuroanatomical correlates. Some differences in neuroanatomy which might be underlying further differences in behavior and cognition between placentals and marsupials are described, followed by a review of the current literature – starting from the initial interest in marsupial behavior and cognition in the beginning of the twentieth century and summarizing the current state of research on different aspects of cognition – perception, learning, memory, attention, decision-making, and executive functions (flexibility, categorization, problem-solving).

What Is Cognition?

Cognition encompasses the abilities of an organism to decode, encode, store and process information from the environment (endogenous and exogenous) in (almost) real time. This usually results in adaptive or flexible behaviors that maximize the species' fitness. These abilities had emerged and evolved as an assembly of different properties of the nervous system in combination with other receptive and perceptive systems multiple times in evolution.

On Neuroanatomical Differences with Placentals

Placentals and marsupials show surprising convergence in neuroanatomy (Karlen and Krubitzer 2007). One major difference is the fact that while all marsupials are relatively lissencephalic (exhibiting smooth cortical surface), placentals do exhibit gyrencephaly (folded cortical surface) more often. It is not clear whether the last common ancestor had a gyrated or smooth cortex, but a case has been made that proposes a secondary loss of gyrencephaly in mammals. If so, this might be an example of secondary loss, that is, lysencephaly might be a derived trait in marsupials and not an indication of "primitiveness" (Kelava et al. 2013).

One notable aspect of marsupial neuroanatomy which sets them apart from placentals is that they lack corpus callosum (Suárez et al. 2018). Most connections between the hemispheres are initiated through the hippocampal tracts or the anterior commissure (diprotodont marsupials, such as kangaroos and koalas have an additional axonal tract called *fasciculus aberrans*), which is more typical of reptiles and birds.

Besides these two significant neuroanatomical differences there is a striking convergence between placentals and marsupials in neuroanatomy, morphology, and behavior in species occupying similar habitats. This indicates a possible set of constraints or limits to the developmental bias on the evolution of the nervous system, resulting in similar solutions to similar pressures of the environment.

On Perception

Vision

Visual acuity in marsupials is quite poor compared to more derived placental mammals. This is mostly explained due to their nocturnal or crepuscular activity pattern which relies more on sensitivity to UV instead of resolution or color vision (Arrese et al. 2006).

Until recently, all marsupials were thought to have dichromatic vision (possessing only two types of cones). Recently, it has been discovered that there are many trichromatic species (i.e., fat-tailed dunnart, honey possum, quenda, and quokka, among others), but up until now it has been impossible to identify the third cone's photopigment unambiguously. The observation that around 20% of the photopigments in the retina of the fat-tailed dunnart (*Sminthopsis crassicaudata*) do not react to short or middle wave opsins has been backed up with behavioral experiments (Arrese et al. 2006). Previously thought to be unique to primates, the third class of cones allow for red–green color discrimination. Interestingly, trichromacy in marsupials is not linked to the X-chromosome, and all cones express a type of rod opsin.

The evolution of trichromacy in marsupials presents an interesting case, where this trait might have evolved at least twice in the infraclass (in polyprotodonts and diprotodonts) if it is assumed that the ancestral marsupial was dichromatic. The explanation as to what might the evolutionary pressures behind that be is challenging – for example, species from similar habitats were shown to have different visual ability. Wallabies have been shown to be dichromats while quokkas trichromats. Further research is needed in order to establish the exact evolutionary pressures behind that phenomenon.

