Behavioural Brain Research 325 (2017) 90–104

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Invited review

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

Elisa Di Giorgio[1], Jasmine L. Loveland[1], Uwe Mayer[1], Orsola Rosa-Salva[1], Elisabetta Versace[1], Giorgio Vallortigara*

Center for Mind/Brain Sciences, University of Trento, Italy

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.

ARTICLE INFO

Article history:
Received 30 June 2016
Received in revised form 6 September 2016
Accepted 8 September 2016
Available online 8 September 2016

Keywords:
Social predispositions (biological motion, face preferences, self-propulsion)
Naïve chicks (*Gallus gallus*)
Newborn babies
Autism spectrum disorders (ASD)
Neural and hormonal correlates
Septum

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.

© 2016 Elsevier B.V. All rights reserved.

Contents

1. Introduction 91
2. Predispositions for the motion of living creatures 92
3. Neural bases of biological predispositions 95
4. Hormones and predispositions 96
5. Impairments in social predispositions early in life and their relevance to the ontogeny of autism spectrum disorders (ASD) 97

* Corresponding author at: Animal Cognition and Neuroscience Laboratory, Center for Brain/Mind Sciences, University of Trento, Rovereto, TN 38068, Italy.
E-mail address: giorgio.vallortigara@unitn.it (G. Vallortigara).

[1] These authors had equal contribution to the work and are listed in alphabetical order.

http://dx.doi.org/10.1016/j.bbr.2016.09.018
0166-4328/© 2016 Elsevier B.V. All rights reserved.

6. Conclusion remarks 98
Acknowledgement 99
References 99

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

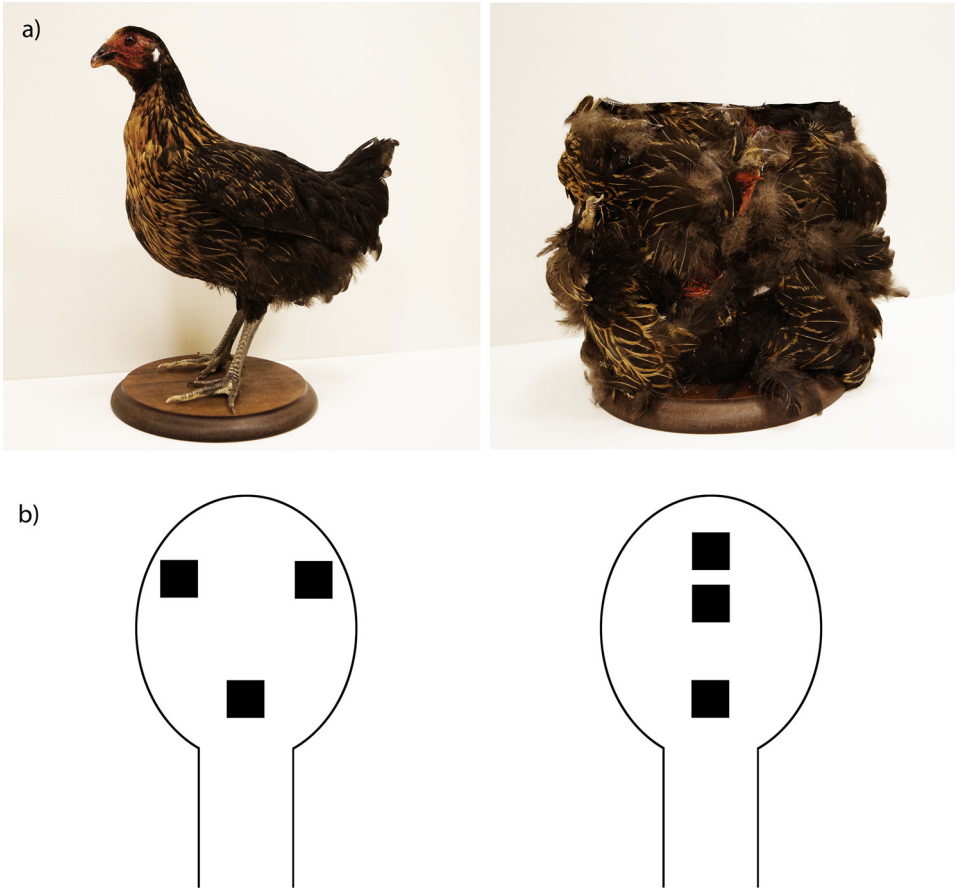

Fig. 1. Visual stimuli employed in tests for predispositions for static configurations of features in naïve chicks: a) stuffed fowl and scrambled version of the stimulus preserving only its visual texture (known as "texture fowl"); b) schematic face-like and non-face-like configurations. Adapted from [31] and from [16] respectively.

we will discuss recent advances in our understanding of the predisposition for the motion of animate creatures. In Sections 3 and 4 we will present the current understanding of how predispositions may be processed by brain nuclei within the visual pathway and the influence of hormones on facilitating and strengthening preferences for predisposed stimuli. Lastly, in Section 5 we will present recent research of biomedical relevance for the early detection of autism spectrum disorder (ASD) that is based on testing preferences for social stimuli, including predisposed stimuli, in newborns that are at high familial risk for developing ASD.

2. Predispositions for the motion of living creatures

In recent years, particular attention has been devoted to the study of social predispositions for motion cues that are typical of animate creatures. A well-known case is that of semi-rigid biological motion, represented by animation sequences of point-light-displays (PLDs) where a few light points are placed on the joints of a digitalised image of a moving animal, and all remaining two-dimensional information about the shape of the moving object is excluded [57] (see Fig. 2). Research in naïve chicks (*Gallus gallus*) revealed spontaneous preferences towards biological motion displays characterised by semi-rigidity, compared to rigid or random motion. Interestingly, also in this case, as for the face-like configurations, chicks' predisposition was not specific for the motion pattern of their own species [12]. However, similar to what is known for human adults [58–62], chicks' processing of PLD of biological motion is orientation-specific (i.e., limited to displays presented in the canonical upright orientation, rather than upside down) [26]. Intriguingly, this orientation sensitivity of chicks is influenced by the degree of brain lateralization and is associated with a right hemispheric dominance, akin to what is known for adult humans and few-month-old infants [63–65]. Furthermore, chicks' preference for semi-rigid PLD of biological motion has been shown to result in increased imprinting learning after exposure to the predisposed motion patterns, suggesting again a role of social predispositions in directing subsequent filial responses and social learning [66] (see also [67]).

Following the initial reports on chicks, subsequent research showed that even medaka fish (*Oryzias latipes*) respond socially to biological motion stimuli [68], while female marmosets (*Callithrix jacchus*) prefer to inspect similar biological motion patterns as chicks do [69]. Also, human newborns are attracted to the same stimuli that elicit chicks' preferential approach (see also Section 5), showing higher looking times for the PLD representations of semi-rigid biological motion of an upright walking chicken over rigid motion, random motion and even over the upside down version of the walking stimulus [8,70]. In adult observers, the inversion effect for biological motion perception depends on whether the vertical acceleration of the dots representing the feet is consistent with gravity direction. The two feet-dots presented in isolation, but with the correct acceleration profile, are sufficient to elicit biological motion processing and animacy perception in adult observers [59,71,72]. It has been theorised that this local motion property, which is independent from the global species-specific shape of the moving animal, is computed by a spontaneous and evolutionarily conserved mechanism for the fast, pre-attentive detection of animacy [73–75] (see also Section 3). This mechanism computing local

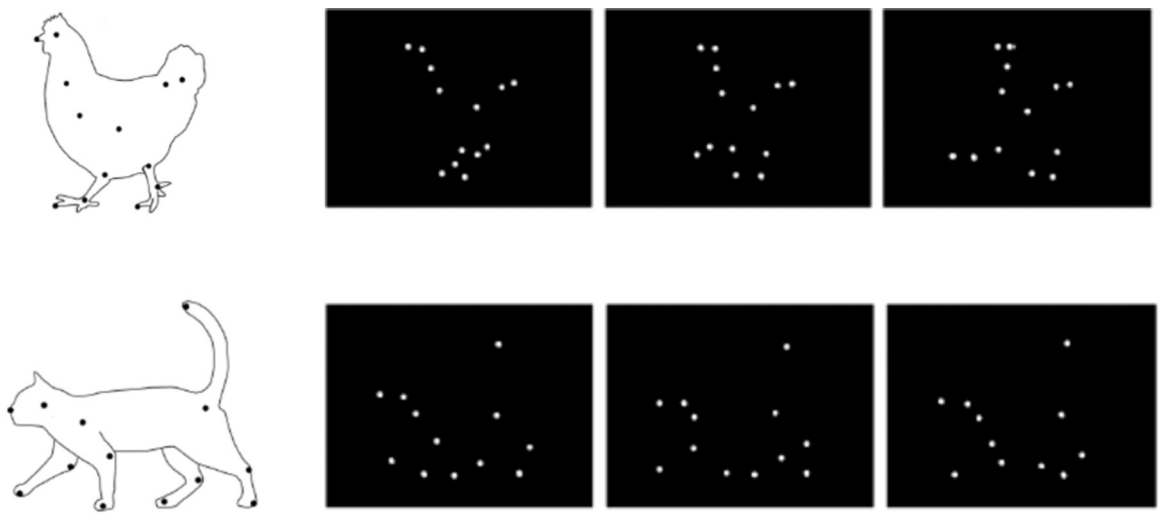

Fig. 2. Point light displays (PLDs) representing biological motion used for domestic chicks. Structure of the PLDs and sample frames for the animation sequences of a walking hen and a walking cat (both examples of biological motion, equally preferred by naïve chicks). The animations were obtained from actual video recordings of the walking of the two animals: the filled dots in the leftmost images indicate the location of each point of light. Adapted from [12].

acceleration profiles interacts with another system that processes the global configuration of the moving body, which is sensitive to the position of the feet-dots in the overall configuration, above or below the body. Due to the activity of this second system, the vertical location of the dots representing the feet might be another cue to discriminate living creatures from inanimate objects [76,77]. The latter mechanism would be individually acquired through experience [72]. In fact, newborn babies' preferences are already tuned to the local vertical acceleration profile of the feet dots when presented in isolation, even though the global body configuration can influence this effect. On the contrary, the vertical location of feet-dots in the array per se is not enough to drive babies' preferences [78].

