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Invited review

Filial responses as predisposed and learned preferences: Early attachment in chicks and babies

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HIGHLIGHTS

- Predispositions orient newborn babies and chicks towards animate objects.
- Subcortical/subpallial structures may be sufficient to support social predispositions.
- Social Behaviour Network areas might be involved in unlearnt social behaviours.
- Hormones facilitate preferences for predisposed stimuli and social attachment.
- Social predispositions are impaired in newborns at high genetic risk for autism.

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ABSTRACT

To what extent are filial responses the outcome of spontaneous or acquired preferences? The case of domestic chicks illustrates the connection between predisposed and learned knowledge in early social responses. In the absence of specific experience, chicks prefer to approach objects that are more similar to natural social partners (e.g. they prefer face-like configurations, biological motion, self-propelled objects and those that move at variable speed). Spontaneous preferences are complemented by filial imprinting, a powerful learning mechanism that enables chicks to quickly learn the features of specific social partners. While neurobiological studies have clarified that the substrates of spontaneous and learned preferences are at least partially distinct in chicks, evidence shows that spontaneous preferences might orient and facilitate imprinting on animate stimuli, such as the mother hen, and that hormones facilitate and strengthen preferences for predisposed stimuli. Preferences towards animate stimuli are observed in human neonates as well. The remarkable consistency between the perceptual cues attended to by newborn babies and naïve chicks suggests that the attentional biases observed in babies are unlikely to result from very rapid post-natal learning, and confirms that research on precocial species can inform and guide human infant research with regards to both typical and atypical development. This has potentially important biomedical implications, opening new possibilities for the early detection of subjects at risk for autism spectrum disorders. We show how the parallel investigation of predispositions in naïve chicks and human infants, both benefiting from contact with social partners since the beginning of life, has greatly improved our understanding of early responses to social stimuli at the behavioural and neurobiological level.

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1. Introduction

Predispositions to preferentially attend to living things, in particular social partners, have been investigated across phylogenetically distant species. These predispositions might be crucial for survival [1,2] and have a role in the typical development of mechanisms for social cognition [3,4]. Predispositions for visual stimuli have been investigated in the chicks of nidifugal bird species, such as galliformes [1,5], in non-human primates [6] and in human neonates (e.g., [7,8]). Precocial avian species offer some notable advantage for this kind of research because their precocial nature allows testing to take place immediately after hatching, before any visual experience has occurred. While in primates (and other mammals) practical and ethical constraints hinder controlled-rearing studies, in precocial chicks a precise control of embryos [9–11] and of newly hatched animals until the moment of test (see for instance [12–14]) is feasible. Despite the clear differences in the level of development at birth between human and non-human primates, on the one hand, and nidifugal birds on the other, to some extent they have similar needs at the beginning of their life. In fact, in a precocial species such as the domestic fowl (*Gallus gallus*), parental care still plays an important adaptive role: even if chicks can move and feed autonomously soon after birth, the mother hen provides warmth, protection and facilitates learning, e.g. about the location or appearance of suitable food items [15]. In this work, we thus focus on the parallel investigation of human newborns' and chicks' early filial responses at the behavioural and neurobiological level.

Predispositions for attending to stimuli associated with animate objects soon after birth were first described for chicks of precocial bird species (e.g. mallard and chicken) and later on confirmed also in newborn babies (reviewed in [1], see Sections 2 and 5). Direct evidence of predisposed preferences comes from naïve animals: in the absence of previous visual experience, dark-hatched chicks prefer to approach a stuffed jungle fowl hen over an artificial object, or even over a scrambled version of the same stimulus [5] (see Fig. 1a). Chicks' spontaneous preferences extend to schematic face-like configurations [16] (see also [17,18]) (see Fig. 1b), similar to what has been reported for newborn babies, who prefer to direct their gaze towards face-like stimuli [7,19–21] (see also [6] for non-human primates). In both cases, this has been attributed to a predisposition for stimuli that match a very broad template of a face, reflecting the action of an early, not learned, orienting mechanism called CONSPEC, as opposed to a subsequent learning mechanism called CONLERN [7].

