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Representational signalling in birds

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Some animals give specific calls when they discover food or detect a particular type of predator. Companions respond with food-searching behaviour or by adopting appropriate escape responses. These signals thus seem to denote objects in the environment, but this specific mechanism has only been demonstrated for monkey alarm calls. We manipulated whether fowl (*Gallus gallus*) had recently found a small quantity of preferred food and then tested for a specific interaction between this event and their subsequent response to playback of food calls. In one treatment, food calls thus potentially provided information about the immediate environment, while in the other the putative message was redundant with individual experience. Food calls evoked substrate searching, but only if the hens had not recently discovered food. An identical manipulation had no effect on responses to an acoustically matched control call. These results show that chicken food calls are representational signals: they stimulate retrieval of information about a class of external events. This is the first such demonstration for any non-primate species. Representational signalling is hence more taxonomically widespread than has previously been thought, suggesting that it may be the product of common social factors, rather than an attribute of a particular phylogenetic lineage.

Keywords: referential signalling;
representational signalling; animal cognition;
food calls

1. INTRODUCTION

Some animal calls have the unusual property of seeming to denote environmental events. Such *referential signals* are produced in response to specific stimuli (e.g. approach of a particular predator and discovery of food) and are sufficient to evoke from companions the full suite of appropriate responses (e.g. adaptive escape behaviour and food search). Given the cognitive sophistication implied by such systems, it was logical for initial research to concentrate on non-human primates, beginning with vervet monkeys (*Cercopithecus aethiops*; Seyfarth *et al.* 1980). A flurry of recent papers has revealed that referential signalling may be relatively widespread. For example, it is also present in other cercopithecines (Zuberbühler 2000*a*,*b*, 2001), tufted capuchins (*Cebus apella nigritus*; Di Bitetti 2003), lemurs (Macedonia 1990), at least one non-primate mammal (suricates (*Suricata suricatta*); Manser 2001; Manser *et al.* 2001) and several species of birds, including fowl (Evans *et al.* 1993; Evans & Marler 1994; Evans & Evans 1999), ravens (Bugnyar *et al.* 2001), yellow warblers (*Dendroica petechia*; Gill & Sealy 2004) and black-capped chickadees (*Poecile atricapilla*; Templeton *et al.* 2005).

Referential signalling is controversial because it potentially extends the parallels between animal communication and language (Hauser 1996; Evans 1997; Fitch 2005), long considered the principal exception to an otherwise clear pattern of evolutionary continuity (Darwin 1871). Some linguists accept that there is evidence for a primitive type of reference in animal communication (Bickerton 1990; Pinker 1994); others stress the apparent lack of volitional control and conclude that such analogies are not compelling (Lieberman 1994). Similarly, some biologists have objected that referential signals may reveal only the subsequent behaviour of the sender (Smith 1991) or that it is not useful to think of animal signals as containing information at all (Owings & Morton 1998). In sum, conventional studies of call production and playback experiments can establish only that animals behave *as if* their signals describe external events.

The central issue in this debate is both straightforward and empirically accessible: it concerns the cognitive processes that must be invoked to explain the observed pattern of receiver behaviour. Words derive their meaning from mental representations that correspond to stimulus categories. If referential signals and language are truly analogous, then they should similarly evoke representations of the eliciting event (i.e. stimulate retrieval of stored information that then determines receiver response). This property would correspond to Gallistel's 'nominal representation' (1990), which is the lowest level of cognitive complexity: it would establish that calls 'stand for' something in the environment. The design of most previous studies has not allowed exclusion of more parsimonious alternatives, such as the possibility that referential signals might simply trigger appropriate motor patterns in a reflexive way (Wallman 1992; c.f. Zuberbühler *et al.* 1999; Zuberbühler 2000*a*,*b*). If this were so, then the apparent similarity with language would be illusory.

Food calls are widespread in primates (e.g. Dittus 1984; Elowson *et al.* 1991; Hauser 1998; Slocombe & Zuberbühler 2005) and social birds (e.g. Williams *et al.* 1968; Stokes 1972; Collias 1987; Bugnyar *et al.* 2001). Previous work with fowl has shown that these structurally distinct sounds are referential signals; they are produced when food is discovered (Evans & Marler 1994) and evoke anticipatory feeding behaviour in receivers (Evans & Evans 1999). To evaluate whether this response is mediated by a representation, we adopted the logic of closely analogous learning experiments (Colwill & Rescorla 1985; Holland 1990; Hall 1996) and used a manipulation of experience. We reasoned that if food calls encode information about feeding opportunities, then the effects of playback should be specifically affected by the prior discovery of food, while the same experience should cause no change in responsiveness to control calls of a different type. Neither of these predictions is generated by the various non-representational models of call processing (Smith 1991; Wallman 1992; Lieberman 1994; Owings & Morton 1998).