Audition and Vocalization

Marsupials use vocalization, mostly directed to conspecifics during mating, agonistic territorial encounters, and mother–young interactions (Aitkin 1998). The size and habitat of different species appears to drastically affect calls. Vocal communication seems to be more important and thus more developed in arboreal species (Aitkin 1998). For example, opossums' calls cover very broad spectra (0.5–8 kHz – growl; 1–16 kHz – screech), while dasyurids' calls are usually in the spectral frequencies below 3 kHz. In contrast, the arboreal striped possum's call (*Dactylopsila trivirgata*) has a tonal peak at 2.5 and 5.5. kHz. There is evidence that some small, terrestrial carnivorous species can use ultrasonic frequencies, but most such calls lack harmonic structure. Brushtail possums' (*Trichosurus vulpecula*) hearing sensitivity increases from 2 to 15 kHz, and they could still hear tones between 20 and 35 kHz. The hearing range in northern quolls (*Dasyurus hallucatus*) has been shown to lie between 8 and 10 kHz, while the best frequency of hearing in the American opossum (*Didelphis virginiana*) was shown to be between 16 and 32 kHz which is much higher compared to the quoll.

Low-frequency hearing and calls are related to recognition of conspecifics, mid-frequency ranges are related to interactions with pouch-young, while upper ranges are mainly used during predator–prey encounters (Aitkin et al. 1994).

Finally, similarly to placental mammals, there seems to be broad diversity of spectral sensitivity in different species of marsupials, corresponding to wide array of vocalization frequencies. This probably reflects the variety of adaptations to habitats that these species occupy. These findings strengthen the argument that auditory perception and production are as diverse in marsupials as they are in placentals, reflecting their ability to perceive, process, and react to complex stimuli in the environment.

Olfaction

Similarly to placentals, marsupials possess main and vomeronasal olfactory system, where the later exhibits pronounced sexual dimorphism in some species, and high structural conservation (Aland et al. 2016). The structure and development of the vomeronasal organ in marsupials indicates that, as in other mammals, the importance of pheromones in reproduction is crucial. This might be especially important for some small dasyurid species, as females from these species are monestrous (only a single estrus in a lifetime) while males are semelparous (sudden death of all males after one reproductive season). Thus, the cost of reproduction in such species is extremely high, and an evolved ability to correctly assess a potential mate should necessarily rely on highly developed olfactory perception for recognition.

In regards to olfactory cognition, there are no studies up to date addressing questions related to olfactory memory, attention, or categorization in marsupials, despite it being a popular topic of research in other mammals (Zucco et al. 2014).

Cognition in Marsupials

In lieu of the fact that most extant marsupials can be found in Australia and New Guinea, one of the most studied species of marsupial in the psychological literature is the common opossum (*Didelphis marsupialis*). Most marsupials are understudied in terms of cognition and behavior and little progress has been made in this area of inquiry since a series of pioneering attempts in the 70s (Kirkby 2015). Before that, it was popularly held that marsupials were a primitive mammalian radiation, representing an intermediate form between sophisticated eutherians and primitive reptiles. Even though that notion is no longer supported, almost no advance has been made in the field of marsupial cognition, and the view that marsupials are somewhat primitive is still widely and wrongly accepted.

Exploration and Problem-Solving

Platt and James (1967) were able to show that adult opossums exhibited preference for novelty, by training them in T or Y mazes with different colors of the different arms. When both arms were changed to congruent color choice, most opossums showed tendency to explore the arm that had changed color. In a larger comparative study Russell and Pearce (1971) exposed 30 animals from 6 different marsupial species to a set of four novel objects with different odor, shape, and texture. Their findings showed similar response to novelty to placental mammals, where repeated exposure led to habituation, with some species showing higher level of reactivity (brush-tailed marsupial rat – *Dasyuroides byrnie*) while others had very quick habituation (i.e., red kangaroo, *Macropus rufus,* or the Tammar wallaby, *Macropus eugenii*). Other studies had also pointed to similarity in exploration toward novelty between mammals and marsupials (Kirkby 2015) with the little differences been attributed mainly to differences in habitats and diets.

