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Socially scripted vocal learning in primates

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Animal learning theory has been enormously influential in setting up laws of how individuals gradually learn associations and instrumentation by reinforcement. Yet, the theory rests on data collected from socially isolated laboratory animals, exposed to artificial cause–effect relations without visible agents. We review the primate vocal learning literature and find that animal learning theory performs poorly in accounting for real-life learning and evolutionarily relevant problem-solving. Instead, learning occurs when conspecifics act as event-causing agents, often without direct consequences for learners. We illustrate this with recent field studies, which suggest that the default mode of learning may not be through reinforcement and repeated trials but by acquiring scripts — mental representations of how events typically unfold. Becoming communicatively competent may be more about learning how events unfold than becoming conditioned to stimuli and responses.

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Abbreviations: OTL, one-trial learning; FM, fast mapping; NHP, non-human primate; ST, script theory; EC, event cognition; C, conditioning; P, predation; VL, vocal learning; MR, mental representation

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Learning to communicate

Since pioneering fieldwork by Ref. [34], primate alarm calls have become a paradigmatic system to study animal cognition and communication. Alarm calls often trigger unique behavioural responses, allowing researchers to study stimulus-responses patterns systematically and experimentally, even under difficult field conditions. For example, both vervet monkeys [36] and sooty mangabeys [29] run and climb into trees when detecting a leopard, seek cover after spotting an eagle and adopt bipedal postures when near a snake. Both species produce acoustically distinctive alarm calls to these predators and playback experiments have demonstrated that calls alone can evoke adaptive antipredator responses in listeners [22,34,28].

As predator attacks are rare and perceptually challenging events, the question is how young primates ever learn to anticipate predators, protect themselves against them and warn others about them. But the problem faced by young monkeys in the predation context is probably characteristic for any situation that requires communication: how does an animal learn to make sense of an event and become a competent communicator?

Acts of communication involve two roles, signallers and receivers, and this most likely involves different types of learning. While a signaller needs to learn how to act in the world, a recipient needs to learn to predict it. Some of this may be done by 'innate' or evolved propensities and simple maturation, but many situations will require personal experience acquired by some form of learning. Again, the predation context is interesting due to the diversity of the threats, the costliness of errors and the restricted learning opportunities. In such situations, natural selection should favour a cognitive apparatus capable of rapid and efficient social learning [17], which has been demonstrated in a range of species from fishes [27] to great apes [32].

Although intuitive and theoretically appealing, learning from others requires a number of important decisions. Most importantly, the learner needs some awareness of its own (in)competence before relying on others. Assessments of others' expertise are therefore required, for instance, who is and is not predator-savvy within the social unit. Pioneering work here is on adult vervet monkeys who will quickly learn to ignore the alarm calls of another that has turned out to be an unreliable signaller [3]. More recently, the same ability has also been shown in another context, by juvenile vervet monkeys directing their social attention to competent group members during foraging [11]. Equally relevant is a field

experiment with vervet monkeys, in which juveniles were exposed to unfamiliar raptor models in the presence of different audiences: mothers, siblings or unrelated group members [24]. Juvenile alarm calling turned out to be audience-dependent, with juveniles calling less in the presence of (competent) mothers and more in the presence of (incompetent) younger siblings, suggesting discriminatory abilities relating to others' competence when dealing with aerial predators.

Once a suitable model has been identified, what does a learner actually learn? Production and comprehension involve different processes, and here, many scholars have highlighted the staggering differences in flexibility between primates as signallers and as recipients, with low flexibility in call production and usage and high flexibility in call comprehension [7,41].

Socially scripted learning

Learning in primates and other animals usually takes place within a social sphere, when individuals are immersed in social interactions. Our claim here is that primates learn from watching others by incorporating new cause–effect relations to existing ones, both as passive observers and as active seekers of information, hereby constructing increasingly complex representations of how events normally unfold [38]. Scripts are often of a social nature, typically agent–patient interactions [44,48]. They contain core knowledge, a sort of innate understanding of the world that includes the perception of psychological intention [4] and physical causality [23], partly acquired from own experiences and partly from observing others. Script theory has recently been proposed as a way to 'deintellectualise' claims of mental-state attribution, including false-belief tasks [38], but it has broader implication for animal cognition, as a general account of how individuals make sense and predict the behaviour of others. In this view, learning is a continuous and incremental process of adding complexity and diversity to an individual's script repertoire by adding newly discovered cause–effect relations to already-existing ones.

