Primer

Do birds have the capacity for fun?

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A crow carries a jar lid to the top of a sloping snowy rooftop in Russia. Sitting on the lid and sliding down the roof, you could think of it as surfing. It picks up the lid and repeats this behaviour again and again (Figure 1A). A group of black swans ride the crest of a wave that also looks like they are surfing. Once the wave reaches the beach, the swans fly back to another wave crest and perform the same actions again (Figure 1B). In both cases, the birds' behaviours do not seem to provide any obvious function apart from enjoyment - they look like they are having fun. Videos of these behaviours received millions of views on YouTube, so we appear to like watching other animals having fun. But is this interpretation of the birds' actions as having fun pure anthropomorphism or is it possible that an animal can act solely for its own enjoyment?

In this Primer, we discuss the idea of whether birds can temporally and energetically afford to have fun, whether they have the neural machinery necessary to feel pleasure, and provide some examples, such as play or singing, that could be interpreted in this way. We also discuss possible ways of making animal emotion more scientifically tractable and consider implications for animal welfare if some of these behaviours can be interpreted as pleasurable.

Having fun

What do we mean by having fun? Play is perhaps the most obvious behavioural manifestation of fun. Despite its many proposed functions in the training of young minds, play must also be rewarding or even pleasurable for it to be repeated. We discuss play later, but first enquire whether there are other avian activities that could be interpreted as fun? Although animals do not necessarily have the time, cognition or neurobiology for pastimes or leisure activities, some behaviours could be seen as being related to having fun, such as experiencing sensory pleasure from eating a preferred food to having sex to experiencing something beautiful, such as art.

Omnivorous animals with a varied diet are the best candidates for experiencing pleasure from their food, as they must possess the capacity to discriminate between different foods, preferring one over another. These preferences do not necessarily reflect differences in nutritional value between the foods (like our own dietary preferences). For example, western scrub-jays are given many different foods, including peanuts, dog biscuits, mealworms and wax worms, during experiments to test their episodic-like memory and future planning: when given a choice, say between mealworms and wax worms, all scrub-jays choose wax worms. One of us (N.S.C.) refers to wax worms as the "Belgian truffles of the scrub-jay world" because they are so preferred over all other foods. Is this because wax worms elicit a greater amount of sensory pleasure than other foods? This is a testable hypothesis.

The anthropomorphic trap

Returning to the two video examples, a simple interpretation of the birds' behaviour based on human introspection is that they are enjoying themselves. For example, the crow performs actions with no obvious function, which are repeated and the crow behaves 'as if' it is experiencing joy, for example, flapping its wings on each descent. For some scientists, such as Mark Bekoff (see his quick guide on play in domestic dogs in this issue), this is as far as we need to go: the bird looks like it's having fun, so of course, it is. From a scientific viewpoint, however, this is far from satisfactory. We cannot only rely on external behavioural cues when attributing emotional or mental states to others; human or otherwise. Relying on such cues alone will quickly cause us to fall in the anthropomorphic trap, which does not get us any closer to finding out what's actually going on inside another's head. We automatically project human thoughts and feelings onto an agent (animate or inanimate) that displays actions resembling those of a human agent, especially within the same context.

This form of anthropomorphic thinking was most strikingly demonstrated by Heidel and Simmel, who presented subjects with crude animations of two triangles and a circle moving around a large box with a movable section. The shapes' actions were erratic and resembled the social interactions of three human figures. Subjects did not dissociate their descriptions of the figures from their use of purposive and intentional language to describe the shape's actions in human terms. "The small triangle was attacking the circle" or "the circle was being chased by the large triangle" were common phrases used to describe the attributed intentional actions of the different shapes. Of course, the shapes could not possess these types of intentions. They were shapes on a film, with no internal mental states that could afford them with purpose, animated by an external agent (the animator).

Even Charles Darwin was prone to making attribution errors in his writings, specifically in relation to emotion. For example, in *The Expression of the Emotions in Man and Animals* (1872), Darwin suggested that a monkey baring its teeth was experiencing joy, whereas we know that this configuration of facial muscles now represents fear (produced by a subordinate monkey in the presence of a dominant). These errors are more easily made for species that are more closely related to us, such as primates or those with whom we share our homes, such as cats and dogs. Yet, even for birds, especially those known to be smart such as crows and parrots, it is very easy to slip into the anthropomorphic trap and attribute them with human emotions without good evidence. The question for this Primer is whether our quick attribution of pleasure and fun to the birds described for the two videos, or indeed any non-verbal creature, is just an example of our introspection biases or whether we can adopt a more scientific approach.