Despite the success of paradigms based on biological motion as depicted by PLD, predispositions for elementary aspects of objects' velocity profile can be better studied with stimuli showing the motion of a single shape. Research on the human perception of animacy and agency based on the cinematic of simple two-dimensional objects dates back to Heider and Simmel [79] and Michotte [80]. With a reference to Aristotle's categorisation of living and non-living entities [81], it has been theorised that automatic animacy perception would happen in response to motions implying an internal energy source to the moving object. The most well studied cue implying self-propulsion is probably "start from rest", displayed by an object when it starts to move autonomously as opposed to being put in motion by physical contact with another object. This visual cue elicits "mandatory" animacy attribution not only in adult observers [82,83], but also in infants, who by a few months of age already seem to attribute an internal energy source to an object that starts to move on its own. In fact, they are not surprised if such object spontaneously changes its trajectory or moves against gravity [84–87]. In line with that, dark-hatched chicks revealed preferential imprintability for an object whose motion started spontaneously from a resting state, over another object, which was set in motion by the push from the first object (see Fig. 3). Control conditions showed that the effect was not influenced by which object started to move first, initiated physical contact (in the absence of physical causation) or had a causal role [13]. In a later study, Di Giorgio et al., [88] showed that even human newborns prefer to look at objects that clearly display movement that starts from rest, compared to objects that appear on the screen already in movement (i.e., without any information about the onset

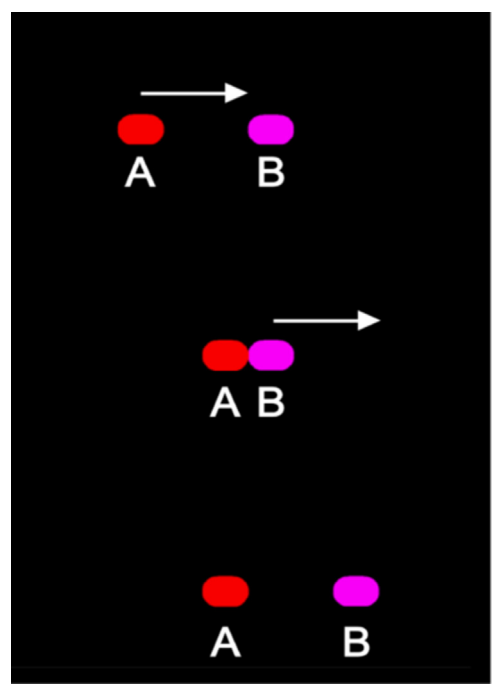

Fig. 3. Schematic representation of the animation sequence presented to chicks in order to obtain imprinting for one of the two objects (A and B, in red and purple, respectively). Subsequent representative frames of the sequence are ordered from top to bottom. In this animation, object A was perceived by human observers as self-propelled, whereas object B seemed to be passively put in motion by the impact with object A. After exposure to this stimulus, chicks tested for their preference between objects A and B, preferred to approach the first, indicating that during the initial exposure they imprinted preferentially on the self-propelled object. Adapted from [13]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of motion). This shows that sensitivity to this cue is present from birth also in humans (see also Section 5). However, movement that starts from a resting state is not the only cue of self-propulsion that elicits animacy perception in human observers. Greater animacy is attributed also to objects that move quickly, move against gravity and change autonomously speed or direction of motion [83,89–92]. Changes in direction and speed automatically attract adults' attention [93], while the visual preferences of infants that

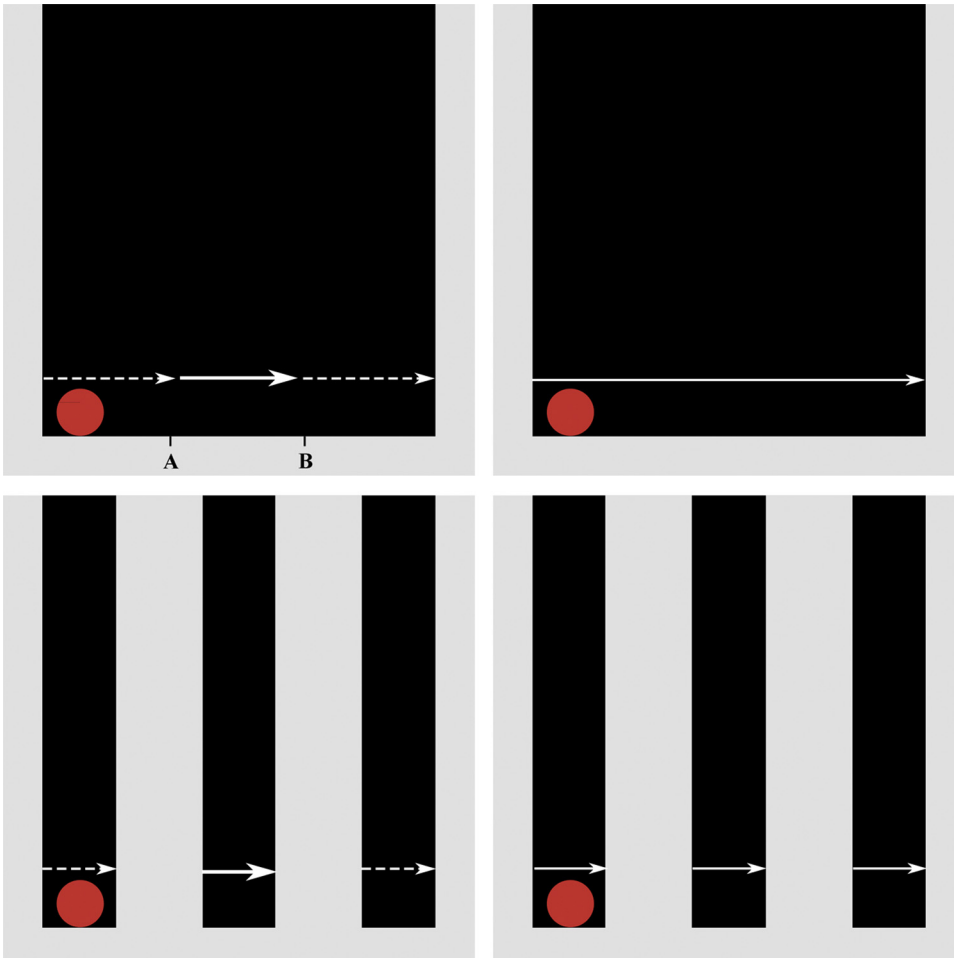

Fig. 4. Schematic representation of the speed-change stimuli (on the left) and of the constant-speed stimuli (on the right) used with chicks. The letters A and B, in the first panel, indicate the points where the visible speed change occurred. Arrows indicate the relative speed of the object for different portions of the trajectory (with thicker continuous lines representing the higher speed, followed by thinner ones and finally by dotted lines). The two top panels represent stimuli in which the moments of speed change are visible, whereas the two bottom ones represent equivalent stimuli where the speed change were occluded. Adapted from [28].

are a few months old seem to be driven more by speed than by direction changes [94]. In line with this, in our recent work we showed that naïve chicks have a preference to attend to objects that change their speed over objects that move at a constant speed [28]. Chicks were presented two displays, in each one a red circle appeared on the screen already in motion, moved linearly along the azimuth, and then disappeared at the opposite side of the screen. In one of the two displays, the object abruptly accelerated at one third of the way and decelerated to the original speed at two thirds of the way. In the second display, the other object moved constantly at the same average speed (see Fig. 4). Dark-hatched chicks showed a clear preference for the object in the first display. In additional control trials, we showed that matching the variability of the control 'speed-constant' stimulus to that of the "speed-change stimulus" did not alter chicks' preference for the latter. In order to do so, two different speeds were alternated for the control stimulus in subsequent cycles. This increased its perceptual variability (the ratio between the lower and the faster speed was also matched between the two stimuli), even though in the control stimulus there were still no visible speed changes. In fact, in the new version of the control stimulus, the red object was still moving at a constant speed for the whole length of its trajectory, but alternating two different speeds in subsequent cycles. That is to say that when traveling in one direction (e.g., appearing from the left side of the screen disappearing from the right one) the stimulus was moving at a constant slow speed. Then, when it appears again from the right side of the screen, the object is traveling back in the opposite direction at a constant speed, which is faster than the previous one, and so on. However, chicks' preference was suppressed by adding two occluders on both displays, positioned along the stimulus trajectory in such a way that the moment of speed change was occluded (Fig. 4), showing that the moment of speed change needs to be directly visible to elicit chicks' preferential approach.

An important distinction between animacy and intentional agency is that the latter property defines entities capable of goal directed, efficient and rational actions. While attribution of animacy should be operated by the core-system for physical reasoning, based on the presence of motion features indicating an internal energy source for self-propelled motion, attribution of intentional agency should depend on the core-system for naïve psychology, based on cues that indicate that the object has autonomous control over its actions [95–97]. This applies to objects that respond contingently to events or environmental constraints, and the relationship between these two levels is not obvious. For example, even though in some instances infants attribute intentional agency based on self-propelled motion (e.g., [98,99]), this is not always sufficient or even necessary (e.g., [95,97,100–102]). Visual patterns determining the attribution of various levels of agency by infants or adult observers usually involve at least two visual objects that move in a spatially or temporally contingent manner, which sug-

gests a social interaction (e.g., [97,101]) or a reaction from the agent to an inanimate element in the environment [89,103,104]. Also, variability of goal-directed behaviour seems to induce agency attribution in infants [95]. Interestingly, chicks of two galliform species (bobwhite quails, *Colinus virginianus*, and Japanese quails, *Coturnix japonica*) revealed preferential visual or auditory imprinting towards stimuli that had motion or acoustical emissions that were contingent on the chicks' own calls [105–107]. Future studies could thus investigate whether direct evidence of social predispositions for contingency and other cues of agency occur also in naïve chicks, in line with what has been suggested by the literature on human infants.

3. Neural bases of biological predispositions

Face preferences of newborn babies have been hypothesised to be mediated by subcortical structures, such as the superior colliculus, the pulvinar complex and the amygdala [3]. This view is based on multiple, but indirect, lines of evidence. First of all, given that in human infants the retino-geniculo-cortical pathway is most likely not fully functional before the age of two months [108–114], until infants reach this age, visual function is mediated mainly by the precortical part of the retino-collicular visual pathway. This age-dependent role of the retino-collicular system is supported by the observation that in human newborns and adults the preferential orienting toward faces is limited to stimuli in the temporal visual hemifield [115]. The retino-collicular system has indeed proportionally greater input from the temporal hemifields, with respect to the geniculo-striate system [116–118]. Moreover, residual face detection abilities persist after cortical lesions in patients suffering from hemi-neglect, prosopagnosia or blindsight [119–122]. These patients lack the ability to process face-identity information, suggesting a mechanism that responds in a non-selective way to any face-like stimulus. Such a mechanism probably operates on low spatial frequency only, which carries the visual information needed for face detection, whereas high spatial frequency provides more detailed information (e.g. face identity) [3]. In fact, neuroimaging studies have shown that neurons in the amygdala, pulvinar and superior colliculus respond exclusively to the low spatial frequency content of face stimuli [123]. Overall, this points to a role of the human retino-collicular system in face preferences and of the cortical structures for learning detailed visual information about these stimuli.