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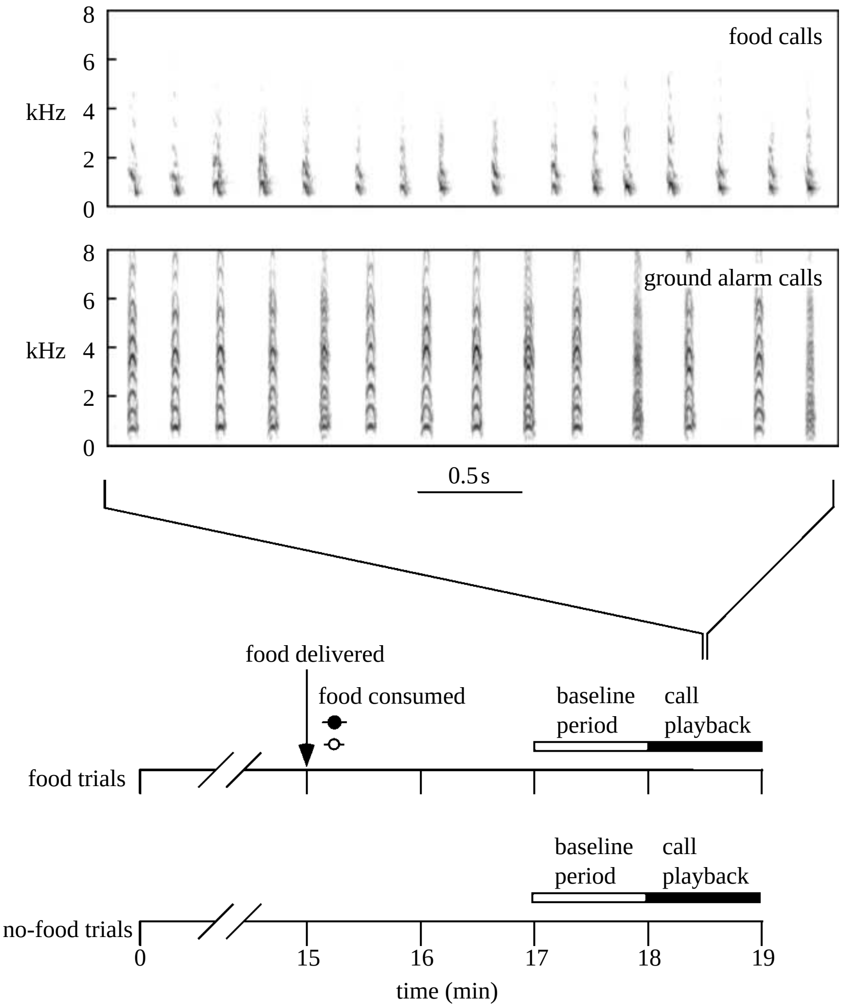

Figure 1. Experimental protocol and playback stimuli. In a randomly determined half of the tests (food trials), food call and ground alarm call sounds were preceded by a delivery of corn kernels. The other half of the tests conducted were controls in which these sounds were played after the same delay, but without a food presentation (no-food trials). Mean (±3 s.d.) duration of feeding bouts is indicated (filled circle, feeding prior to food calls; open circle, feeding prior to ground alarm calls). Food searching behaviour was measured during the playback and an equivalent baseline period. Spectrograms (frequency resolution 350 Hz) depict short sections from one pair of exemplars.

2. MATERIAL AND METHODS

(a) *Subjects*

Our subjects were adult golden Sebright bantam hens, a strain selected because it has not been subjected to artificial selection for rapid growth or egg production. There are no differences in call structure or repertoire size between Sebrights and the red jungle fowl (*Gallus gallus*), from which all domesticated breeds have been derived. We tested 17 birds individually in a sound-attenuating chamber (see electronic supplementary material for additional details).