Building a brain for fun

How may fun be represented in the brain? At first, this seems a daunting question, yet although fun is a relatively new concept with respect to neuroscience and comparative cognition, there is precedence in its study. Fun involves doing something rewarding —it elicits a tendency to repeatedly approach a reward-inducing stimulus (*wanting*) — and it provides a sense of pleasure — a hedonic response eliciting a positive affective feeling (*liking*). We know much about how the mammalian brain processes reward and pleasure, and how it controls an animal's actions toward pleasure-seeking. Our revised knowledge of the evolution and anatomy of the avian brain can help us to make extrapolations from mammalian to avian brain with respect to the neuroanatomy of pleasure.

What could be going on in the brain of the Russian crow that we described earlier? Studies on the neurobiology of play in mammals, such as rats, have recorded neural activity, sampled neurotransmitters or mapped early gene activation in brain regions said to be involved in play. Although such studies have yet to be performed in birds, similar brain regions are found in the avian brain, with neurotransmitters, such as dopamine, that are essential for reward and endogenous opiates, such as enkephalins, which are essential for experiencing pleasure, flooding equivalent areas in the avian brain. As illustrated schematically in Figure 2, dopamine neurons originate in the midbrain (VTA and SN) and project to areas throughout the striatum (basal ganglia) and pallium; dopamine receptors are found in the greatest number in the nidopallium (especially NCL, suggested to be equivalent to the prefrontal cortex), striatum, pallidum, arcopallium, hyperpallium, mesopallium and various areas within the song control system (Area X, HVC and RA).

As in most animals, dopamine appears to play an essential role in reward in birds and is found in analogous brain regions, suggesting that dopamine also controls the search for reward-inducing stimuli in birds. Similarly, as also illustrated in Figure 2, bird brains are populated with receptors for opiates; μ opiate receptors are found in the VTA and SN, striatum, LMAN, nidopallium and mesopallium, whereas κ opiate receptors are found in the VTA and SN, striatum, and nidopallium, but also the hypothalamus, various parts of the thalamus, arcopallium, HVC and

Area X. With respect to our argument that birds have brains capable of experiencing pleasure (and so having fun), it is noteworthy that receptors for *both* dopamine and opiates are found in overlapping brain regions in those areas equivalent to hedonic brain regions in rodents and primates.

Do birds play?

When we imagine fun, perhaps the first behaviour to come to mind is play. It is seen throughout the animal kingdom, but the diversity, frequency and intensity of play increases dramatically in two groups; birds and mammals. As there are few examples of play in reptiles, and even fewer in amphibians, it is likely that play evolved independently in these two taxa. Within birds and mammals, those larger-brained species appear to play more frequently. Play also seems more prevalent in altricial species (those that take longer to develop and cannot fend for themselves). Within birds, of 27 orders, play has been reported in 13, two of them precocial and ten altricial (one could not be attributed). Play thus seems to be relatively uncommon in birds, seen in only 1% of the approximately 10,000 species and largely restricted to species with an extended developmental period, such as crows and parrots. In these two groups of birds, which have the most documented cases of play, play is typically similar to what has been observed in primates and carnivores, the two mammalian groups with the highest incidences of play: examples included elaborate acrobatics, manipulating objects and different types of social play, including play fighting. As in mammals, play in crows and parrots also involves specialised play signals that may differentiate play behaviours from their ‘real’ counterparts.

Birds engage in three types of play. First, locomotor play, which includes all types of flight-related play such as aerial acrobatics, hanging and flying upside down, as well as the two examples in Figure 1. Ravens and raptors are the most frequent performers of locomotor play, displaying all sorts of acrobatic acts whilst flying.

Second, object play, which can be difficult to differentiate from neophilia — exploration, curiosity and object manipulation — as it can involve the close inspection of objects to learn about their structure, whether they are edible and how they work. Could tool use in captive birds that do not use tools in the wild be considered object play? Such birds have to approach and manipulate objects not usually encountered in their natural environment (or in a different context), investigate then discover their appropriateness as functional objects in a tool-using context. Keas have a strong neophilic response to all objects and are notorious for their encroachment into human settlements in New Zealand, destroying external fixtures on cars, raiding rubbish bins on campsites, and so on. In their wanton destruction, it is difficult not to anthropomorphise that they are having fun in their destructive behaviour.

