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Review

Representation in development: From a model system to some general processes

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ABSTRACT

The view that filial imprinting might serve as a useful model system for studying the neurobiological basis of memory was inspired, at least in part, by a simple idea: acquired filial preferences reflect the formation of a memory or representation of the imprinting object itself, as opposed to the change in the efficacy of stimulus-response pathways, for example. We provide a synthesis of the evidence that supports this idea; and show that the processes of memory formation observed in filial imprinting find surprisingly close counterparts in other species, including our own.

Contents

1. Filial imprinting as a representational process

The choice to use filial imprinting in chicks as a model system to study the neurobiological basis of memory is one that Gabriel Horn recounted with undiminished enthusiasm, both privately and publicly (e.g., Horn, 1985, 2004). It is undoubtedly the case that watching chicks develop a preference to approach a familiar object creates a vivid impression; but it also enables the kind of experimental control that is perhaps unrivaled in vertebrate species: day-old chicks enter the experimental setting having experienced rather little, but being highly mobile and ready to learn. As with the choice of many model systems, however, one immediately faces a conundrum: will the unique appearance of the system be a consequence of some relatively specialized underlying conceptual or neural process, or will its surface characteristics belie the generality of the processes that are involved. From a purely academic stance, the two scenarios are of equivalent interest; but a model system should provide information that transcends itself. Why should the study of filial imprinting yield such generality?

We review evidence that provides support for the idea that filial imprinting involves, among other things, processes of representation formation, wherein the different views afforded by interaction with the imprinting object become bound to one another and distinguished from otherwise equivalent novel objects. Gabriel Horn's academic partner and friend Patrick Bateson coined the terms 'classification together' and 'classification apart' for these processes of representational change (Bateson and Chantrey, 1972; see also, Bateson, 1964, 1990; Hollis et al., 1991). And in many ways this characterization of filial imprinting anticipated that its study would provide general insights: at a behavioral and neurobiological level. The early fruits of their collaboration (e.g., Bateson et al., 1969; Horn et al., 1971) set the tone for the continuing interaction between the study of behavioral and brain processes (for a review, see Bolhuis and Honey, 1998; Horn, 1998) that would serve as a model to others. Before describing some of the striking parallels between the behavioral processes involved in filial imprinting and those that contribute to other forms of learning, it is informative to contrast its characterization as involving representational processes with a more prosaic analysis. In

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doing so, we introduce theoretical analyses and behavioral procedures that provide immediate points of contact between filial imprinting and other forms of (perceptual and associative) learning.

The bare fact that chicks develop a tendency to approach a familiar object in preference to other novel objects might simply reflect the rapid strengthening of a set of stimulus-response links involving the features of the training object and the approach response. Indeed, in the neural net model developed in Bateson and Horn (1994), but conceived at a much earlier date, there are such links that generate (nonselective) approach at the outset of imprinting training. The inclusion of such links is not only consistent with the behavior of naïve chicks, but also reflects Horn's earlier analysis of habituation. In this case, it was the decline (rather than a strengthening) in the efficacy of the stimulus-response links that was held to play a central role in behavioral habituation (Horn and Hill, 1964; Horn, 1967; see also, Groves and Thompson, 1970). Returning to imprinting, an increase in the strength of stimulus-response links will explain, for example, the orderly generalization of an imprinting preference to objects that share features with the training object (see Bolhuis and Horn, 1992). One compelling reason to doubt the adequacy of a purely stimulus-response analysis comes from examining the influence that imprinting training has on the acquisition of a reinforced discrimination; and specifically a discrimination where direct transfer of the tendency to approach the imprinting stimulus should confer no direct benefit. Under these conditions, there are no obvious grounds for a stimulus-response analysis to predict any effect. In contrast, the view that imprinting involves processes of representation formation anticipates that chicks possessing a representation of the imprinting object might learn such a discrimination more rapidly; assuming that the representations formed during imprinting are also available to the processes of associative learning. Such processes of representation formation were captured within the Bateson and Horn (1994) model by the formation of links between the different features of the imprinting stimulus and a shared "recognition" unit that sat between the feature analysis units and response units that generate behavior.