This view, derived mainly from the human literature, is also supported by indirect evidence from different animal models, which we will briefly review below. One important first point is that the candidate subcortical structures' response properties may enable recognition of predisposed stimuli. In fact, even early stations of the visual system respond to complex objects, including biologically relevant stimuli. For example, the superior colliculus, which shows remarkable functional conservation among different vertebrate species [124], contains neurons with diverse and complex functional properties that respond to both static and moving stimuli [125–135]. Already at this level, the visual system recognises different categories of visual stimuli [125,126,128,133,136–140]. The superior colliculus (optic tectum in other vertebrates) is also essential for the spontaneous recognition of biologically relevant stimuli. In mice, collicular cells respond to each of the simple visual configurations commonly used in studies of amphibian prey and predator recognition [141–144]. In a more recent study with primates, also pulvinar neurons have been shown to differentiate between categories of biologically relevant stimuli, such as snakes, monkey faces, monkey hands or geometric shapes [145]. Likewise, neurons have been found in the monkey amygdala that respond selectively to stimuli such as faces and direct gaze [146,147]. Overall, in birds, as in mammals, visual information is simultaneously processed by two major visual pathways [148,149]. The thalamofugal pathway runs from the retina via the nucleus opticus principalis thalami (OPT) to the visual Wulst. The OPT is assumed to be homolog of the mammalian lateral geniculate nucleus (LGN) and the visual Wulst is considered to be a homolog to the primary visual cortex (V1) [150–152]. The tectofugal pathway proceeds from the optic tectum in the mesencephalon, through the nucleus rotundus, within the thalamus to the entopallium in the telencephalon [153]. Optic tectum is considered homologous to the superior colliculus in mammals, while the nucleus rotundus is homologous to the pulvinar complex. The entopallium is probably equivalent to several areas of mammalian extra striate cortex [150,154]. Of particular interest for the topic of this review, among the motion properties to which tectal neurons of domestic chicks respond are some motion cues that elicit the display of social predispositions in this species, such as changes in speed [155] (see Section 2).

Another crucial observation, based on the literature on animal models, is that the candidate subcortical structures may be sufficient to elicit the behavioural responses required for the expression of predispositions. For example, it is well known that the superior colliculus is necessary for orienting responses towards stimuli [156–158], which are at the basis of social predispositions' expression. At a very general level, there is evidence that subcortical structures can support visually guided behaviours independently from cortical structures. Moreover, of particular relevance for the current topic, these behaviours seem to not be learned, as they are displayed by naïve individuals and/or shortly after birth (hatching). For example, in rats, behaviours that are observed in naïve rodents after exposure to a predator for the first time [159,160], can be also elicited by stimulation of the superior colliculus [161–163]. Anurans, which have been more heavily studied for their spontaneous forms of visual recognition of biologically relevant objects, such as conspecifics, preys and predators [141], do not have a visual cortex as such. Their visually guided behaviours are presumably mediated by medullary, pontine, mesencephalic and thalamic structures [164], with a major contribution of optic tectum, since lesions to this structure cause a total loss of responses to moving predator and prey objects [165–167]. However, for the discrimination of 'prey-like' and 'predator-like' stimuli, pretectal areas are also important [168].

In birds, many visually guided behaviours do not require pallial structures, because they can be displayed after complete removal of the telencephalon [169]. These behaviours seem to be not dependent on experience, because they are displayed by naïve-decerebrated animals right after hatching. For example, decerebrated newly hatched chicks show the same spontaneous preferences for colour and shape combinations of potential food items as intact chicks do [170]. Also, after bilateral hemispherectomy domestic chicks and quails continue to approach moving objects or flickering lights [169,171]. Spontaneous early colour preferences of newly hatched quails have been studied to investigate the mechanisms by which the brain stores and processes preference information [172,173]. It has been discovered that, while removal of the telencephalic hemispheres prevents Japanese quail chicks from forming a memory of coloured imprinting stimuli, it spares the spontaneous preference for particular colours and patterns [171,174]. In a more detailed study, lesions of several diencephalic structures diminished quail chicks' spontaneous preference for the colour red [175]. Although the authors do not specify which brain regions of the medial diencephalon were lesioned, it is reasonable to assume the preoptic area was also lesioned, and perhaps even the anterior and/or the ventro-medial hypothalamus. It has been argued [124] that these particular deficits in quail chicks may be due to the loss of motivational inputs to premotor and motor structures: at least the preoptic area is involved in

motivational processes [176,177] and also in mammals lesions to homologous structures cause deficits in behavioural responses to external stimuli [160,178–180].

It can thus be expected that also chicks' visual predispositions for social stimuli should involve subcortical structures, with the optic tectum and the tectofugal visual pathway having particular importance. On the contrary, subsequent imprinting learning of the detailed visual information originated by exposure to those stimuli (see Section 1) would require pallial structures of the telencephalon (homologous to the mammalian cortex). Several pallial structures of the avian brain are involved in learning this kind of detailed visual information. For example, the intermediate medial mesopallium, IMM (IMHV, intermediate medial hyperstriatum ventral in the old nomenclature) is crucial for filial imprinting in chicks [181–186], whereas the lateral meso-nidopallium (LMN) is involved in sexual imprinting in zebra finches [187–189]. On the contrary, bilateral lesioning of IMM does not affect chicks' predisposition for approaching stuffed hens [190], in line with the evidence on spontaneous colour preference in quails. Interestingly, we recently found that IMM activity in naïve chicks is differently modulated by exposure to a predisposed or a non-predisposed stimulus (a stuffed hen or a scrambled version of the same stimulus, in which the face configuration is absent) (Fig. 1) [31]. Nevertheless, the data on IMM lesions suggest, again, that preference for hen-like objects is processed in earlier brain stations.

The diencephalic areas likely affected in the study of Csillag and colleagues [175] on quails spontaneous colour preferences, represent some of the nodes of the social behaviour network (SBN) [191]. In the literature on the neural bases of animal social behaviour, this is defined as a network of areas that contain sex steroid receptors and are reciprocally interconnected, also comprising the subcortical part of the amygdala (medial extended amygdala), that controls multiple forms of social behaviour [192]. The social behaviour network is present in all vertebrates and exhibits extensive similarities between mammals and birds in its connections, histochemistry, and locations of sex steroid receptors [193–204]. Given the importance of this network for social functions, it is surprising that so far no studies directly investigated its role in early social behaviours of newborn animals (see also Section 4).

In order to shed some light on this issue we have recently started to study septal activity of newly hatched visually naïve chicks exposed to different social stimuli. The lateral septum represents one of the nodes of the social behaviour network [191] and is also connected to the mesolimbic reward system, making it a key element in a larger social decision making network [205]. Indeed, many studies in mammals and in birds have implicated the lateral septum in a variety of social behaviours, such as social memory, communication, gregariousness, individual recognition, dominance hierarchies, territoriality, aggression, sexual behaviour, pair-bonding, parental and anxiety-related behaviours, which are mainly mediated through neuropeptide signalling based on vasopressin and oxytocin receptors (or its avian homologous vasotocin and mesotocin) [199,202,206,207–237]. We found that simple exposure of visually naïve animals to an alive, behaving conspecific selectively activated septal areas, showing their involvement in recognition of animate creatures directly after birth [238,274]. In a second experiment, we found that the animate motion of an alive social partner alone is sufficient to activate septal nuclei, as opposed to the rigid motion of a similarly looking stimulus (i.e., a stuffed chick rotating at a constant speed). To narrow down the interpretation of these results, in a further study we also investigated if a simple object that changes its speed (by accelerating or decelerating), which is known to be preferred by newly hatched visually naïve chicks to an identical object that moves at constant speed [28], will selectively activate septal nuclei. Also in this case, we found higher activity in septum of chicks that were exposed to the preferred social stimulus [239]. This new evidence of septal involvement in response to animate motion indicates that previous visual experience and specific learning events are not necessary to establish this septal function, which is present shortly after birth.

4. Hormones and predispositions

Hormones are key in controlling the timing of hatching, yet little is known about whether they play a permissive role in the expression of predispositions. Although there are few studies on the effects or roles of hormones in predispositions per se, findings from imprinting studies that have been generated to date, have provided evidence that circulating hormones and their effects in specific brain nuclei may very well be linked to facilitating conditions that allow the expression of predispositions.

In chicks, the periods that comprise the sensitive window for imprinting (post-hatch days 1–4) as well as the eventual detachment from imprinted objects (weeks 6–10), are characterised by specific hormonal profiles [240,241]. For instance, a couple days before hatching, corticosterone and thyroid hormone T4 begin a transient increase that peaks on the day before hatching, and the peaking time of circulating levels of T3 coincides with the day of hatching [242]. Interestingly, chicks exposed to corticosterone prenatally (by injecting the egg) fail to successfully imprint, but they also spend more time close to the live stimulus chick that is used for imprinting training compared to vehicle-injected control chicks [243]. These authors interpreted these results as showing that corticosterone increased approach behaviour towards predisposed stimuli despite subsequent impairment of imprinting.

Yamaguchi et al. [242] made an important discovery regarding the role of thyroid hormone (T3): it is necessary for the onset of the sensitive period for imprinting learning (post-hatch days 1–4) and if it is injected intravenously in non-imprinted chicks after day 4, it is sufficient for reopening the sensitive window and chicks are able to imprint as if they were intact chicks within the naturally occurring sensitive window. Interestingly, injection of inhibitors of thyroid hormone signalling in the IMM (intermediate medial mesopallium) prevented successful imprinting. However, with respect to predispositions, it has been shown that the IMM is not required for the display of the spontaneous preferences (see Section 3). Specifically, predispositions are unaffected by IMM ablations, whereas filial imprinting is completely abolished with such lesions [190]. Therefore, although thyroid hormone signalling is critical for enabling imprinting learning, whether and how it is involved in the display of predispositions remains an open question.