What do primates learn?

Learning to predict

Regarding comprehension, primates (and many other animals) appear to be able to easily learn relations between arbitrary signals and external events, as demonstrated by great apes' understanding of human speech and sign language [48] or monkeys' understanding of other species' vocalisations [47]. Overall, primates behave as if their own and other species' calls contain (event-related) meaning, perhaps not unlike how human speech utterances convey (lexical) meaning [49]. But how do primates acquire such knowledge?

Early work on vervet monkeys showed that infants were more likely to respond correctly to alarm calls if they first looked at their mothers [33], suggesting that learning requires proactively seeking out cause–effect relation, for example, predator-specific alarm calls and the mother's reaction to them. Although already quite complex, the reality is probably even more challenging because alarm calls often refer to a multitude of events with different referents [1], suggesting that comprehension learning is a scaffolded and incremental process of refinement. This is well illustrated by a recent study during which young vervet monkeys, already familiar with conspecific leopard alarms, were experimentally exposed to a new danger, an unfamiliar animal model. During this simple experience, juveniles did (or did not) hear another group member's leopard alarms. The results showed that juveniles who encountered the model in conjunction with leopard alarms showed higher levels of vigilance in subsequent encounters, compared with juveniles without alarm calls [5]. One interpretation of this finding is that the meaning of a semantically already-defined alarm call can be further enriched during ontogeny to include new references. Importantly, the experience offered to the monkeys neither contained repeated trials nor negative or positive reinforcement, two pillars of associative learning accounts [30].

Learning to act

For production learning, that is, the ability to control the structure of sounds, primates rank at the other extreme end of flexibility in animal communication. Numerous studies have found that species, including great apes, are simply unable to mould their vocal output in any meaningful way, incapable of producing recognisable phonetic units or any similar properties of human speech (for potential precursors see, for example, Ref. [43]). The only consistent kind of documented production learning is in terms of subtle modifications of existing call types that are already part of the vocal repertoire [20]. Such accommodation or convergence of calls are typically responses to relationship variables, sometimes at the expense of individual recognition [50] and appear to be fairly widespread in primates, the result of sensory–motor integration also seen in humans [14,31,50,8]. Vocal production learning, in short, is very modest in primates, a likely consequence of poorly evolved motor control of the sound-production apparatus [19].

Nevertheless, primates are avid communicators with often rich, species-specific vocal and gestural repertoires. As a general pattern, different call types serve specific biological functions that emerge during tightly controlled developmental processes. Learning to use the calls mostly concerns the ability to inhibit call production under unfavourable circumstances. For example, chimpanzee females appear to be strategic in the production of their copulation calls [40], an ability that is

learned with increasing social cognition [6]. A second form of usage learning concerns the nature of the referents linked to a particular call type. Here, primates appear to have some flexibility in enriching the referential space of some call types. In a recent example, sooty mangabeys were presented with an unfamiliar danger — a chimeric animal model comprising both snake-like and leopard-like features — to which some juveniles responded in snake-like and others in leopard-like ways [21]. Adults, on the other hand, consistently ignored the model. In the experiment, juveniles were introduced to the chimera with playbacks of either snake or leopard alarms from another group member. A few hours later, juveniles were then retested with the chimera, and the results showed that their antipredator responses corresponded to the alarm-call type they heard during the experiment. Importantly, some juveniles actively produced their own (corresponding) alarm calls, demonstrating usage learning. Moreover, when retested again nearly two years later, most subjects continued to respond in the same way, suggesting stable and long-term social learning from one single learning experience. As with the previous vervet study [5], the experiment showed that primates can enrich the meaning of their own calls, in response to new evidence acquired from the behaviour of others. As for chimpanzee copulation calls, usage learning appears to follow comprehension learning.