One striking example of problem solving, where possums outperform even primates involves retrieval of a food reward tied to string when the only solution to the task requires the animal to face away from the goal object (Wynne and McLean 1999). In terms of spatial learning, marsupials, and especially opossums, have been shown to be especially apt. On specific maze tasks they seem to perform better than rats, chickens, and even dogs. In rare study in wild animals (Morrant and Petit 2012) the nectar feeding western pygmy possum (*Cercartetus concinnus*) were shown to exhibit very complex exploratory behavior in their natural environment, combined with diet-switching in order to cope with fluctuation in resource availability. Pygmy possums have been detected to travel up to 4.7 km in a single night in search of flowering plants, and when certain food sources were unavailable, they could identify alternative flowering plants to feed on.

Conditioning and Learning

Attempts for classical conditioning in marsupials had been more controversial in their outcomes. Initially, researchers could not successfully train animals to respond to conditioned stimuli but recent attempts have shown that this is possible, concluding that a suitable choice of stimuli is crucial for conditioning in marsupials (Papini 2005). On the other hand, several species of marsupials had been shown to react very similarly to placentals in regards to acquiring both positive and negative operant responses (Angermeier et al. 1987; Powell and Doolittle 1971). Red opossums (*Lutreolina crassicaudata*) were even shown to acquire similar preference to a box with sugar solution versus an empty box, after only a few daily training trials (Papini et al. 1987). This was not the case in Virginia opossums, which exhibited better performance with more trials per session (Friedman and Marshall 1965), indicating variation in context learning in marsupials.

In another study (Bonney and Wynne 2004) both herbivorous quokkas (*Setonix brachyurus*) and carnivorous fat-tailed dunnarts (*Sminthopsis crassicaudata*) showed impressive cognitive flexibility. Both species were successful in learning discriminations, learning sets and reversal sets. Dunnarts showed exceptionally fast learning abilities successfully learning reversal sets in one trial, and were the only species which succeeded in transverse patterning tasks (in which each stimulus has a different property contingent on other stimuli with which it is presented) and negative patterning tasks (tasks in which an animal is conditioned to respond to one of two stimuli, but not to the simulations presentation of both). This difference between the two species might be due to the better developed cortical association areas in dunnarts as compared to quokkas.

Such findings lead to the conclusion that operant learning ability does not appear to have evolved after the split between eutherians and metatherians, and that more encephalized animals do not show improvement as compared to less encephalized ones. This might be related to the fact that experimental operant and classical conditioning mostly rely on food as reward. It is a very basic stimulus related to survival, that even the most basic vertebrates should be capable of efficient conditioning to.

Lateralization

Lateralization of behavior (preferential usage of one side of the body during execution of certain repertoires like extracting fruit, offspring care, etc.) has been shown to be a property of most bilaterally symmetrical vertebrates. It has many implications for behavior and cognition and has been suggested to be a result of an evolutionary stable strategy under social pressures, where asymmetrical organisms need to coordinate their behavior with other conspecifics or other species (Vallortigara and Rogers 2005).

In a study on southern hairy-nosed wombats (*Lasiorhinus latifrons*) right auditory bias was detected when the animals were presented with eight sounds from different contexts (Descovich et al. 2013). Interestingly, once used to the sounds, the animals reversed their bias to the left side. This is in concert with other studies, indicating that most vertebrates exhibit left hemisphere/right sensory bias for vigilance (Vallortigara and Rogers 2005) and right hemisphere/left sensory bias for familiar objects (Robins and Phillips 2010).

Strong manual lateralization had also been shown to be present in some bipedal marsupials both on individual and on population level (Giljov et al. 2017). Left-limb preference was observed in several species of macropods, and it was shown to be present from the pouch-young stage. These finding suggest that manual preference and lateralization in this group is not determined by habitual bipedality, but it is a result of developmental processes precluding postural and locomotor bipedality. This is in strike difference to most studied placental mammals, where manual lateralization usually manifests with advancing age, with the one exception in primates, where the scenario resembles marsupial's early development. In that sense, both humans and macropods manifest handedness before the adult stage which becomes evident before the development of bipedality.