The effects of testosterone on imprinting, especially for predisposed stimuli, have been shown through its administration under a number of conditions. For example, chicks treated with intramuscular testosterone injections upon hatching and then trained to imprint on a stuffed fowl, have higher preference scores compared to vehicle-injected, stuffed fowl imprinted controls [244]. In that study, circulating levels of testosterone were also shown to correlate with the strength of imprinting for animal-like stimuli, but not artificial stimuli like coloured boxes. Interestingly, the effects of testosterone depend on when it is administered, either prior to imprinting or after imprinting has taken place. Specifically, after chicks have been imprinted on a specific object, testosterone injections given on the third and fourth weeks post-hatch will induce detachment from the imprinted object, which in intact chicks does not begin until the sixth week of age [241]. Altogether, this suggests that brain regions sensitive to androgens may change significantly during the first days and weeks of development, and most impor-

tantly, the effects of testosterone on preferences for imprinted stimuli are both stimulus and age dependent.

These data suggest that knowledge of the distribution of androgen receptors in the brain, at the time of hatching may reveal areas that are functionally associated with the proper development of predispositions. Preliminary immunohistochemical analyses show that on the day of hatching, cells in the paraventricular nucleus (PVN) show relatively higher expression of androgen receptors compared to other hypothalamic brain nuclei (Loveland, J. L. and Vallortigara, G., unpublished). Given mesotocin- and vasotocin-producing cells are located in this nucleus, future investigations that focus on discerning whether the activation of these neurons shows any specific pattern associated with predisposed stimuli are needed. Furthermore, the potential roles of these nonapeptides in predispositions is promising given evidence of their effects on gregariousness in adults of other bird species. For example, in the zebra finch, *Taeniopygia guttata*, independent experiments show that bilateral injections of vasopressin V1a antagonist to the lateral septum, as well as the transient knockdown of vasotocin levels in neurons of the medial bed nucleus of the stria terminalis (BSTm) by injection of vasotocin antisense oligos, result in a reduction in gregariousness compared to saline-injected controls [245]. As an initial step in this direction, based on the model that peripheral release of substance P (SP) mediates the effects of vasotocin on approach behaviour [246], we have investigated how intraperitoneal SP injections affect preferences for the stuffed jungle fowl hen (predisposed stimulus, see Fig. 1a). We have found that in males, but not females, SP injection increased the preference for the predisposed stimulus compared to vehicle-injected controls [247].

Although much of the evidence for how hormones affect the preference for predisposed stimuli is indirect, that is, it is derived from imprinting studies where examining predispositions was not the central focus, it is reasonable to speculate that certain aspects of neural activation (or inhibition) that are required for predispositions to be expressed, as a precursor to imprinting may be at least in part, under hormonal control. Therefore, further research on the neuroendocrine system and underlying mechanisms of hormonal effects on the behaviour of visually naïve chicks to prefer predisposed stimuli promises to yield important advances.

5. Impairments in social predispositions early in life and their relevance to the ontogeny of autism spectrum disorders (ASD)

Human newborns, like newly-hatched chicks (see Section 1 and 2), soon after birth, preferentially orient to faces [7] and also demonstrate a preference for biological motion patterns over rigid or random motion patterns [8]. Based on these phenomena, it has been hypothesised that the expression of these predispositions is controlled, in part, by subcortical attention orienting mechanisms that are influenced by, and responsive to, social stimuli [3,7,73,248,249] (see also Section 3). These mechanisms may serve not only to detect the presence of social stimuli and enable newborns to orient towards them, but also to bias the relevant input to the developing cortical circuitry over the first weeks and months of life to promote proper development of brain regions that will become specialised for processing social stimuli [3]. From this point of view, social predispositions that are restricted to the first days of life may be considered as a precursor to the typical development of social cognition and communication. Accordingly, some authors have put forth the hypothesis that impairments in one or more of these early-emerging mechanisms (i.e., around the time of birth) prevent newborns from focusing their attention on social stimuli and as a consequence, typical development of social abilities become compromised and symptoms associated with autism spectrum disorder (ASD) are more likely to appear [250–252].

A challenge in testing this hypothesis is that, although ASD is an early-onset neurodevelopmental disorder, to date, confirmed diagnoses can only be made once children have reached, roughly, two to three years of age, despite the fact that some behavioural traits that culminate in ASD symptoms are evident in the first year of life [253]. Therefore, particular interest has recently been devoted to the study of social attention impairments in infants who have older siblings with a confirmed diagnosis of ASD. These subjects are considered at high-risk for developing ASD because as a group, 1 out of 5 will go on to be diagnosed with ASD [254,255]. In contrast, for 'low-risk' infants who have older siblings that have developed in a typical manner (and have never been diagnosed with ASD), the likelihood that they will develop ASD is much lower compared to the high-risk group.

Interestingly, the overall picture that emerges from studies that use the low- and high-risk group distinction is not conclusive. Some studies report early social attention impairments in infants at high risk for ASD [256–258]. For example, 6-month-old high-risk infants when presented with talking faces showed reduced visual attention to facial features [258] compared to low-risk infants. In another study with infants of the same age, compared to low-risk infants, the high-risk group exhibited diminished visual attention to a social scene. Even when high-risk infants were paying attention to the scene, they looked less at the actress in general, and at her face in particular [256]. Further, significant differences in the attention engagement to social stimuli during a habituation task were observed between infants who did and did not receive ASD diagnosis by 24 months [257]. Specifically, at 6 months of age, infants who later met the criteria for ASD had shorter looking times than other infants, suggesting impairments in sustained attention and a delay in when they start paying more attention to faces over objects, suggesting delayed engagement of "sensitization" to social stimuli. Of note, these differences were less apparent at 12 months, in line with other studies that demonstrated that some deficits in basic aspects of development present early in life appear to resolve during later stages [259,260].

In contrast, other studies have failed to find social orienting impairments early in life in infants at high risk for autism. For instance, one study reported that both 7- and 14-month-old infants from high- and at low-risk groups showed typical patterns of orienting to a target face when it was presented among other objects that were intended to function as distractors [261]. Another study showed that at 2 months of age, there was no difference between high- and low-risk groups in time spent looking at eyes. However, over time, a difference in looking at the eyes of others emerges between 2 and 6 months of age: infants later diagnosed with ASD showed a decrease in looking at the eyes of others whereas typically developing infants showed an increase in looking at the eyes of others during this period [262]. The authors interpreted these data as evidence that infants at high and low risk for ASD share the same social predisposition to attend to social stimuli at 2 months of age, and accordingly, the early-emerging orienting mechanisms must be "intact" in infants of this age even if they will later be diagnosed with ASD. However, it is important to note that 2-month-old babies have already had plenty of visual experience with social stimuli, which may allow for learning related compensatory mechanisms to occur and, further, that at that age developing cortical areas already influence responses to social stimuli [3,7]. For this reason, data collected from newborns is key for testing hypotheses about the state of social orienting mechanisms at a developmental stage when very little (i.e. from a few hours to a few days) opportunity for visual experience has been present.

In a recent report, Di Giorgio et al. [4] found that the predispositions to attend to and prefer social stimuli and biological

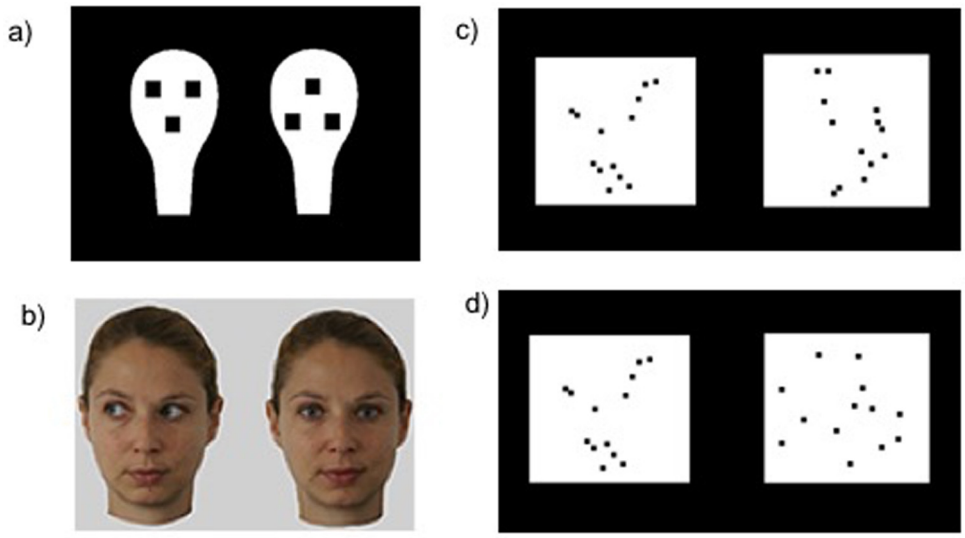

Fig. 5. Pairs of visual stimuli used to test newborn babies at low- and high-risk for ASD. Each baby was presented with all the four pairs, in random order: a) schematic face-like and non-face-like stimuli; b) face pictures with direct and averted gaze; c) representative frame of the animation sequence for PLDs of semi-rigid biological motion and rigid motion d) for semi-rigid biological motion and random motion. Significant differences in visual attention between the two risk groups were evident for the comparison between the predisposed and non-predisposed stimuli of the pairs a) and d).

motion differed between newborns at high- and at low-risk for ASD. Visual preferences, already employed with typically-developing newborns, towards face-like stimuli [7,263], images of real faces displaying direct eye-gaze [264], and biological motion stimuli [8,70] were investigated in high- and low-risk newborns. The prediction was that if some impairment in one of the early-emerging mechanisms for social visual orienting is present from birth in infants at high-risk for ASD, then their visual preferences for social face stimuli and biological motion should be absent or reversed and consistently lower compared to the low-risk group. Results showed that visual predispositions to attend to social stimuli, such as upright face-like patterns (compared to inverted ones) and biological motion (compared to the random motion pattern), differ between high-risk and low-risk newborns (Fig. 5). Specifically, it has been observed that high-risk newborns, compared to low-risk ones, were more interested in paying attention to the inverted face-like pattern and the random motion stimulus. This is the first evidence that impairments in the orienting mechanisms responsible for biasing newborns' visual attention to social stimuli, in this case the mechanism mediating orientation toward face-like configurations and the mechanism mediating orientation toward biological motion, are present very early in life in newborns at high-risk for autism. We are hopeful that with continued work and progress in this line of research we will be able to develop a standard setup and screening protocol that is simple to use and could be implemented by clinicians, allowing for a widespread application of early screening for ASD.

