Experimental field studies with non-human primates

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Abstract

One way to study language evolution is to compare human communication with closely related non-human primate species. This comparative approach has turned to be especially productive if subjects are studied under natural field conditions in which they have evolved. Various observation techniques have been developed, but field experiments are often needed to clarify underlying cause-effect relations. Here, I review the main experimental designs that are suitable for primate fieldwork and discuss some scientific advancements that they have generated. Field experiments are notoriously difficult to carry out for a range of reasons that are discussed. Nonetheless, considerable progress has been made in recent years, including with great apes, which have traditionally been neglected in experimental research in the wild.

Introduction

How and why did humans evolve a communication system so radically different from other primates? An evolutionarily parsimonious scenario is that the key capacities, such as the abilities to control and combine articulatory manoeuvres, to take the audience into account, or to make inferences about the intended meaning of an utterance, have gradually evolved during human evolution and are derived from earlier forms of more primate-like communication systems. Investigating all this is not a trivial task, mainly because the fossil record generally reveals little about behavioural evolution. An alternative approach is to compare the communication behaviour of closely related modern primates; the comparative method. This requires detailed and careful field observations combined with focussed field experiments, ideally also with the great apes, our nearest living relatives.

This chapter reviews some of the scientific progress achieved by studying wild primates experimentally, including a discussion of the difficulties encountered by field workers, who address research questions this way. Lack of control over subject movements and audience composition, working with intelligent animals, and ethical issues relating to endangered species are some of the main obstacles that need to be addressed.

Primate communication and human language

Initially, researchers studying the relation of primate communication and language have largely worked in the laboratory, using artificial language systems [1]. Although this has led to substantial insights, an important concern has always been

that subjects had been trained to respond to various requests from their human trainers in order to earn food rewards, which has raised questions about evolutionary relevance. Unless similar capacities are expressed during natural communication, results from captivity may be irrelevant for theories of language evolution and better explained as the product of human enculturation or excessive training.

The natural communication of primates has been of longstanding scientific interest, perhaps starting with fieldwork by Carpenter in the 1930s [2]*. It has quickly become clear, from this and later research, that primates possess rich, species-specific repertoires with vocal, visual, and tactile signals that have specific social functions. Studying primate communication is of course worthy in its own right but many researchers have also wondered about the relation between primate and human communication and especially language. One relevant early finding came from fieldwork with vervet monkeys, which were observed to produce a range of acoustically distinct alarm calls to different predators [3]. Historically also important was a methodological breakthrough provided by a field study on gray-cheeked mangabeys in Uganda, which demonstrated to a wide scientific audience that playback techniques could be used to investigate the function of primate signals [4]*. Although playbacks had been used before with primates, possibly first by Garner in 1890 [5], the mangabey study demonstrated that the technique was suitable to address major questions in the field. Subsequently, Seyfarth et al. [6]* then carried out a first systematic playback study with fully habituated vervet monkeys to test whether their alarm calls conveyed something about the type of predator encountered by the caller. The striking finding was that subjects responded to the different alarm call playbacks as if the corresponding predator were present, which indicated that these calls conveyed very specific meanings. This landmark study thus provided the first conclusive evidence that non-human primates possessed communicative abilities to refer to external events with recipients capable of extracting meaning from the calls. Non-human primates, it was concluded, are capable of semantic communication, not fundamentally different from how humans extract meaning from speech utterances.

This early success was followed by a substantial, experimentally based research programme on free-ranging vervet monkeys, which revealed that the mental and social world of these primates was much richer than anyone could have imagined from mere behavioural observations [7]**. For example, it could be shown that monkeys recognised each other individually by their vocalisations [8], that some calls consisted of acoustic variants with distinct functions [9], that individuals were more willing to aid unrelated individuals if those individuals have behaved affinitively towards them in the past [10], or that individuals who had learned to ignore one call type by an unreliable signaller subsequently also ignored other calls by the same individual [11].

Playback techniques soon became a popular research tool for primate fieldworkers to address a range of biological questions, which resulted in a large literature by the end of the 20th century, including studies on intergroup interactions in titi monkeys [12], gibbons [13], howler monkeys [14] and pig-tailed macaques [15]; long-distance communication in orang-utans [16], mating strategies in gibbons [17], [18], [19] and Barbary macaques [20], call perception and categorisation in Japanese and Barbary macaques [21] [22]; call exchanges in Japanese macaques [23]; alarm calling in lemurs [24], [25], diana monkeys [26], Barbary macaques [27], bonnet macaques [28]; polyspecific grouping and anti-predator behaviour in forest monkeys [29], [30], [31]; social cognition in baboons [32]; mental representations in diana monkeys [33], [34,35]; individual recognition in Barbary macaques [36], rhesus

macaques [37], [38] and spider monkeys [39], [40]); foraging behaviour in gray-cheeked mangabeys ([41]); or inter-specific communication in macaques [42] and guenons [43]. This development has continued almost exponentially into the new millennium with an increasing number of species being tested with experimental techniques with one interesting exception, the great apes. The reasons for this will be discussed below.

