



## Review

# Roots of a social brain: Developmental models of emerging animacy-detection mechanisms



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## ABSTRACT

Here, we review evidence of unlearned predispositions to orient toward visual and auditory cues associated with the presence of animate creatures. We concentrate on studies on chicks of galliform species, whose behavioural preferences for social partners are analyzed in a comparative perspective with respect to the human developmental literature. The emerging nature of chicks' social predispositions is discussed in relation to the underlying physiological mechanisms and to the role of genetic and environmental factors in their development. In the second part of the review, we summarize evidence on the neural substrate of the animacy detectors, again focusing on our animal model of election, the domestic chick. On the basis of a substantial amount of indirect evidence, subpallial structures, among which the optic tectum (homologous to the mammalian superior colliculus), seem to comprise the most probable candidates. We also discuss some preliminary evidence of different brain activity, measured by IEG expression, in chicks exposed to predisposed or a non-predisposed stimulus.

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## Contents

1.	Behavioural evidence of social predisposition.....	151
1.1.	Visual predispositions for colours, shapes and configurations.....	151
1.2.	Visual predispositions for different kinds of motion.....	152
1.3.	Acoustical predispositions.....	154
2.	Sensory stimulation and the emergence of predispositions.....	155
2.1.	Developmental origins of the species-specific predispositions of galliform chicks.....	155
2.2.	Developmental origins of the general predispositions for animacy of galliform chicks.....	155
3.	Neuronal bases of social predispositions.....	156
3.1.	The visual system of birds.....	158
3.2.	Processing of innate predispositions in birds.....	159
4.	Conclusions.....	161
	Acknowledgements.....	162
	References.....	162

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## 1. Behavioural evidence of social predisposition

A series of seminal papers published almost three decades ago by Gabriel Horn and his collaborators laid the foundations for our current investigation of unlearned social predispositions and their neural substrate in domestic chicks. While studying the neural bases of filial imprinting, researchers in Horn's group serendipitously noticed a surprising variability in their results, depending on the type of object employed as an imprinting stimulus (Bolhuis and Horn, 1997; Bolhuis et al., 1985, 1989; Davies et al., 1992; Hampton et al., 1995; Horn, 2004; Johnson and Horn, 1986, 1988; Johnson et al., 1985, 1989). This suggested the presence of pre-wired preferences for certain kinds of visual objects. In controlled laboratory settings imprinting can be obtained for a variety of artificial objects. Despite that, it is not completely unconstrained in its object: notoriously, filial imprinting can be better obtained for visually salient objects of the appropriate size (e.g., visual stimuli that are small enough for being a food item do not elicit filial imprinting, with the optimal size for eliciting following being around 10 cm; Schulman et al., 1970). In addition, moving stimuli are preferred as imprinting objects over static ones (Ten Cate, 1986, 1989). Three-dimensional objects produce better imprinting than two-dimensional moving objects, presented via motion picture films (Klopfer, 1971). In the following paragraphs, we will review behavioural evidence of unlearned predispositions guided by different visual features of the imprinting stimuli in chicks of galliform and other nidifugos species.

### 1.1. Visual predispositions for colours, shapes and configurations

Overall shape affects the a priori attractiveness of an imprinting object, with circular objects preferred to square ones (Salzen and Meyer, 1968; see also Hess and Hess, 1969; Huber, 1967; Ramsay and Hess, 1954; Waller and Waller, 1963). Over the 1960s and the 1970s, researches have also invested quite some time to investigate unlearned colour preferences in imprinting (e.g., Goodwin and Hess, 1969; Gray, 1961; Kovach, 1971; Schaefer and Hess, 1959; Smith and Bird, 1964). A frequent finding in domestic chicks is a preference for red stimuli over yellow or green ones (Bateson, 1983; Bateson and Jaekel, 1976; Kovach, 1971; Salzen et al., 1971). Nevertheless, contradictory results are present in the literature on colour preferences (Bateson, 1966; Salzen and Cornell, 1968), which could be partially explained by the contrast between stimuli and background. In particular, a preference for blue stimuli was reported, but appeared to be a response to contrast rather than hue (Salzen et al., 1971). These preferences are not learned through any specific prior experience with the preferred colour, which suggested that they should be under genetic control. Direct evidence of a genetic component for this trait is provided by artificial selection studies in which Japanese quail chicks (*Coturnix coturnix japonica*) were selected to create different lines showing divergent approach preferences for and imprintability to particular colours and patterns (Kovach, 1990, 1993; Kovach and Wilson, 1988, 1993). Interestingly, quail's colour preferences are mediated by mechanisms at the level of the central nervous system (Kovach, 1977, 1983), implying that genetic influences on visual preferences must actually affect brain circuitry, rather than peripheral sensory mechanisms. In Japanese quails, motivation to social reinstatement (measured by distance walked to reach a group of other chicks) seems also to be under genetic control (Faure and Mills, 1998). In domestic chickens, similar traits have been studied comparing their behaviour to that of the non-domesticated but closely related species (red jungle-fowls). Filial motivation per se could be a stable trait (not affected by domestication), whereas colour preferences and flexibility in imprinting (capacity to imprint on not preferred