To conclude, since some of the key behavioural traits that characterise ASD, which is an early-onset neurodevelopmental disorder defined by core deficits in social cognition and communication, are severe impairments in the perception and processing of social stimuli, there is growing interest in the study of ASD as a model syndrome to investigate the ontogenesis of the social brain [265]. Within the *interactive specialization framework* (see [266–268]), it is plausible to hypothesise that, as a developmental disorder, ASD likely emerges from a complex interaction between initial genetic vulnerabilities and the infant's environment (interestingly, differences in the approach response towards predisposed stimuli has been found by investigating genetically distinct breeds of domestic fowl, which suggests there may be a genetic basis to this behaviour [32]). This alters the development of brain structure and function, compromising the infant's ability to learn from its social world [267]. Early impairments in some of the social orienting mechanisms prevent newborns from paying attention to the relevant social stimuli, changing their experience of the social environment and, as a consequence, restricting its social learning opportunities [269]. Of note, this is in line with a vast literature on human early sensitive periods related to social exposure (i.e., stress, maltreatment, abuse, etc.) and its consequences on neural and cognitive/affective development [270,271]. For instance, children reared in institutions show diminished intellectual (mental retardation) and affective performance (i.e., facial expression processing), as well as reduced metabolic activity in both the temporal and frontal cortical areas [272], compared to children reared in foster care or in their families of origin [273].

6. Conclusion remarks

Here we have reviewed, in parallel for human newborns and naïve precocial chicks, behavioural evidence of predispositions for various static and dynamic features typical of animate creatures (e.g. [7,12,13,16,88]). We have also considered the neural and physiological mechanisms underlying the expression of social predispositions, with particular attention to the data made available by research in animal models, suggesting a set of candidate areas and hormonal mechanisms that might be involved. We argue that the response properties of candidate subcortical structures, potentially involved in social preferences, are such to indeed enable recognition of predisposed stimuli (see also [1]). Moreover, the available evidence indicates that the candidate subcortical structures may also be sufficient to elicit the behavioural responses required for the expression of predispositions. We also highlight a partial overlap between some of the traditional candidate areas suggested for predispositions and the so-called social behaviour network, comprising interconnected areas, rich in sex steroid receptors and controlling multiple forms of social behaviour in adult animals [192]. By reviewing some of our most recent evidence, we suggest an involvement of one of the network's nodes in naïve chicks' responses to animate, biological motion. Moreover, we suggest that the distribution of androgen receptors in the brain of newly hatched

chicks might reveal areas that are functionally associated with the development of predispositions. Finally, we have explored the role of predispositions in the typical and atypical development of subsequent, more sophisticated, mechanisms of social cognition in our species, by comparing social attention in babies at high- and low-risk for autism spectrum disorders (ASD) [4].

Some general points emerge from all these diverse approaches. First of all, there is a remarkable consistency between the perceptual cues attended to by newborn babies and naïve nidifugal chicks, confirming on the one hand that these are appropriate models for the investigation of social predispositions in the human species, and suggesting on the other hand that the attentional biases observed in babies are unlikely to result from very rapid post-natal learning. Moreover, in both models there seems to be an analogous dissociation between early detection mechanisms for orienting towards the most basic properties that characterise animate creatures, and subsequent learning mechanisms for finer processing of social stimuli. The early detection mechanisms seem to be tuned very broadly to the recognition of few fundamental perceptual templates of animacy. Finer distinctions, for example between the motion or appearance of conspecifics and other species, as well as individual recognition of social companions, depend on subsequent learning (see Sections 1 and 2). This dissociation is also apparent in the division between the neural substrates of predispositions, which are hypothesised to be mostly subcortical (subpallial), and the neural mechanisms of learned social behaviours (e.g., individual recognition of the familiar imprinting object), in which cortical (pallial) regions have an important role (e.g., [190], Section 3). Suggestive dissociations are also apparent when considering the hormonal correlates of predisposed preferences and filial imprinting learning in chicks (e.g., [244], Section 4). However, there is a crucial interplay between the action of the early predispositions and the subsequent development of social learning mechanisms. This is clearly apparent in animal models, where we find recurrent demonstrations of a facilitation for imprinting on predisposed stimuli (e.g., [13,66]). This supports the view that one of the adaptive functions of the early biases for predisposed stimuli may be to direct subsequent learning mechanisms towards appropriate objects (Sections 1 and 2). This interaction between the two sets of mechanisms is also reflected at the neuroanatomical level, as revealed by our recent evidence that activity in an area responsible for imprinting learning is modulated by exposure to predisposed versus non predisposed stimuli ([31], Section 3). The evidence of anomalies in visual attention for predisposed social stimuli in babies at high risk of ASD ([4], Section 5) further supports and confirms this hypothesis, indicating that social predispositions in human newborns might be instrumental for the typical functional and neural specialisation of cortical circuitry specifically devoted to the perception and processing of social stimuli.

Acknowledgement

Giorgio Vallortigara was supported by a grant from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / Advanced Grant ERC PREMESOR G.A. n° 295517.

References

[1] O. Rosa-Salva, U. Mayer, G. Vallortigara, Roots of a social brain: developmental models of emerging animacy-detection mechanisms, Neurosci. Biobehav. Rev. 50 (2015) 150–168, http://dx.doi.org/10.1016/j.neubiorev.2014.12.015.
[2] F. Simion, E. Di Giorgio, I. Leo, L. Bardi, The processing of social stimuli in early infancy: from faces to biological motion perception, Prog. Brain Res. 189 (2011) 173–193.
[3] M.H. Johnson, Subcortical face processing, Nat. Rev. Neurosci. 6 (2005) 766–774, http://dx.doi.org/10.1038/nrn1766.
[4] E. Di Giorgio, E. Frasnelli, O. Rosa-Salva, S. Maria Luisa, M. Puopolo, D. Tosoni, NIDA-Network, F. Simion, G. Vallortigara, Difference in visual social predispositions between newborns at low- and high-risk for autism, Sci. Rep. 6 (2016) 26395, http://dx.doi.org/10.1038/srep26395.
[5] M.H. Johnson, G. Horn, Development of filial preferences in dark-reared chicks, Anim. Behav. 36 (1988) 675–683, http://dx.doi.org/10.1016/S0003-3472(88)80150-7.
[6] Y. Sugita, Face perception in monkeys reared with no exposure to faces, Proc. Natl. Acad. Sci. U. S. A. 105 (2008) 394–398, http://dx.doi.org/10.1073/pnas.0706079105.
[7] J. Morton, M.H. Johnson, CONSPEC and CONLERN: a two-process theory of infant face recognition, Psychol. Rev. 98 (1991) 164.
[8] F. Simion, L. Regolin, H. Bulf, A predisposition for biological motion in the newborn baby, Proc. Natl. Acad. Sci. U. S. A. 105 (2008) 809–813, http://dx.doi.org/10.1073/pnas.0707021105.
[9] G. Gottlieb, Imprinting in relation to parental and species identification by avian neonates, J. Comp. Physiol. Psychol. 59 (1965) 345.
[10] A.M. Janczak, B.O. Braastad, M. Bakken, Behavioural effects of embryonic exposure to corticosterone in chickens, Appl. Anim. Behav. Sci. 96 (2006) 69–82.
[11] C. Chiandetti, J. Galliussi, R.J. Andrew, G. Vallortigara, Early-light embryonic stimulation suggests a second route, via gene activation, to cerebral lateralization in vertebrates, Sci. Rep. 3 (2013) 2701.
[12] G. Vallortigara, L. Regolin, F. Marconato, Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns, PLoS Biol. 3 (2005) e208, http://dx.doi.org/10.1371/journal.pbio.0030208.
[13] E. Mascalzoni, L. Regolin, G. Vallortigara, Innate sensitivity for self-propelled causal agency in newly hatched chicks, Proc. Natl. Acad. Sci. U. S. A. 107 (2010) 4483–4485, http://dx.doi.org/10.1073/pnas.0908792107.
[14] J.G. Goldman, J.N. Wood, An automated controlled-rearing method for studying the origins of movement recognition in newly hatched chicks, Anim. Cogn. 18 (2015) 723–731.
[15] C.J. Nicol, The Behavioural Biology of Chickens, CABI, Oxfordshire, UK, 2015.
[16] O. Rosa-Salva, L. Regolin, G. Vallortigara, Faces are special for newly hatched chicks: evidence for inborn domain-specific mechanisms underlying spontaneous preferences for face-like stimuli, Dev. Sci. 13 (2010) 565–577, http://dx.doi.org/10.1111/j.1467-7687.2009.00914.x.
[17] O. Rosa-Salva, T. Farroni, L. Regolin, G. Vallortigara, M.H. Johnson, The evolution of social orienting: evidence from chicks (*Gallus gallus*) and human newborns, PLoS One 6 (2011) e18802, http://dx.doi.org/10.1371/journal.pone.0018802.
[18] O. Rosa-Salva, L. Regolin, G. Vallortigara, Inversion of contrast polarity abolishes spontaneous preferences for face-like stimuli in newborn chicks, Behav. Brain Res. 228 (2012) 133–143, http://dx.doi.org/10.1016/j.bbr.2011.11.025.
[19] T. Farroni, M.H. Johnson, E. Menon, L. Zulian, D. Faraguna, G. Csibra, Newborns' preference for face-relevant stimuli: effects of contrast polarity, Proc. Natl. Acad. Sci. U. S. A. 102 (2005) 17245–17250.
[20] C. Turati, F. Simion, I. Milani, C. Umiltà, Newborns' preference for faces: what is crucial? Dev. Psychol. 38 (2002) 875.
[21] E.S. Spelke, K.D. Kinzler, Core knowledge, Dev. Sci. 10 (2007) 89–96, http://dx.doi.org/10.1111/j.1467-7687.2007.00569.x.
[22] L.A. Eiserer, Development of filial attachment to static visual features of an imprinting object, Anim. Learn. Behav. 8 (1980) 159–166.
[23] C. ten Cate, Stimulus movement hen behaviour and filial imprinting in japanese quail (*Coturnix coturnix japonica*), Ethology 82 (1989) 287–306, http://dx.doi.org/10.1111/j.1439-0310.1989.tb00509.x.
[24] P. Bateson, The characteristics and context of imprinting, Biol. Rev. 41 (1966) 177–220.
[25] J.J. Bolhuis, Mechanisms of avian imprinting: a review, Biol. Rev. 66 (1991) 303–345, http://dx.doi.org/10.1111/j.1469-185X.1991.tb01145.x.
[26] G. Vallortigara, L. Regolin, Gravity bias in the interpretation of biological motion by inexperienced chicks, Curr. Biol. 16 (2006) R279–R280, http://dx.doi.org/10.1016/j.cub.2006.03.052.
[27] E. Mascalzoni, L. Regolin, G. Vallortigara, F. Simion, The cradle of causal reasoning: newborns' preference for physical causality, Dev. Sci. 16 (2013) 327–335.
[28] O. Rosa-Salva, M. Grassi, E. Lorenzi, L. Regolin, G. Vallortigara, Spontaneous preference for visual cues of animacy in naïve domestic chicks: the case of speed changes, Cognition 157 (2016) 49–60.
[29] G. Vallortigara, Aristotle and the chicken: animacy and the origins of beliefs, in: Theory Evol Its Impact, Springer, 2012, pp. 189–199.
[30] E. Versace, G. Vallortigara, Origins of knowledge: insights from precocial species, Front. Behav. Neurosci. 9 (2015).
[31] U. Mayer, O. Rosa-Salva, E. Lorenzi, G. Vallortigara, Social predisposition dependent neuronal activity in the intermediate medial mesopallium of domestic chicks (*Gallus gallus domesticus*), Behav. Brain Res. 310 (2016) 93–102, http://dx.doi.org/10.1016/j.bbr.2016.05.019.
[32] E. Versace, I. Fracasso, G. Baldan, A. Dalle Zotte, G. Vallortigara, Newborn chicks show inherited variability in early social predispositions for hen-like stimuli, in: 5th CogEvo – Rovereto Workshop Cogn. Evol., University of Trento, Rovereto, Italy, 2016, http://dx.doi.org/10.1101/071456.