Experimental designs

Before planning a field experiment, researchers typically spend considerable time describing the natural behaviour patterns using traditional, well established observation methods [44]. Once the main patterns become visible, a number of choices are available to test the causal structure of the data with specific hypotheses.

A general point to consider for any experimental intervention is the quality and authenticity of the stimuli. Ideally, subjects should not realise that they are being tested, which requires stimuli that closely resemble the real object or event that they simulate. For playback experiments, high quality recordings are therefore very essential, while the loudspeaker should not be visible but broadcasting from a plausible direction (see below, [45]).

Natural experiments

Fieldworkers often struggle with the fact that evolutionarily important events, such as encounters with predators, are rare or difficult to observe. The problem can be addressed by what is sometimes called a 'natural experiment'. This is not a true experimental manipulation but an intervention conducted to produce a systematic and large dataset. Strictly speaking, natural experiments are just observational studies as they lack the controls of a randomised experiment.

An early, dramatic example for an natural experiment is Kortlandt's report of antipredator behaviour by wild chimpanzees involving cooperative defence and the use of weapons, triggered by presenting a mobile stuffed leopard [46]*. A related more recent example is a study with free-ranging leopards to investigate primate alarm calling behaviour [47]. Here, the 'natural experiment' consisted of capturing and radio-tagging wild leopards in Tai Forest, Ivory Coast, and following them through the forest to monitor their hunting behaviour and the primates' corresponding anti-predator responses (fig. 1). One finding was that leopards spent extended periods of time hiding in the vicinity of monkey groups, but moved on as soon as detected by the monkeys -- valuable information that would have been extremely difficult to obtain with naturalistic observations alone.

-- Figure 1 --

Controlled experiments

Habituating wild primates to human observers is a lengthy, difficult and often costly process, which can take several years [48]. As a result, primate fieldwork is almost always plagued by small sample size, to the effect that within-subject designs are often the only possibility. Between-subjects designs are also possible, for example if a large number of primate groups are available for sampling [49]. The advantage is that each group can only be tested once, which removes concerns about dependent data. A recent example for a within-subjects design is a study with five putty-nosed

monkey females. This monkey species is interesting because adult males combine two vocalisations, pyows and hacks, into different call sequences that are linked to specific external events [50]*. Series consisting of 'pyows' are a common response to leopards, while 'hacks' or 'hacks' followed by 'pyows' are regularly given to crowned eagles. However, males also produce sequences consisting of several 'pyows' followed by several 'hacks', which reliably predicts forthcoming group progression, regardless of context [51], [52]. In playback experiments, the females' reactions to their own male's 'pyows', 'hacks' and 'pyow-hack' sequences were tested. It was found that the subjects started group progressions after hearing 'pyow-hack' sequences and also responded appropriately to the other call series [53]. This within-subjects design revealed that, in this primate, meaning is encoded at the level of call sequences, not just the individual calls, despite a very small number of subjects (fig. 2).

-- Figure 2 --

Complex designs

Sound playbacks have also been used in more elaborate designs, for instance in combination with real-life events or to in order to simulate two separate events. A recent example is a study on triadic awareness in chimpanzees [54]. Here, a subject was followed until a real agonistic interaction occurred with another group member. Provided no reconciliation took place, the researchers then continued to follow the subject and, after an average of two hours, they played back the aggressive barks of an ally (or non-ally) of their former opponent (fig. 3). Subjects responded in ways that suggested they were aware of the social relationships of other group members, i.e., who was likely to support whom, regardless of genetic ties.

-- Figure 3 --

An example of a two-events design is a playback study on mate guarding behaviour in baboons [55]. In this species, dominant males try to monopolise access to oestrous females to form 'consortships'. In the experiment, subjects heard a consorting male's grunts and an oestrous female's copulation calls in close succession but from two different speakers positioned 40m apart. This suggested to listeners that the male and female had separated and that she was now copulating with another male. As predicted, subjects reacted more strongly to this situation compared to when the female's copulation calls were combined with the grunts of a non-consorting or a formerly consorting male.

Two-events designs have also been used to simulate rank reversal in social groups [56]**, [57] and temporal separation between events [34]. For example, in putty-nosed monkeys, two disturbances (eagle attack or falling tree) were combined with male alarm calls about 30s later [58]. Results showed that listeners considered the previous contextual information as the likely cause for the subsequent alarm calls, suggesting that pragmatic factors are important in call interpretation in primates. An important type of two-event design is the 'habituation-dishabituation' experiment. Here, the goal is to study the effects of experience with one type of stimulus on how subjects respond to a second type of stimulus. These designs are suitable, for example, to investigate perceptual discrimination [22], psychoacoustics [59], or the conceptual organisation underlying communication [33].

Visual stimuli

Although playbacks are probably the most popular type of field experiments, they are by no means the only ones. In the early days of primatology, researchers carried out experiments by capturing and translocating live animals [60]*. Nowadays, this is usually done by broadcasting vocalisations, mainly because of the stress caused by capturing and moving animals between social groups.