(b) *Experimental design and test protocol*

Hens received playbacks of food calls and ground alarm calls in separate trials (see electronic supplementary material for examples of these sounds). Ground alarm calls were selected as a control because they match closely the acoustic structure of food calls (figure 1), but they have very different eliciting conditions (Evans *et al.* 1993). Each call type was played back both shortly after three fresh corn kernels had been delivered from a concealed hopper onto the cage floor and without such a pre-playback experience (figure 1). This manipulation was designed to change the hens' experience of the test environment, so that a preferred food item had just been discovered in one condition, but not the other. Planned statistical comparisons tested for an interaction between pre-playback experience and signal type.

(c) *Analysis of video-recorded responses*

We examined test session videotapes frame-by-frame (temporal resolution 40 ms) and measured the time that hens spent in close frontal inspection of the substrate (figure 2) to measure the anticipatory feeding response evoked by sound playbacks. This behaviour is characteristic of the search for small food items in fowl (Andrew & Dharmaretnam 1993; Evans & Evans 1999). Scoring was done blind to experimental condition.

3. RESULTS

Hen responses varied significantly as a function of experimental treatment (repeated measures ANOVA: $F=4.406$, d.f. $=3,48$, $p=0.008$) and the effects of manipulating their recent experience interacted with those of call type, precisely as predicted by a representational model. Playback of food calls evoked anticipatory feeding behaviour at almost three times the baseline rate, but only when this signal had not been preceded by discovery of food (figure 2). In no-food trials, hens responded to food calls by searching the substrate significantly more than in trials with matched ground alarm calls (paired $t=2.98$, d.f. $=16$, $p=0.009$). This difference was completely abolished by consumption of a few corn kernels 3 min before sound playback (paired $t=0.25$, d.f. $=16$, $p=0.808$).

Discovery of food also reduced the subsequent response to food calls specifically (figure 2). Substrate search during food call playback in food trials was

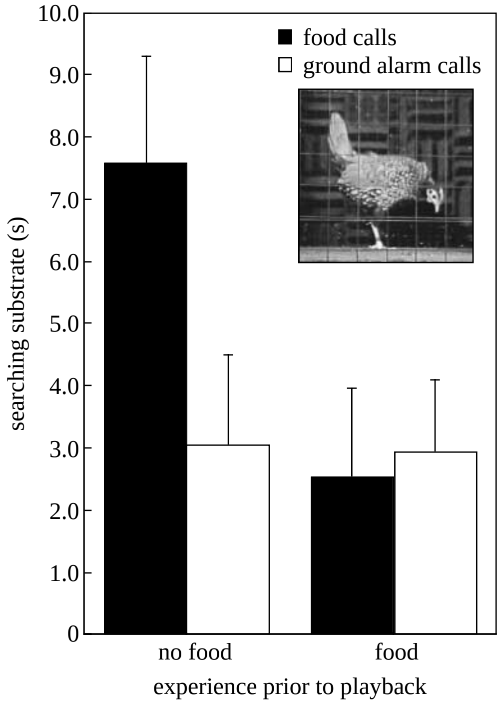

Figure 2. Effects of food call and ground alarm call playback. Hens responded to food calls with close frontal inspection of the substrate (inset), but only when these sounds had not been preceded by a food delivery. Results plotted are mean (+s.e.) difference in duration of substrate search, relative to the 60 s baseline period. Inset was taken from a single test session video frame.

significantly less than that in no-food trials (paired $t=3.87$, d.f. $=16$, $p=0.001$). In contrast, the duration of substrate search during control ground alarm call playbacks was unaffected (paired $t=0.08$, d.f. $=16$, $p=0.935$). This comparison allows us to reject the possibility that ingesting preferred food caused some global change in responsiveness to conspecific calls.

4. DISCUSSION

These results demonstrate that chicken food calls evoke selective retrieval of information about the discovery of food. When heard in a setting in which corn had not recently been found, they triggered characteristic searching behaviour (figure 2). In contrast, the same signal heard minutes after ingesting a small quantity of food had no effect. Our interpretation is that under these conditions, the food calls provided no new information about the hens' immediate environment. We conclude that the cognitive processes engaged by these avian signals include nominal representations, which may prove to have properties in common with those that have been revealed in studies of associative learning (Gallistel 1990; Shettleworth 1998). To our knowledge, this is the first demonstration of representational signalling in any non-primate species.

It may be surprising that these data have been obtained in studies of a social bird, rather than in a group phylogenetically closer to humans. We suggest that representational signalling is not as taxonomically limited as the pattern of previous findings might imply, but rather a property of several quite diverse taxa, perhaps arising from particular patterns of relatedness within stable social groups (Fitch 2005). Our findings encourage comparative studies to identify the common factors responsible for the evolution of such signal systems.

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