[33] N.G. Hampton, J.J. Bolhuis, G. Horn, Induction and development of a filial predisposition in the chick, Behaviour 132 (1995) 451–477, http://dx.doi.org/10.1163/156853995x00667.
[34] M.H. Johnson, J.J. Bolhuis, G. Horn, Interaction between acquired preferences and developing predispositions during imprinting, Anim. Behav. 33 (1985) 1000–1006.
[35] J.J. Bolhuis, M.H. Johnson, G. Horn, Effects of early experience on the development of filial preferences in the domestic chick, Dev. Psychobiol. 18 (1985) 299–308.
[36] O.V. Egorova, K.V. Anokhin, Experimental analysis of the processes of systems genesis: expression of the c-fos gene in the chick brain during treatments inducing the development of the species-specific results-of-action acceptor, Neurosci. Behav. Physiol. 33 (2003) 209–216.
[37] J.J. Bolhuis, Mechanisms of avian imprinting: a review, Biol. Rev. Camb. Philos. Soc. 66 (1991) 303–345.
[38] G. Horn, Pathways of the past: the imprint of memory, Nat. Rev. Neurosci. 5 (2004) 108–120, http://dx.doi.org/10.1038/nrn1324.
[39] B.J. McCabe, Imprinting, Wiley Interdiscip. Rev. Cogn. Sci. 4 (2013) 375–390, http://dx.doi.org/10.1002/wcs.1231.
[40] T. Matsushima, E.-I. Izawa, N. Aoki, S. Yanagihara, The mind through chick eyes: memory, cognition and anticipation, Zoolog. Sci. 20 (2003) 395–408, http://dx.doi.org/10.2108/zsj.20.395.
[41] G. Gottlieb, Development of species identification in ducklings: XI. Embryonic critical period for species-typical perception in the hatchling, Anim. Behav. 33 (1985) 225–233.
[42] P. Bateson, How do sensitive periods arise and what are they for? Anim. Behav. 27 (1979) 470–486.
[43] C. Huchzermeyer, P. Husemann, C. Lieshoff, H.-J. Bischof, ZENK expression in a restricted forebrain area correlates negatively with preference for an imprinted stimulus, Behav. Brain Res. 171 (2006) 154–161.
[44] K. Immelmann, Sexual and other long-term aspects of imprinting in birds and other species, Adv. Study Behav. 4 (1972) 147–174.
[45] K. Immelmann, R. Pröve, R. Lassek, H.-J. Bischof, Influence of adult courtship experience on the development of sexual preferences in zebra finch males, Anim. Behav. 42 (1991) 83–89.
[46] J.-M. Vidal, The relations between filial and sexual imprinting in the domestic fowl: effects of age and social experience, Anim. Behav. 28 (1980) 880–891.
[47] P.P.G. Bateson, E.P. Reese, Reinforcing properties of conspicuous objects before imprinting has occurred, Psychon. Sci. 10 (1968) 379–380.
[48] K. Lorenz, Der kumpan in der umwelt des vogels, J. Ornithol. 83 (1935) 289–413.
[49] K.Z. Lorenz, The companion in the bird's world, The Auk 54 (1937) 245–273.
[50] D.A. Spalding, Instinct: with original observations on young animals, Br. J. Anim. Behav. 2 (1954) 2–11.
[51] T.D. Johnston, G. Gottlieb, Development of visual species identification in ducklings: what is the role of imprinting? Anim. Behav. 29 (1981) 1082–1099.
[52] R. Boakes, D. Panter, Secondary imprinting in the domestic chick blocked by previous exposure to a live hen, Anim. Behav. 33 (1985) 353–365, http://dx.doi.org/10.1016/S0003-3472(85)80059-2.
[53] J.J. Bolhuis, W.J. Trooster, Reversibility revisited: stimulus-dependent stability of filial preference in the chick, Anim. Behav. 36 (1988) 668–674.
[54] J.J. Cherfas, A. Scott, Impermanent reversal of filial imprinting, Anim. Behav. 29 (1981) 301, http://dx.doi.org/10.1016/s0003-3472(81)80180-7.
[55] J.P. Kent, Experiments on the relationship between the hen and chick (*Gallus gallus*): the role of the auditory mode in recognition and the effects of maternal separation, Behaviour 102 (1987) 1–13.
[56] E.A. Salzen, C.C. Meyer, Reversibility of imprinting, J. Comp. Physiol. Psychol. 66 (1968) 269.
[57] G. Johansson, Visual perception of biological motion and a model for its analysis, Percept. Psychophys. 14 (1973) 201–211.
[58] B.I. Bertenthal, J. Pinto, Global processing of biological motions, Psychol. Sci. 5 (1994) 221–225, http://dx.doi.org/10.1111/j.1467-9280.1994.tb00504.x.
[59] D.H. Chang, N.F. Troje, Perception of animacy and direction from local biological motion signals, J. Vis. 8 (2008) 3.
[60] M. Pavlova, A. Sokolov, Orientation specificity in biological motion perception, Percept. Psychophys. 62 (2000) 889–899.
[61] T.F. Shipley, The effect of object and event orientation on perception of biological motion, Psychol. Sci. 14 (2003) 377–380.
[62] S. Sumi, Upside-down presentation of the Johansson moving light-spot pattern, Perception 13 (1984) 283–286.
[63] M. Hirai, K. Hiraki, An event-related potentials study of biological motion perception in human infants, Cogn. Brain Res. 22 (2005) 301–304.
[64] V.M. Reid, S. Hoehl, T. Striano, The perception of biological motion by infants: an event-related potential study, Neurosci. Lett. 395 (2006) 211–214.
[65] R. Rugani, O. Rosa-Salva, L. Regolin, G. Vallortigara, Brain asymmetry modulates perception of biological motion in newborn chicks (*Gallus gallus*), Behav. Brain Res. 290 (2015) 1–7.
[66] M. Miura, T. Matsushima, Biological motion facilitates filial imprinting, Anim. Behav. 116 (2016) 171–180.
[67] M. Miura, T. Matsushima, Preference for biological motion in domestic chicks: sex-dependent effect of early visual experience, Anim. Cogn. 15 (2012) 871–879.
[68] T. Nakayasu, E. Watanabe, Biological motion stimuli are attractive to medaka fish, Anim. Cogn. 17 (2014) 559–575.
[69] J. Brown, G. Kaplan, L.J. Rogers, G. Vallortigara, Perception of biological motion in common marmosets (*Callithrix jacchus*): by females only, Anim. Cogn. 13 (2010) 555–564.
[70] L. Bardi, L. Regolin, F. Simion, Biological motion preference in humans at birth: role of dynamic and configural properties, Dev. Sci. 14 (2011) 353–359.
[71] D.H.F. Chang, N.F. Troje, Acceleration carries the local inversion effect in biological motion perception, J. Vis. 9 (2009), http://dx.doi.org/10.1167/9.1.19.
[72] D.H. Chang, N.F. Troje, Characterizing global and local mechanisms in biological motion perception, J. Vis. 9 (2009) 8.
[73] M.H. Johnson, Biological motion: a perceptual life detector? Curr. Biol. 16 (2006) R376–R377.
[74] N.F. Troje, C. Westhoff, The inversion effect in biological motion perception: evidence for a life detector? Curr. Biol. 16 (2006) 821–824.
[75] L. Wang, K. Zhang, S. He, Y. Jiang, Searching for life motion signals visual search asymmetry in local but not global biological-motion processing, Psychol. Sci. 21 (2010) 1083–1089.
[76] M. Hirai, D.H. Chang, D.R. Saunders, N.F. Troje, Body configuration modulates the usage of local cues to direction in biological-motion perception, Psychol. Sci. (2011) (0956797611417257).
[77] M. Hirai, D.R. Saunders, N.F. Troje, Allocation of attention to biological motion: local motion dominates global shape, J. Vis 11 (2011) 4.
[78] L. Bardi, L. Regolin, F. Simion, The first time ever I saw your feet: inversion effect in newborns' sensitivity to biological motion, Dev. Psychol. 50 (2014) 986–993, http://dx.doi.org/10.1037/a0034678.
[79] F. Heider, M. Simmel, An experimental study of apparent behavior, Am. J. Psychol. 57 (1944) 243–259.
[80] A. Michotte, The Perception of Causality, Basic Books, Oxford England, 1963.
[81] Aristotle, Physics, Harvard University Press, 1980. 307.
[82] J.A. Stewart, Perception of Animacy, University of Pennsylvania, 1982.
[83] R.A. Abrams, S.E. Christ, Motion onset captures attention, Psychol. Sci. 14 (2003) 427–432.
[84] S. Carey, Conceptual differences between children and adults, Mind Lang. 3 (1988) 167–181.
[85] R. Gelman, First principles organize attention to and learning about relevant data: number and the animate-inanimate distinction as examples, Cogn. Sci. 14 (1990) 79–106.
[86] A.M. Leslie, ToMM ToBy, and Agency: core architecture and domain specificity, Mapp. Mind Domain Specif. Cogn. Cult. (1994) 119–148.
[87] Y. Luo, L. Kaufman, R. Baillargeon, Young infants' reasoning about physical events involving inert and self-propelled objects, Cognit. Psychol. 58 (2009) 441–486.
[88] E. Di Giorgio, M. Lunghi, F. Simion, G. Vallortigara, Visual cues of motion that trigger animacy perception at birth: the case of self-propulsion, Dev. Sci. (2016), http://dx.doi.org/10.1111/desc.12394.
[89] E. Gyulai, Considerations on perception of animacy in the motion of a single object, Percept. Mot. Skills 99 (2004) 1014–1026.
[90] P.A. Szego, M.D. Rutherford, Actual and illusory differences in constant speed influence the perception of animacy similarly, J. Vis. 7 (2007) 5.
[91] P.A. Szego, M.D. Rutherford, Dissociating the perception of speed and the perception of animacy: a functional approach, Evol. Hum. Behav. 29 (2008) 335–342.
[92] P.D. Tremoulet, J. Feldman, Perception of animacy from the motion of a single object, Perception 29 (2000) 943–951.
[93] J. Pratt, P.V. Radulescu, R.M. Guo, R.A. Abrams, It's alive! Animate motion captures visual attention, Psychol. Sci. 21 (2010) 1724–1730.
[94] W.E. Frankenhuis, B. House, H.C. Barrett, S.P. Johnson, Infants' perception of chasing, Cognition 126 (2013) 224–233.
[95] G. Csibra, Goal attribution to inanimate agents by 6.5-month-old infants, Cognition 107 (2008) 705–717.
[96] G. Gergely, G. Csibra, Teleological reasoning in infancy: the naıve theory of rational action, Trends Cogn. Sci. 7 (2003) 287–292.
[97] S.C. Johnson, Y.A. Shimizu, S.-J. Ok, Actors and actions: the role of agent behavior in infants' attribution of goals, Cogn. Dev. 22 (2007) 310–322.
[98] Y. Luo, Three-month-old infants attribute goals to a non-human agent, Dev. Sci. 14 (2011) 453–460.
[99] Y. Luo, R. Baillargeon, Can a self-propelled box have a goal? Psychological reasoning in 5-month-old infants, Psychol. Sci. 16 (2005) 601–608.
[100] S. Biro, G. Csibra, G. Gergely, The role of behavioral cues in understanding goal-directed actions in infancy, Prog. Brain Res. 164 (2007) 303–322, http://dx.doi.org/10.1016/S0079-6123(07)64017-5.
[101] Y. Shimizu, S.C. Johnson, Infants' attribution of a goal to a morphologically unfamiliar agent, Dev. Sci. 7 (2004) 425–430.
[102] P. Setoh, D. Wu, R. Baillargeon, R. Gelman, Young infants have biological expectations about animals, Proc. Natl. Acad. Sci. U. S. A. 110 (2013) 15937–15942, http://dx.doi.org/10.1073/pnas.1314075110.
[103] G. Gergely, Z. Nádasdy, G. Csibra, S. Bíró, Taking the intentional stance at 12 months of age, Cognition 56 (1995) 165–193.
[104] P.D. Tremoulet, J. Feldman, The influence of spatial context and the role of intentionality in the interpretation of animacy from motion, Percept. Psychophys. 68 (2006) 1047–1058.