Avoidance Learning and Generalization

Predator avoidance in marsupials it one of the best studied areas of cognitive ability in that group with all observations and experiments suggesting that learning processes in marsupials might be convergent with those in placentals. One of the largest members of the Macropodoids, the eastern grey kangaroo (*Macropus giganteus*) was shown to flee if there are dingos or farm dogs in proximity. The fear response toward the farm dogs had also been shown to generalize toward the vehicle the dog always appears around (Jarman and Wright 1993). Several other marsupial species had been shown to successfully learn to recognize introduced predators. Rufous hare-wallabies (*Lagorchestes hirsutus*) could learn to recognize a stuffed model of a fox and a cat, and quokkas (*Setonix brachyurus*) had been shown to be able to generalize their fear toward dogs to a stuffed model of a cat (McLean et al. 2000). Tamar wallabies (*Macropus eugenii*) were shown to become fearful of a model fox then generalize the response to a cat, but not to a non-predator (goat) (Griffin et al. 2002). The authors interpret this finding as an adaptive predisposition to acquire a fear of predators, based on their subsequent experiments with an array of control stimuli.

Social Cognition and Play

Tammar wallabies (*Macropus eugenii*), a highly gregarious and social species, can socially transmit knowledge on avoiding a predator model (fox) and can generalize between contexts (Griffin and Evans 2003) – they subsequently avoid cats, but not goats. This was the first instance where social learning was demonstrated in a marsupial species. Another study (Cordoni and Norscia 2014) demonstrated that in the red-necked wallaby (*Macropus rufogriseus*) reconciliation was not only present, but it was also modulated depending on the intensity of the conflict. While low intensity conflicts were reconciled, high intensity ones were not. These findings indicate that the red-necked wallaby can evaluate the costs of conflict and reconciliation and can engage actively in peace-making in an attempt to maximize the pay-offs.

Play has been considered one of the indicators of complex cognition in mammals and birds (Iwaniuk et al. 2001). Despite the scarcity of data, a survey of play behavior among marsupials revealed that play was common in larger-bodied members of Dasyuridae, in *Myrmecobiius*, in Vombatidae, and in all Macropodoidea (Watson 2009). They exhibit a diverse range of social (play fighting, sexual play, and parallel locomotion), nonsocial (locomotor or object play), and interspecific play. It was shown that the presence of play was related to relative brain mass, but a point was also made that there might be a confusion in classification of play fight versus real fight, for example in macropodoids (Watson 2009). Some ritualized behaviors in fights categorized as real ones, might have been indicators of play fight instead.

The evolution of play in marsupials, and macropods more specifically, has been analyzed from the scope of their specific social system. Most of the playing macropodoids are polygynous, which necessitates a certain level of competition between both males and females, which can be "rehearsed" while playing. Another contributing factor might have been predation pressure, as macropodoids have been preyed upon by a range of mammals, avians, and reptilian predators throughout their evolution. Training different predator avoidance strategies through locomotor play might be an adaptation alternative to crypsis in some non-playing species (e.g., potoroids).

Conclusion

The area of marsupial cognition is remarkably underexplored, and despite many potential species that can be studied as model animals the infraclass remains poorly understudied. For example, in species that show evidence of enhanced learning abilities and cognitive flexibility, studying pouch young in their early development provides a great opportunity for research on development and evolution of cognitive abilities. Many species had never been studied in terms of cognition, and there is a substantial gap in our knowledge of memory, cognitive flexibility, social learning, innovation or most types of complex cognition in the group, such as emotions, moral judgment, prospection and planning, theory of mind, and consciousness. Metatherians in general provide a wonderful study system for research on convergence in cognitive ability, and given their differences and similarities in neuroanatomy, they deserve more attention from scholars interested in evolutionary comparative studies, such as neuroecology and cognitive ethology.

Cross-References

▶ Cognition
▶ Marsupial Sensory Systems
▶ Marsupial Communication

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