



Violated expectancies: Cause and function of exploration, fear, and aggression



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ABSTRACT

To be able to reproduce, animals need to survive and interact with an ever changing environment. Therefore, they create a cognitive representation of that environment, from which they derive expectancies regarding current and future events. These expected events are compared continuously with information gathered through exploration, to guide behaviour and update the existing representation. When a moderate discrepancy between perceived and expected events is detected, exploration is employed to update the internal representation so as to alter the expectancy and make it match the perceived event. When the discrepancy is relatively large, exploration is inhibited, and animals will try to alter the perceived event utilizing aggression or fear. The largest discrepancies are associated with a tendency to flee. When an exploratory, fear, or aggressive behaviour pattern proves to be the optimal solution for a particular discrepancy, the response will become conditioned to events that previously preceded the occurrence of that discrepancy. When primary needs are relatively low, animals will actively look for or create moderately violated expectancies in order to learn about objects, behaviour patterns, and the environment. In those situations, exploratory tendencies will summate with ongoing behaviour and, when all primary needs are satiated, may even be performed exclusively. This results in behavioural variability, play, and active information-seeking.

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1. Introduction

After I received my PhD at the University of Groningen in the Netherlands (van Kampen, 1993), I spent almost a year at the University of Toronto in Canada, working in the lab of Prof. Jerry Hogan. While I was there, I wrote a paper on filial imprinting, in which I analyzed the process through which newly hatched precocial birds learn to recognize their mother, by referring to the same mechanisms as are generally assumed to play a role in perceptual and associative learning (van Kampen, 1996). For this analysis of imprinting and the development of social attachments I used the framework formulated by Hogan (1988) to study the development of behaviour systems in general. Hogan (1988, 2001) proposes that the behaviour we observe is the result of some interaction between three basic mechanisms that are all viewed as corresponding to structures within the central nervous system: the perceptual, motor, and central mechanisms. Any organization of these

mechanisms that acts as a unit during a particular basic motivational state, such as hunger or sex, is defined as a behaviour system, in this case the feeding system and the sexual system. The reason I went to Toronto in the first place was to study courtship food-calling in Burmese red junglefowl (*Gallus gallus spadiceus*) (van Kampen, 1994, 1997; van Kampen and Hogan, 2000). Interestingly, for both imprinting and food-calling the involvement of exploration, fear, and aggression appeared to be an important factor.

Much literature is available on the relationship between exploration and fear on the one hand and aggression and fear on the other. Exploration-fear is often referred to as “approach-avoidance” (Montgomery, 1955) and is mostly described for non-social contexts. Montgomery hypothesized that behaviour elicited by unfamiliarity is the result of a competition between the conflicting motivations to approach out of curiosity and to avoid out of fear. Aggression-fear is often referred to as “fight-or-flight” (Cannon, 1929) and is mostly described for social contexts. Cannon described the “fight-or-flight” response as an automatic physiological reaction to potentially dangerous situations, preparing the body for immediate action.

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The papers I wrote aroused my curiosity as to the relationship between exploration, fear, and aggression, and prompted me into exploring the available literature. The result of my exploration will be presented here. However, it is not my intention to provide a comprehensive review of the existing literature and theories; rather, I want to present the selective overall picture that imposed itself upon me, and that is consistent with the results of my experiments. The literature shows that an adequate analysis of these three behaviour systems cannot be formulated in behavioural terms alone, but must for instance utilize cognitive concepts (cf. Berlyne, 1954; Hebb, 1946). In the present context I use the term “cognition” to refer to the central processes that mediate between perception, predispositions, and experience to produce behaviour (cf. Zajonc, 1984), without wanting to imply – or deny for that matter – any form of conscious processing. Furthermore, cause and function of exploration, fear, and aggression can only be fully understood when put into the broader perspective of the causation and function of behaviour in general.

First I will describe imprinting and food-calling in some more detail, as case studies on the interaction between exploration, fear, and aggression and other behaviour systems. Next, I will provide a theoretical background on the causation of behaviour from a cognitive perspective that fits well with the ethological concept of behaviour systems that I used to analyze imprinting and food-calling in the original papers. More specifically, I will describe how an animal creates an internal cognitive representation of its environment and how the interaction between this representation and the perception of external and internal stimuli results in a decision to perform certain behaviour. Along the way, but at different points in the story, exploration and fear on the one hand and aggression and fear on the other will be discussed in their causal and functional context. In a concluding section I will bring together the relationship between cause and function of exploration, fear, and aggression into an overall picture utilizing the presented cognitive concepts.