[105] C. ten Cate, Does behavior contingent stimulus movement enhance filial imprinting in Japanese quail? Dev. Psychobiol. 19 (1986) 607–614, http://dx.doi.org/10.1002/dev.420190611.
[106] C. Harshaw, R. Lickliter, Interactive and vicarious acquisition of auditory preferences in Northern bobwhite (*Colinus virginianus*) chicks, J. Comp. Psychol. 121 (2007) 320.
[107] C. Harshaw, I.P. Tourgeman, R. Lickliter, Stimulus contingency and the malleability of species-typical auditory preferences in Northern bobwhite (*Colinus virginianus*) hatchlings, Dev. Psychobiol. 50 (2008) 460–472.
[108] J. Atkinson, Human visual development over the first 6 months of life. A review and a hypothesis, Hum. Neurobiol. 3 (1984) 61–74.
[109] J. Atkinson, O.J. Braddick, Where and what in visual search, Perception 18 (1989) 181–189.
[110] J. Atkinson, B. Hood, J. Wattam-Bell, O. Braddick, Changes in infants' ability to switch visual attention in the first three months of life, Perception 21 (1992) 643–653.
[111] O. Braddick, J. Atkinson, J. Wattam-Bell, Normal and anomalous development of visual motion processing: motion coherence and dorsal-stream vulnerability, Neuropsychologia 41 (2003) 1769–1784.
[112] O. Braddick, J. Atkinson, B. Hood, W. Harkness, G. Jackson, F. Vargha-Khadem, Possible blindsight in infants lacking one cerebral hemisphere, Nature 360 (1992) 461–463, http://dx.doi.org/10.1038/360461a0.
[113] O.J. Braddick, J. Wattam-Bell, J. Atkinson, Orientation-specific cortical responses develop in early infancy, Nature 320 (1986) 617–619, http://dx.doi.org/10.1038/320617a0.
[114] M. Kraemer, A. Sjöström, Lack of short-latency-potentials in the VEP reflects immature extra geniculate visual function in delayed visual maturation (DVM), Doc. Ophthalmol. Adv. Ophthalmol. 97 (1998) 189–201.
[115] F. Simion, E. Valenza, C. Umiltà, B. Dalla Barba, Preferential orienting to faces in newborns: a temporal-nasal asymmetry, J. Exp. Psychol. Hum. Percept. Perform. 24 (1998) 1399–1405.
[116] R. Rafal, A. Henik, J. Smith, Extrageniculate contributions to reflex visual orienting in normal humans: a temporal hemifield advantage, J. Cogn. Neurosci. 3 (1991) 322–328, http://dx.doi.org/10.1162/jocn.1991.3.4.322.
[117] R. Rafal, J. Smith, J. Krantz, A. Cohen, C. Brennan, Extrageniculate vision in hemianopic humans: saccade inhibition by signals in the blind field, Science 250 (1990) 118–121.
[118] C. Williams, P. Azzopardi, A. Cowey, Nasal and temporal retinal ganglion cells projecting to the midbrain: implications for blindsight, Neuroscience 65 (1995) 577–586.
[119] B. de Gelder, I. Frissen, J. Barton, N. Hadjikhani, A modulatory role for facial expressions in prosopagnosia, Proc. Natl. Acad. Sci. 100 (2003) 13105–13110, http://dx.doi.org/10.1073/pnas.1735530100.
[120] J.S. Morris, B. DeGelder, L. Weiskrantz, R.J. Dolan, Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field, Brain 124 (2001) 1241–1252, http://dx.doi.org/10.1093/brain/124.6.1241.
[121] P. Vuilleumier, Faces call for attention: evidence from patients with visual extinction, Neuropsychologia 38 (2000) 693–700.
[122] P. Vuilleumier, N. Sagiv, Two eyes make a pair: facial organization and perceptual learning reduce visual extinction, Neuropsychologia 39 (2001) 1144–1149.
[123] P. Vuilleumier, J.L. Armony, J. Driver, R.J. Dolan, Distinct spatial frequency sensitivities for processing faces and emotional expressions, Nat. Neurosci. 6 (2003) 624–631, http://dx.doi.org/10.1038/nn1057.
[124] T.V. Sewards, M.A. Sewards, Innate visual object recognition in vertebrates: some proposed pathways and mechanisms, Comp. Biochem. Physiol. A: Mol. Integr. Physiol. 132 (2002) 861–891.
[125] M. Cynader, N. Berman, Receptive-field organization of monkey superior colliculus, J. Neurophysiol. 35 (1972) 187–201.
[126] S.V. Girman, R.D. Lund, Most superficial sublamina of rat superior colliculus: neuronal response properties and correlates with perceptual figure-ground segregation, J. Neurophysiol. 98 (2007) 161–177, http://dx.doi.org/10.1152/jn.00059.2007.
[127] F. González, R. Pérez, J.M. Alonso, J.L. Labandeira-García, C. Acuña, Responses of visual single cells in the superior colliculus of the albino rat to bright bars, Arch. Ital. Biol. 130 (1992) 249–261.
[128] J.T. McIlwain, P. Buser, Receptive fields of single cells in the cat's superior colliculus, Exp. Brain Res. 5 (1968) 314–325.
[129] M.A. Meredith, B.E. Stein, The visuotopic component of the multisensory map in the deep laminae of the cat superior colliculus, J. Neurosci. Off. J. Soc. Neurosci. 10 (1990) 3727–3742.
[130] C.R. Michael, Functional organization of cells in superior colliculus of the ground squirrel, J. Neurophysiol. 35 (1972) 833–846.
[131] R.D. Mooney, B.G. Klein, R.W. Rhoades, Correlations between the structural and functional characteristics of neurons in the superficial laminae and the hamster's superior colliculus, J. Neurosci. Off. J. Soc. Neurosci. 5 (1985) 2989–3009.
[132] R.D. Mooney, M.M. Nikoletseas, T.D. King, S.V. Savage, X. Huang, Correlations between the receptive field properties and morphology of neurons in the deep layers of the hamster's superior colliculus, J. Comp. Neurol. 335 (1993) 214–227, http://dx.doi.org/10.1002/cne.903350206.
[133] F. Prévost, F. Lepore, J.-P. Guillemot, Spatio-temporal receptive field properties of cells in the rat superior colliculus, Brain Res. 1142 (2007) 80–91, http://dx.doi.org/10.1016/j.brainres.2007.01.041.
[134] Y.C. Tiao, C. Blakemore, Functional organization in the superior colliculus of the golden hamster, J. Comp. Neurol. 168 (1976) 483–503, http://dx.doi.org/10.1002/cne.901680404.
[135] L. Wang, R. Sarnaik, K. Rangarajan, X. Liu, J. Cang, Visual receptive field properties of neurons in the superficial superior colliculus of the mouse, J. Neurosci. Off. J. Soc. Neurosci. 30 (2010) 16573–16584, http://dx.doi.org/10.1523/JNEUROSCI.3305-10.2010.
[136] L. Arendes, Superior colliculus activity related to attention and to connotative stimulus meaning, Brain Res. Cogn. Brain Res. 2 (1994) 65–69.
[137] R.W. Rhoades, L.M. Chalupa, Differential effects of stimulus size on on and off responses of superior collicular neurons, Exp. Neurol. 57 (1977) 57–66.
[138] G. Rizzolatti, Two functional types of neurons in the superficial layers of monkey superior colliculus, Arch. Ital. Biol. 116 (1978) 235–240.
[139] G. Rizzolatti, H.A. Buchtel, R. Camarda, C. Scandolara, Neurons with complex visual properties in the superior colliculus of the macaque monkey, Exp. Brain Res. 38 (1980) 37–42.
[140] P.H. Schiller, M. Stryker, Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey, J. Neurophysiol. 35 (1972) 915–924.
[141] J.-P. Ewert, Neuroethology of releasing mechanisms: prey-catching in toads, Behav. Brain Sci. 10 (1987) 337–368, http://dx.doi.org/10.1017/S0140525x00023128.
[142] J.-P. Ewert, A. von Wietersheim, Einfluß von Thalamus/Praetectum-Defekten auf die Antwort von Tectum-Neuronen gegenüber bewegten visuellen Mustern bei der Kröte *Bufo bufo* (L.), J. Comp. Physiol. 92 (1974) 149–160, http://dx.doi.org/10.1007/BF00694503.
[143] G. Manteuffel, S. Fiseifis, Configuration-sensitive visual responses in the superior colliculus of the house mouse (*Mus musculus domesticus*), Brain. Behav. Evol. 35 (1990) 176–184.
[144] N. Matsumoto, W.W. Schwippert, J.-P. Ewert, Intracellular activity of morphologically identified neurons of the grass frog's optic tectum in response to moving configurational visual stimuli, J. Comp. Physiol. A. 159 (1986) 721–739, http://dx.doi.org/10.1007/BF00603726.
[145] Q. Van Le, L.A. Isbell, J. Matsumoto, M. Nguyen, E. Hori, R.S. Maior, C. Tomaz, A.H. Tran, T. Ono, H. Nishijo, Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes, Proc. Natl. Acad. Sci. U. S. A. 110 (2013) 19000–19005, http://dx.doi.org/10.1073/pnas.1312648110.
[146] C.P. Mosher, P.E. Zimmerman, K.M. Gothard, Neurons in the monkey amygdala detect eye contact during naturalistic social interactions, Curr. Biol. 24 (2014) 2459–2464, http://dx.doi.org/10.1016/j.cub.2014.08.063.
[147] E.T. Rolls, Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces, Hum. Neurobiol. 3 (1984) 209–222.
[148] T. Shimizu, H.J. Karten, The avian visual system and the evolution of the neocortex, in: H.P. Zeigler, H.-J. Bischof (Eds.), Vis. Brain Behav. Birds, MIT Press, Cambridge, Massachusetts, 1993, pp. 103–114.
[149] H.-J. Bischof, S. Watanabe, On the structure and function of the tectofugal visual pathway in laterally eyed birds, Eur. J. Morphol. 35 (1997) 246–254.
[150] A.B. Butler, W. Hodos, Comparative Vertebrate Neuroanatomy: Evolution and Adaptation, John Wiley & Sons, 2005.
[151] L. Medina, A. Reiner, Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? Trends Neurosci. 23 (2000) 1–12.
[152] A. Reiner, K. Yamamoto, H.J. Karten, Organization and evolution of the avian forebrain, Anat. Rec. A: Discov. Mol. Cell Evol. Biol. 287 (2005) 1080–1102.
[153] L.I. Benowitz, H.J. Karten, Organization of the tectofugal visual pathway in the pigeon: a retrograde transport study, J. Comp. Neurol. 167 (1976) 503–520.
[154] H.J. Karten, T. Shimizu, The origins of neocortex: connections and lamination as distinct events in evolution, J. Cogn. Neurosci. 1 (1989) 291–301.
[155] J. Verhaal, H. Luksch, Processing of motion stimuli by cells in the optic tectum of chickens, Neuroreport 26 (2015) 578–582, http://dx.doi.org/10.1097/WNR.0000000000000391.
[156] L.R. Harris, The superior colliculus and movements of the head and eyes in cats, J. Physiol. 300 (1980) 367–391.
[157] P.H. Schiller, The role of the monkey superior colliculus in eye movement and vision, Invest. Ophthalmol. 11 (1972) 451–460.
[158] G.E. Schneider, Two visual systems, Science 163 (1969) 895–902.
[159] R.J. Blanchard, D.C. Blanchard, Defensive reactions in the albino rat, Learn. Motiv. 2 (1971) 351–362, http://dx.doi.org/10.1016/0023-9690(71)90016-6.
[160] N.S. Canteras, S. Chiavegatto, L.E. Ribeiro do Valle, L.W. Swanson, Severe reduction of rat defensive behavior to a predator by discrete hypothalamic chemical lesions, Brain Res. Bull. 44 (1997) 297–305.
[161] P. Dean, I.J. Mitchell, P. Redgrave, Responses resembling defensive behaviour produced by microinjection of glutamate into superior colliculus of rats, Neuroscience 24 (1988) 501–510.
[162] P. Redgrave, P. Dean, W. Souki, G. Lewis, Gnawing and changes in reactivity produced by microinjections of picrotoxin into the superior colliculus of rats, Psychopharmacology (Berl.) 75 (1981) 198–203.
[163] N. Sahibzada, P. Dean, P. Redgrave, Movements resembling orientation or avoidance elicited by electrical stimulation of the superior colliculus in rats, J. Neurosci. Off. J. Soc. Neurosci. 6 (1986) 723–733.
[164] A. Straube, T. Brandt, T. Probst, Importance of the visual cortex for postural stabilization: inferences from pigeon and frog data, Hum. Neurobiol. 6 (1987) 39–43.
[165] D. Ingle, Two visual systems in the frog, Science 181 (1973) 1053–1055.