Finally, social play, which can easily be confused with fighting and courtship, and tends to involve a lot of chasing, tussling and rough and tumble. Social play frequently involves objects, where favoured objects are stolen or fought over. For example, captive rooks will often play tug-of-war with strips of newspaper, even when the birds are standing in thousands of examples of the same material. This strongly suggests that the birds were having fun with little function outside a pleasurable experience.

A perennial problem for play research concerns its function. An ultimate, evolutionary explanation for play does not have to supersede a proximate, mechanistic explanation. Birds, like us, may also play because it is fun; it produces a pleasurable experience — releasing endogenous opioids. It does not necessarily have to prepare an animal for later life. We may even suggest that adult play should be outside the need to learn about the world, and that sensory experience may be a more parsimonious explanation for why play remains in some adult animals. If we ascribe various functions to play that circumvent enjoyment, then perhaps we need to focus on adult play. Time for play is a rare commodity for adults. Although some adult play may function in affording the practice of certain behaviours, especially subtle social interactions, adult animals cannot afford the luxury of spending time doing something without benefit. However, play may reduce stress, may aid social bonding or it may just be immediately pleasurable; these possibilities have so far been little researched.

Singing a joyful song

Birds are highly motivated to sing. Indeed, for some species, singing is the only way to attract a mate, either directly, with the female discriminating between different males based on the content of their song or the size of their song repertoire, or indirectly, using song to maintain a territory. Although these are purely functional reasons for song, there is strong evidence that singing may also be rewarding, possibly even pleasurable. Although the ultimate explanation for the evolution of singing is to attract a mate or defend a territory, the proximate explanation may be that is produces a pleasurable affect in the brain. Studies have suggested that dopamine provides the drive or motivation to sing (equivalent to the wanting system) and that opiates cause singing to be rewarding (equivalent to the liking system).

Of most interest is what has been termed *directed song:* song that directly influences the behaviour of another individual, namely causing a female to approach and solicit mating from the singing male. Once directed song has attracted the attention of a female resulting in mating, song production decreases, as the goal of mating has been achieved, leading to satiation and a reduction in the motivation to sing. The more that behaviour X (for example, singing) results in a specific rewarding action Y (for example, mating), the more likely that behaviour X will be repeated. Dopamine will trigger or maintain the production of song when stimulated by the presence of a female, whereas opiates will inhibit the song when it has achieved its purpose (mating).

What is the evidence that dopamine (reward-seeking) and opiates (reward attainment) are involved in the song control system? The peripheral injection of dopamine agonists (opening dopamine receptor channels) increases the production of female directed song, whereas a similar injection of dopamine antagonists (blocking dopamine receptor channels) decreases the production of female directed song. What is going on in the song control system in the songbird brain during directed song? Dopamine and opiates are found widely across the song control system (Figure 2). Dopamine neurons in the midbrain areas of the VTA and the Medial Preoptic Area (mPOA) innervate dopamine and opiate rich regions throughout the song system, including Area X in the striatum and HVC and RA in the mesopallium. The VTA and mPOA are vital to other reward-seeking behaviours in rodents and Japanese quail, such as feeding and sexual behaviour. In the song control system, dopamine activation is significantly increased in Area X prior to the initiation of female directed song, and dopamine receptor immediate early gene expression increases during directed song. By comparison, opioid receptor agonists suppress female directed song, whilst opiate receptor antagonists increase female directed song. If opioids are involved in the pleasure response, this might seem counter-intuitive. But if the male songbird has low levels of opiates, this causes the male to seek socio-sexual contact from a female using song. Once this has been achieved, opioids are released producing a reward response, which has an inhibitory effect on socio-sexual contact and decreases female directed singing.

This relatively new research suggests a physiological mechanism by which males become motivated to sing (and keep singing) and may cause a pleasurable experience, but it is still not known whether (some) males sing for fun (that is, without a female stimulus). Singing does occur outside breeding and territorial contexts (*undirected song*), yet the evidence for a role of dopamine and opiates in this form of song are unknown.

Time for fun

Modern humans maybe the only species that have some form of leisure time. We spend large amounts of time in the pursuit of pleasure; pastimes, games and activities that we find fun. We have been afforded this extra time because of the vagaries of modern life. We no longer have to hunt or grow our own food; we buy it from others through the development of trade and commerce. We live in large communities, with laws and systems of government and protection from attack. We have largely eradicated predators. We each have a designated role in our society and our time is dictated by the work we have to perform in order to provide the things we need (for food, protection, and so on); those things that our ancestors had to provide for themselves. We spend huge amounts of time playing games, watching sports, TV or movies, reading, painting, exercising, cooking and other pastimes. In humans, fun is the result of technological, agricultural, commercial and cultural advances effecting our time, rather than an evolved trait.