The first evidence that directly implicated such representational processes in the development of filial preferences came from an early study by Bateson (1964), who demonstrated that imprinting training improved later discrimination learning under the circumstances outlined in the previous paragraph: where the approach behavior generated by imprinting training should certainly not directly improve discrimination performance. This effect has been replicated and extended (Honey et al., 1993; see also, Chantrey, 1972; Kovach et al., 1966; Polt, 1969) in the context of developing an automated behavioral assay of imprinting and discrimination learning that was later used to assess the neurobiological basis of memories formed during imprinting training (Honey et al., 1995). Honey et al. (1993) first gave chicks imprinting training with either one visual image (B; e.g., a geometric figure) or another image (C; a different figure); with the chicks sitting in a running wheel facing the screen onto which these images were projected. Both groups of chicks then received a discrimination in which two geometric forms (A and B) were simultaneously presented in a chamber that was sufficiently chilly (15 °C) to motivate them to learn to approach A (and not B) in order to receive the delivery of a stream of warm air (see also, McCabe et al., 1982; Zolman, 1968). Those chicks that had received imprinting training with B acquired the discrimination more rapidly than those given imprinting training with C. This finding is an example of a phenomenon known as perceptual learning (e.g., Gibson, 1969) and establishes a *prima facie* case that filial imprinting involves processes of representation development that have been taken to underpin this phenomenon.[1] Additional findings, that we now describe, have shaped a more detailed understanding of the nature of the processes involved. These findings and the conclusions that follow from them appear to have broad generality.

2. Classification together and representational updating

As already noted, the fact that naïve chicks quickly form a stable attachment to the mother hen, and other more arbitrary and mundane objects (see below), are desirable features for a model system of memory formation. That these features are evident in spite of the visual characteristics of the mother hen (for example) changing in the short term (e.g., with the vantage points of the chick; e.g., Lorenz, 1937) has guided theoretical analyses of the nature of the processes of memory formation: the specific physical characteristics of the mother hen are clearly rapidly encoded and the resulting memories updated when these characteristics gradually change (see, for example, Bateson and Horn, 1994). How animals remember individuals (e.g., caregivers) who change over time (in either the short or longer term) is an interesting general issue in the context of understanding of developmental processes including filial imprinting, but it also has broad theoretical significance: influential 'exemplar' models of memory assume that each new pattern of characteristics is establishes a new memory (e.g., Hintzman, 1986; Jamieson et al., 2012; Kruschke, 1992; Logan, 2002; Medin and Schaffer, 1978; Nosofsky, 1986; Pearce, 1994).

Bateson and Chantrey (1972) reported evidence that was consistent with the idea that imprinting involves a process of classification together, wherein different imprinting objects presented close together in time become bound together: chicks given exposure to two imprinting stimuli close together in time, within the same experimental sessions, found it more difficult to learn a rewarded discrimination between them than chicks who had no experience with those objects (see also, Honey et al., 1994, 1995). The idea that such results are underpinned by a process of classification together that operates during imprinting training, making it more difficult to establish different responses to the two imprinting stimuli, parallels theoretical analyses of sensory preconditioning: where, after pairing two (or more) neutral stimuli (e.g., a tone with light, Brogden, 1939; or one flavor with another, Rescorla and Cunningham, 1978) a conditioned response established to one of them (e.g., the light) is reflected in behavior to the other (e.g., the tone). Within the Bateson and Horn (1994) model, classification together is held to reflect the fact that residual activity in the recognition units (arising from the presentation of one stimulus) will increase the likelihood that the new features of a temporally contiguous imprinting stimulus becoming linked to the same recognition unit (or units). The capacity to activate such a shared unit/s will allow new learning about one imprinting stimulus to be conferred onto the other, to the extent that this new learning recruits a shared recognition unit. There is now evidence that such a process of mediated learning plays an important role in some instances of sensory preconditioning in rats (e.g., Iordanova et al., 2011; Lin et al., 2013) and people (Wimmer and Shohamy, 2012). Moreover, mediated learning can be dissociated (behaviorally and neurobiologically) from learning that need not involve such mediation (for a review, see Honey et al., 2014).

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[1] To maintain a stimulus-response analysis one would need to assume that establishing an approach response to the imprinting object (e.g., B) served to discriminate that object from others through a process of acquired distinctiveness generated by response-produced cues (for a recent review, see Honey et al., 2010). It will become evident that such an analysis fails to anticipate other empirical observations that we will come to shortly.

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