2. Case studies

2.1. Filial imprinting

Filial imprinting is the process through which early social behaviour of precocial birds becomes restricted to the mother and siblings (Lorenz, 1935). This process begins when the first conspicuous object encountered captures the attention of a hatchling, resulting in the gradual formation of a representation of that object in the memory system through perceptual learning (see below). First approach to such a stimulus is “prefunctional” (Schiller, 1949/1957); that is, functional experience is not necessary for its occurrence (Hogan, 1988). Approach appears to be the result of exploration (Sluckin, 1972), mediated by the reinforcing properties of sensory stimulation (van Kampen, 1996). Indeed, “information content” (Matthews and Hemmings, 1963) or “conspicuousness” (Baerends, 1982; Bateson, 1964a) is crucial in determining the effectiveness of an artificial object as imprinting stimulus (van Kampen, 1996).

After the first internal representations of external stimuli have been stored, unfamiliar stimuli start eliciting fear, thereby ending the “sensitive period” of imprinting (Bateson, 1966; Salzen, 1962). Functional experience with the fear-reducing property of the familiar imprinting stimulus will condition its representation to the central mechanism of the filial, or attachment, system through associative learning (van Kampen, 1996; see below). Similarly, it has been suggested that in the development of feeding and

dustbathing,¹ first attention to relevant external stimuli is mediated by exploration and subsequently representations become attached to the respective central mechanisms as a result of at least some functional experience (Hogan, 1994a; Vestergaard and Hogan, 1992).

The central mechanism of the filial system contains two parts, an appetitive mechanism that is activated by fear (Salzen, 1962; van Kampen, 1996) and a consummatory mechanism that propagates exploration by inhibiting fear (Rajecki et al., 1978; van Kampen, 1996). In this way the imprinting object functions as a “secure base” (Bowlby, 1969; Harlow, 1958) and the filial system regulates the balance between exploration and fear (van Kampen, 1996). An optimal balance between exploration and fear affects the cognitive development of an animal by mediating the amount and quality of early experience (Denenberg, 1967), leading to optimal adaptive behaviour in adulthood (Schultz, 1965; Hofer, 1987; Kraemer, 1992). Moreover, besides inhibiting fear, secure attachment also inhibits the activation of aggression (Bowlby, 1969; Hoffman et al., 1975), suggesting that the filial system may also play a role in the development of a balance between aggression and fear (van Kampen, 1996). An optimal balance between aggression and fear has been shown to be crucial for the development of adequate social behaviour (Bowlby, 1969; Kruijt, 1964).

2.2. Courtship food-calling

In the previous subsection, I mentioned that in the development of the feeding system of chickens first attention to relevant external stimuli is mediated by exploration. Indeed, newly hatched chicks peck at a wide variety of objects, although certain colours and shapes are preferred. Interestingly, items with certain striking characteristics, such as feathers, dried faeces, mealworms and other insects, elicit “food-running” in young chicks (Hogan, 1965, 1966; Kruijt, 1964). During food-running, a chick picks up an item and starts running around keeping it in its bill, meanwhile producing loud, rapidly repeated peeping. Other chicks and the mother hen often pursue the food-running chick. Mother may take over the prey, kill it, and smash it to edible pieces. Kruijt (1964) interpreted food-running as a conflict between the tendencies to manipulate the item and to flee, and showed that juvenile food-running is the ontogenetic precursor of maternal and courtship food-calling.

Food-calling, also known as tidbitting (Domm, 1927), typically consists of rhythmically repeated calls made while frequently picking up and dropping an edible or inedible object that is usually not swallowed (Kruijt, 1964). Besides being performed by a mother hen (Stokes, 1971), it is also one of the displays generally performed by male fowl during courtship, together with for instance waltzing and rear-approach (Kruijt, 1964; Wood-Gush, 1956). Waltzing is a complex lateral display during which a male advances sideways in a circular movement with his back and shoulders nearest to the female kept lower than the outer side, and the primaries of the outer wing lowered. In rear-approach a male abruptly approaches a female from behind with his ruff raised. Both displays, but especially rear-approach (McBride et al., 1969; van Kampen, 1994), may induce the female to perform the sexual crouch, which is a specific squatting posture with slightly raised wing bows, allowing the male to mount and copulate. During ontogeny, crouching is likely to have developed out of “squatting,” which is also the precursor of freezing (Kruijt, 1964), suggesting the involvement of fear.

¹ Dustbathing is a maintenance behaviour consisting of a sequence of coordinated movements of wings, feet, head, and body, which serves to spread dust through the feathers in order to remove excess lipids and maintain good feather condition (e.g. Vestergaard and Hogan, 1992).

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