We cannot say the same for (most) animals. Indeed, one argument against the possibility of animal fun is whether fun is adaptive. Wild animals, unlike modern humans, live within a strict time budget in which they have to perform a number of biological imperatives in order to survive and pass on their genes. They have to find and process food, find water, avoid predators (and/or locate prey), court and mate, raise offspring, and so on. Perhaps wild animals have little time to devote to pleasure-seeking. By contrast, captive animals, such as pets, working animals or those in zoos do not have to fend for themselves. Many of their biological needs are provided by their human captors, thus affording them with time for other pursuits. Indeed, pets are often encouraged by their owners to play, providing toys and other avenues of enjoyment to reduce boredom. Zoo animals are provided with environmental enrichment, reducing the potential for boredom, which can lead to mental problems such as repetitive behaviours like pacing and feather plucking.

How to measure pleasure in an alien mind

Although we have suggested how birds may experience pleasure, we still have very little data on whether they share similar experiences to us. We have to base our assumptions on similarities in neurochemistry and in the physical expressions of pleasure. We can make suggestions as to the adaptive nature of having fun, but we won't make real progress without the development of new methodologies. One stumbling block is the engrained idea that studying animal emotion is unscientific. This view has prevailed despite Darwin making animal emotion the subject of one of his three primary texts. How do we progress? One suggestion is to tie the study of emotion to cognition. This has produced intriguing, but limited results so far using the cognitive bias paradigm, but may be more fruitful with studies of metacognition (for example, frustration effects).

The study of bird emotion is more embryonic than for mammals. We do not share a similar external anatomy with birds. Unlike primates, birds do not possess a facial musculature revealing precise details about their emotional state. However, that does not mean that birds do not have the means for expressing emotions using their head or body. Some species have head crests, facial feathers, wings and tails they manipulate; they produce vocalizations, gestures and displays; some can even change the intensity of colour of their plumage or reveal hidden colours, even within the ultraviolet. This seems to be an untapped area for study, placing these potential emotional expressions into a behavioural context.

Our revised understanding of the organization of the avian brain also provides us with an opportunity to investigate the neural basis of emotion in birds. We could also apply physiological techniques used with mammals to record autonomic responses to emotional material or affective experiences. However, these would suffer from the same problems as mammals, as changes in heart rate, blood pressure, skin conductance, cortisol levels, and so on can be weak correlates of a specific emotional response. For example, heart rate can increase both as a result of being frightened and the result of seeing a loved one. The best opportunity for progress is to bring all these techniques together into a comprehensive study of emotional states, one species at a time.

What are the implications if we conclude that birds do not have fun? Our animal welfare laws are based largely around an attempt to provide animals with an absence of pain and suffering. We would also like them to be happy. Although a noble pursuit, as yet there is very little scientific evidence to bear on what a happy animal would look like if we saw one. It is therefore of primary importance that we develop sensible, scientifically-based methods to determine precisely what constitutes an animal feeling happy, sad, joyful and whether it can have fun. We can then use such information to enhance their lives, rather than attributing our own ideas on what they do and do not need based on introspection and anthropomorphism.

Further Reading

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Figure 1. Screenshots from YouTube videos of birds appearing to have fun.

(A) A crow slides down a snowy rooftop in Russia (from www.youtube.com/watch?v=_2rjolhgWmw). (B) A flock of swans ride the crest of a wave, appearing to 'surf' (from www.youtube.com/watch?v=pja3UPINHN8).