stimuli) differ between domesticated chickens and red jungle fowls (Kirkden et al., 2008).

These spontaneous preferences (for a given shape, colour, etc.) are likely to favour imprinting for the mother hen in the natural environment. Indeed, the presence of one of these preferred attributes enhances the learning of other non-preferred features of the imprinting object (Van Kampen et al., 1994). Some precocial species seem to be even endowed with a more constraining set of preferences that limit the possibility to imprint on sub-optimal objects in the absence of the mother hen. Already Lorenz (1937) reported that, contrary to other related species that he studied, newly hatched chicks of the curlew (*Numenius arquata*) could not be made to imprint to a human caregiver (or to his boots) (see Göth and Hauber, 2004 for a review of species-specific social preferences).

Of particular interest, domestic chicks seemed to have a predisposition to imprint on naturalistic objects, such as a hen or a stuffed red jungle-fowl (*Gallus gallus spadiceus*, the wild ancestor of domestic chicks; Zeuner, 1963), with respect to artificial stimuli. Imprinting is reversible after the exposure to a second object, if both the first and the second objects to which the young animal is exposed are either naturalistic hen-like objects (live or stuffed hens; Kent, 1987) or artificial objects (Cherfas and Scott, 1981; Salzen and Meyer, 1968). The same is true if the first object to which the chick is exposed is an artificial object followed by a hen-like object. On the contrary, a chick imprinted on a naturalistic stimulus will not shift its preference for an artificial object (Bolhuis and Trooster, 1988; Boakes and Panter, 1985; but see de Vos and van Kampen, 1993). Such differential reversibility of filial imprinting is due to the interaction of two independent mechanisms: the learning process of imprinting and a predisposition to approach hen-like objects that emerges in the first days of life, revealing an unlearned representation of the appearance of a social object in chicks. In the absence of any specific visual experience, chicks show a preference to approach a stuffed red jungle fowl hen with respect to highly salient artificial stimuli, such as an illuminated red box (e.g., Johnson and Horn, 1986, 1988; Johnson et al., 1985). Notably, in most studies, the predisposition for hen-like objects emerged at about 48 h after hatching. In natural settings, this is exactly the time when chicks start to leave the nest and follow the mother hen (Guyomarc'h, 1974).

In 1988, Johnson and Horn investigated which features of the predisposed stimulus were actually eliciting chicks' preferences, demonstrating a crucial role of the configuration of features contained in the head and neck of a hen using, among others, stimuli that were controlled for complexity, texture, outline, presence of structure, object-like appearance, approximate symmetry and presence of specific configurations of feature clusters. In order to do so, chicks were tested for their preference between the canonical stuffed fowl and: (i) disarticulate fowls (whose limbs and body parts were reassembled in anatomically unusual ways, maintaining a complex outline); (ii) a box-fowl (limbs and body parts of the fowl were mounted on the box, so that the outline of the stimulus was that of a box, but all body elements of a fowl were recognizable); (iii) a texture-fowl (the pelt of a jungle fowl cut up in small pieces and attached to the sides of the box in scrambled order, preserving visual texture, colours and luminance, but eliminating any spatial relationships between single features); (iv) a head-fowl (in which the head and neck of a fowl was mounted on the top of a featureless box) and finally (v) stuffed duck and polecat. The intact fowl was preferred only with respect to the texture-fowl, revealing that neither anatomical plausibility nor outline complexity or textural cues could be at the basis of chicks' preferences. Remarkably, chicks' preferences appeared not to be selective for their own species (see also Gray et al., 1980) and could be elicited by the configuration of features contained in the head and neck alone. The role of the neck-head region in chicks' preferences can be

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