Although predispositions were originally identified for approaching static features (see also Section 3), in general moving objects are more attractive than static objects [22,23], and predispositions have been observed for both static and dynamic cues [24,25]. The more recent investigations on dynamic cues (see Section 2) have refined our understanding of the predisposition for moving stimuli, namely that biological motion is preferred over rigid and random motion [12,26], self-propelled objects are more attractive than objects that do not initiate motion [27], and accelerating/decelerating objects are more attractive than linear moving objects [28]. Overall, chicks' preferences for static and dynamic cues reveal an attraction for animacy cues, that is, features associated with the presence of animate objects [1]. This corpus of evidence, obtained in naïve subjects, has allowed the establishment of this animal as a behavioural and neurobiological model for the origins of knowledge, the so-called core-knowledge systems, and the corresponding substrates, including social cognition (reviewed in [1,29–31]). Recent research showed that chicks from different breeds differ in their approach responses towards a stuffed-hen stimulus (i.e., predisposed stimulus) [32]. A substantial body of evidence shows that the expression of predisposed visual preferences changes during the course of the first few days of life, often increasing a few hours after a specific stimulation [5,33–35]. Although the preference for hen-like stimuli does not require any experience with similar stimuli, different kinds of stimulation can enhance the predisposed preferences: motor activity, experience with diffuse or patterned light, acoustic stimulation, handling of the subjects [5,33,35,36].

It has been suggested that one of the adaptive functions of early approach preferences could be to ensure attachment towards social companions over inanimate objects (see Section 2). This is particularly relevant for precocial avian species endowed with the dedicated system of filial imprinting [24,37–40], a learning mechanism that restricts subsequent affiliative responses to the first conspicuous objects experienced (in the case of acoustic stimuli, this process can start even before hatching, during the last days of incubation [41]). After a brief exposure, chicks learn the features of their imprinting object and develop a social preference for it (this learning mechanism is important for the development of sexual preferences too, a phenomenon called sexual imprinting, see [42–46]. Crucially, naïve chicks do not merely absorb information from the environment but actively search for stimulation from conspicuous objects (e.g. [47]). In natural conditions, chicks usually imprint on the mother hen, but the mechanism of imprinting is general enough that they can develop filial responses both for naturalistic objects, including members of other species (before Konrad Lorenz [48,49], there was already a widespread interest on this phenomenon, as it had already been noticed by Spalding [50]; and see [51] for ducklings), and artificial visual and acoustical stimuli, reviewed in [24]).

The interplay between spontaneous predispositions and acquired preferences is well exemplified by the case of chicks' spontaneous preferences for naturalistic vs. artificial objects, which is driven mostly by the configuration of features present in the head region [5], and the filial imprinting phenomenon. While chicks exhibit a spontaneous preference for naturalistic stuffed animals, without any selectivity for the own mother or species, the recognition and preference for specific individuals emerges after the imprinting process [7]. Asymmetrical reversibility of imprinting towards naturalistic objects (a mother hen) compared to artificial objects is one of the first, although indirect, pieces of evidence on the presence of social predispositions. When naïve domestic chicks were initially exposed to an artificial imprinting object followed by a naturalistic object, they could reverse their preference, while this did not happen when the naturalistic object was the first object presented [52–56]. This evidence suggests a close link, as well as a difference, between spontaneous and learned preferences (see also Sections 2 and 5). Neurobiological evidence also suggests that learning a preference for a specific stimulus through filial imprinting and predispositions to approach certain stimuli in the absence of any exposure to them are separate processes [3] (see also Section 3).

In this review, we discuss how the parallel investigation of predispositions in naïve chicks and human infants has greatly improved our understanding of early responses to social stimuli at the behavioural and neurobiological level. Specifically, in Section 2

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