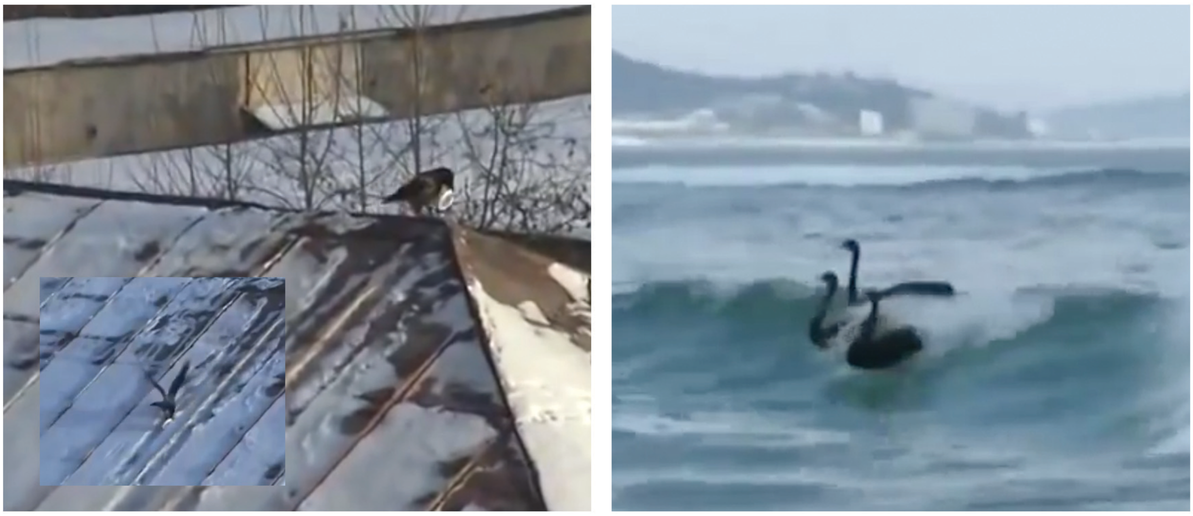
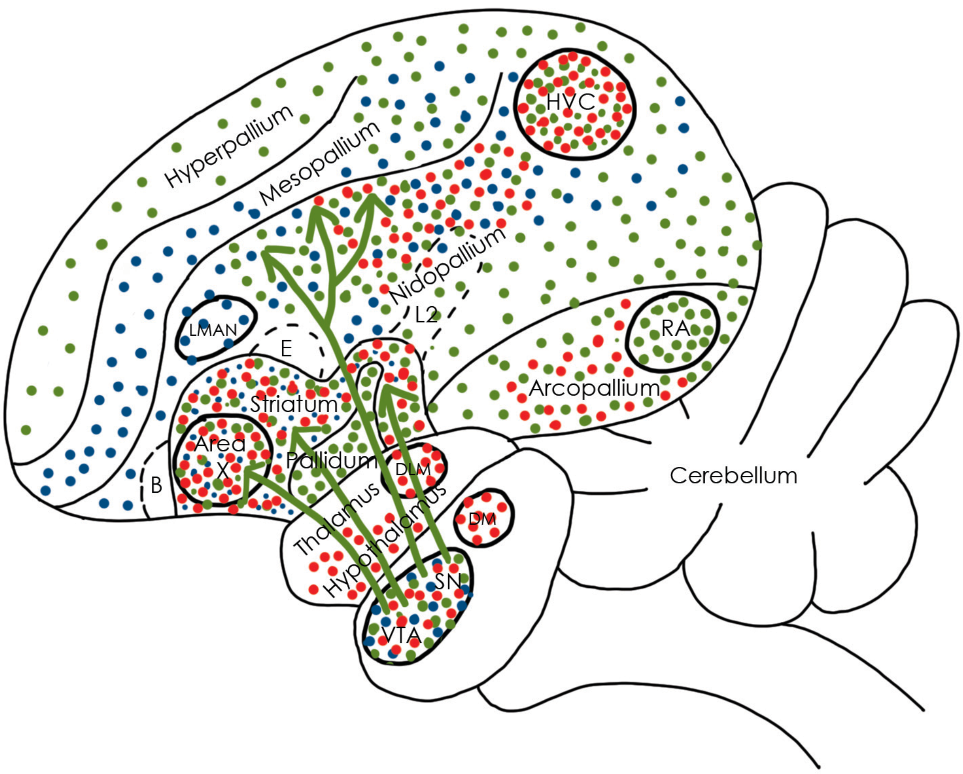


Figure 2. A schematic representation of a songbird brain (sagittal view).

The sketch shows the distribution of dopamine receptors (green circles) and projections (green arrows), κ opiate receptors (red circles) and μ opiate receptors (blue circles). These receptors are distributed across the reward and pleasure centres of the brain. Most interesting for our present argument is that dopamine and opioid receptors are found within the same brain areas, especially nidopallium, striatum, VTA and various nuclei of the song control system. Abbreviations: Area X, Area X of the striatum; B, basolateralis; DM, dorsal medial nucleus of the midbrain; DLM, dorsal lateral nucleus of the dorsomedial thalamus; E, entopallium; HVC, higher vocal centre (nucleus HVC); L2, Field L2; LMAN, lateral magnocellular nucleus of the anterior nidopallium; NCL, nidopallium caudolaterale; RA, robust nucleus of the arcopallium; SN, substantia nigra; VTA, ventral tegmental area.



In Brief:
In this Primer, Emery and Clayton consider whether birds can afford to have fun, with examples, such as play or singing, that could be interpreted in this way.