Further relevant for usage learning is a long research tradition with the goal of conditioning primates to use calls in contexts for which they have not evolved, mainly to address questions about volitional control [37]. In a recent study, [12] managed to train two juvenile rhesus monkeys to vocalise on command, in order to obtain food rewards from their human caretakers. Interestingly, both individuals lost this ability in later adulthood, which led to the suggestion that the evolution of human vocal control was enabled by an evolutionary expansion of the juvenile period.

Although such studies demonstrate usage learning, it is important to point out that this is very different from how human infants learn to produce speech, by gaining increasing control over a highly flexible vocal repertoire, independent of emotional states or biological function [26]. But even though humans mainly communicate with speech, they have not lost their old, primate-like vocal behaviour. In a cross-cultural study, prelinguistic infants produced consistent vocal structures during key social acts — sharing, declaring, protesting or requesting — which were recognised cross-culturally by parents and, to a lesser degree, nonparents [18]. Such results suggest that the transition from primate vocal signals to human speech was probably gradual, fostered by an evolution of motor control of the vocal apparatus, much beyond what is available to nonhuman primates.

How do primates learn?

Animal learning theory

A pigeon in a skinner box will gradually learn to peck a key in response to light, provided the light reliably results in food: the pecking becomes operantly (instrumentally) conditioned. The same reasoning applies for classical conditioning when animals observe cause–effect relations: if a sound reliably precedes food, a dog will learn to perceive the sound as a predictor of food. Both types of conditioning, classical and instrumental, are gradual insofar as conditioning increases with each trial, provided there is occasional reinforcement [30]. This model of learning has been enormously influential and is still routinely invoked as the default mechanism, by reference to Lloyd Morgan's canon of parsimony [13,25].

Relevant in some of the previously discussed studies is that learning was often instant, requiring one single exposure, akin to fast mapping in language acquisition [16] with no obvious reinforcement. One-trial learning has long been known in taste-aversion learning [9], which has always constituted a problem for theories of conditioning. Rapid learning has also been shown in predatory situations [10,42], for example, when a predator is reintroduced to an environment, which requires rapid learning by prey species [2]. In sum, learning is possible from single experiences, in the absence of trial-and-error reinforcements, and can nevertheless be stably 'stamped into the mind'. This suggests that, under ecologically relevant situations, animal learning does not follow the basic laws of classic and instrumental conditioning theory.

Although there is no doubt that animals, including humans, can become conditioned in ways described by the Rescorla–Wagner model, there are reasons to remain sceptical about whether this is the default mechanism of learning. Many events, including sounds that predict food, are in reality caused by animate actors, and it is very likely that primates and other animals operate on this assumption [44]. Equally relevant is that in order to survive, animals have to learn countless evolutionarily relevant patterns that cannot be reduced to simple stimuli and do not offer systematic reinforcement experiences. This has been shown for spatio-temporal problems [15,39], social patterns [35,45] and predation events [46]. In sum, learning opportunities and learning demands in the real world are incredibly messy, hugely variable in appearance and massively inconsistent in their consequences and, yet, animals learn such patterns reliably, rapidly and effectively.

Conclusion

Learning and memory (i.e. mental representations) are fundamental notions in animal cognition. Yet, animal

learning theory is based on ecologically irrelevant experimental paradigms and data collected under highly unnatural situations, characterised by confronting animals to obscure cause–effect relations detached from real-world problems. However, primates and other groups of animals grow up in social worlds rich with events that unfold in predictable ways, suggesting that a major challenge during ontogeny is to assemble dispersed cause–effect relations into coherent scripts. Learning, in other words, is a social event that scaffolds on increasingly more complex mental representations of reality. Although there is a substantial literature on social learning in primates, empirical research has heavily relied on manipulative behaviour and physical cognition, mainly from great apes, resulting in theories with limited scope. Although the mechanisms of other essential skills, such as finding food, orienting in space, understanding social relations and so forth, are often extremely well studied, the development and learning of these skills are much less well understood. From the current literature, we conclude that classical conditioning theories are unable to explain many of these natural processes in the wild. Field experiments addressing questions in learning and social awareness are likely to result in better theories able to delineate the mental representations that primates are able to acquire and maintain.

Conflict of interest statement

No conflict of interest.

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