Field experiments can also be based on the systematic presentation of objects with specific significance, such as food, predators, conspecifics or tools. Visual stimuli have been used to study economic decision-making [61], social learning [62], individual learning [63], cultural behaviour [64]; [65], or decision-making [66]. Predator presentations also have a long history in primate fieldwork [46], for instance to study anti-predator behaviour, mixed-species grouping or cognition [67], [68]*, [69], [70], [71], [51]. Finally, object presentations can be particularly useful in studies of tool use, with a large number of examples in the recent literature, especially on chimpanzees and capuchin monkeys [72], [73], [74].

Experimenting with intelligent species

Much scientific progress has been made in the last 40 years since field playbacks have been introduced to primatology. At the same time, however, researchers working with great apes have tended to shy away from field experiments, and it is interesting to explore the underlying reasons. One concern has to do with the advanced mental capacities of great apes, and the related question of whether it is possible (and morally acceptable) to produce meaningful results by interfering with their natural lives. Indeed, recent experience has shown that one great difficulty of working experimentally with great apes is to create plausible and credible situations, so that subjects do not realise that they are being tested, as is routinely done in human social psychology.

Some of the first field experiments with great apes have been in relation to long-distance calls, which are relatively easy to carry out (orang-utans [16]; chimpanzees [75], [76]), but it has long remained controversial whether playbacks are equally suitable to study close-range communication and cognition. A first attempt was a study by Slocombe et al [77]**, who tested whether chimpanzees could discriminate between different types of screams. The study is mainly relevant for its methodological advance because it illustrates, in great detail, the conditions that have to be in place for a successful playback experiment with socially highly aware animals (fig. 4).

-- Figure 4 --

Another reason why researchers of great apes have avoided field experiments is the possibility that experimental manipulations may have unwanted long-term effects. For example, Clarke et al. [78] found that Lar gibbons showed long-term behavioural effects hours after exposure to a predator model. A sensible way to avoid negative consequences is to work with stimuli that already occur regularly in the animals' natural lives. For example, although it is possible to simulate rank reversals in primates [56]**, designing such an experiment that involves the alpha male of a

chimpanzee group may be ethically irresponsible. Changes in the alpha position can have severe, sometimes violent, implications for other group members, suggesting that this topic should not be investigated experimentally. This example again highlights the fact that playback experiments need to be grounded in careful, long-term behavioural observations and a profound knowledge of the study animals in order to be effective and appropriate.

Another difficulty with working with great apes is that administering experimental trials is often extremely time-consuming, necessitating careful planning. For this reason alone, the number of trials per individual needs to be kept to a minimum, ideally to one trial per condition. Retesting subjects with the same stimulus can be problematic, due to unwanted learning effects across trials. But sometimes this is necessary, for example if responses are subtle or to capture important intra-individual variation. To determine the maximally acceptable exposure rate per individual, a sensible approach is to determine the mean rate at which a test stimulus occurs under natural conditions. These principles have recently been applied to study the cognition, communication and culture of the Sonso chimpanzee community in Budongo Forest, which led to some progress regarding their cognitive capacities underlying communication and culture [50,52-54,64,67,68,72,79-81].

Ethics

Field experiments are an intrusion into the natural life of an animal and this can raise ethical issues. Some primate groups may contain vulnerable members or are ecologically challenged, so that researchers may decide against experimental interventions. For example, it may be unwise to induce anti-predator behaviour in mothers with newborn offspring, who may accidentally harm them during escape or be prevented from feeding. Some interventions, such as providing food, can facilitate disease transmission, alter the feeding habits of subjects or change their relationship to humans. Some populations are threatened by extinction, which may suggest that conservation research should be prioritised over basic research.

It is essential that researchers consider carefully whether a planned experimental intervention may be harmful and could have adverse long-term effects. Predation, aggression and intergroup encounters are natural components of a primate's life and there is no reason these topics should not be investigated in a scientifically rigorous way. However, it is good practice to have field experiments assessed by an independent ethics review board, which has the necessary expertise, so that adequate ethical standards are guaranteed. This is also in the self-interest of the researcher as it provides protection from judgement errors and is often a precondition for publication.

Conclusions

Field experiments are a powerful tool to study primate behaviour. Various procedures have been developed over the years, but virtually all depend on a robust understanding of the natural behaviour patterns of the study animals. As such, field experiments are usually the final step in a research programme, to test the causality of hypotheses obtained from observational studies. The most common techniques involve simulating the presence and behaviour of other individuals, by playing back

their vocalisations, but object presentations have also been used in various ways. Careful planning and piloting is almost always essential and researchers are advised to have their plans reviewed by an ethics board. A good strategy is to develop an experimental design that allows test stimuli to be blended into the subject's natural environment. This way, field experiments are likely to create responses that are evolutionarily relevant, socially meaningful and theoretically interpretable.

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