[166] D. Ingle, Detection of stationary objects by frogs (*Rana pipiens*) after ablation of optic tectum, J. Comp. Physiol. Psychol. 91 (1977) 1359–1364.
[167] S.K. Kostyk, P. Grobstein, Visual orienting deficits in frogs with various unilateral lesions, Behav. Brain Res. 6 (1982) 379–388.
[168] J.P. Ewert, E. Schürg-Pfeiffer, W.W. Schwippert, Influence of pretectal lesions on tectal responses to visual stimulation in anurans: field potential, single neuron and behavior analyses, Acta Biol. Hung. 47 (1996) 89–111.
[169] E.G. Martin, W.H. Rich, The activities of decerebrate and decerebellate chicks, Am. J. Physiol. 46 (1918) 396–411.
[170] G. Zachar, A. Schrott, P. Kabai, Context-dependent prey avoidance in chicks persists following complete telencephalectomy, Brain Res. Bull. 76 (2008) 289–292, http://dx.doi.org/10.1016/j.brainresbull.2008.02.017.
[171] J.K. Kovach, P. Kabai, Effects of bilateral hemispherectomy on genetically variable stimulus preferences and imprinting in quail chicks, Brain Res. 629 (1993) 181–188, http://dx.doi.org/10.1016/0006-8993(93)91319-N.
[172] J.K. Kovach, Constitutional biases in early perceptual learning: I. Preferences between colors patterns, and composite stimuli of colors and patterns in genetically manipulated and imprinted quail chicks (*C. coturnix japonica*), J. Comp. Psychol. Wash. DC 97 (1983) 226–239.
[173] J.K. Kovach, Constitution-environment interactions modelled by artificially selected colour preferences and imprinting in quail, Neth. J. Zool. 43 (1992) 46–67, http://dx.doi.org/10.1163/156854293x00205.
[174] P. Kabai, J.K. Kovach, Persistence of approach response after decerebration in newly hatched quail chicks, Physiol. Behav. 53 (1993) 699–707, http://dx.doi.org/10.1016/0031-9384(93)90176-G.
[175] A. Csillag, P. Kabai, J.K. Kovach, Effects of diencephalic lesions on approach responses and color preferences in quail, Physiol. Behav. 58 (1995) 659–667, http://dx.doi.org/10.1016/0031-9384(95)00113-W.
[176] P.V. Simonov, Brain mechanisms of emotions, Neurosci. Behav. Physiol. 27 (1997) 405–413, http://dx.doi.org/10.1007/BF02462942.
[177] E.S. Valenstein, V.C. Cox, J.W. Kakolewski, Reexamination of the role of the hypothalamus in motivation, Psychol. Rev. 77 (1970) 16–31.
[178] D.A. Edwards, B. WALTER, P. LIANG, Hypothalamic and olfactory control of sexual behavior and partner preference in male rats, Physiol. Behav. 60 (1996) 1347–1354, http://dx.doi.org/10.1016/S0031-9384(96)00260-0.
[179] J. Panksepp, A. Dickinson, On the motivational deficits after medial hypothalamic lesions, Physiol. Behav. 9 (1972) 609–614, http://dx.doi.org/10.1016/0031-9384(72)90019-4.
[180] R.G. Paredes, L. Highland, P. Karam, Socio-sexual behavior in male rats after lesions of the medial preoptic area: evidence for reduced sexual motivation, Brain Res. 618 (1993) 271–276, http://dx.doi.org/10.1016/0006-8993(93)91275-W.
[181] J.J. Bolhuis, R.C. Honey, Imprinting, learning and development: from behaviour to brain and back, Trends Neurosci. 21 (1998) 306–311.
[182] G. Horn, Imprinting, learning, and memory, Behav. Neurosci. 100 (1986) 825–832.
[183] G. Horn, Neural bases of recognition memory investigated through an analysis of imprinting, Philos. Trans. R. Soc. Lond. B: Biol. Sci. 329 (1990) 133–142, http://dx.doi.org/10.1098/rstb.1990.0158.
[184] G. Horn, B.J. McCabe, Predispositions and preferences. Effects on imprinting of lesions to the chick brain, Anim. Behav. 32 (1984) 288–292, http://dx.doi.org/10.1016/S0003-3472(84)80349-8.
[185] B.J. McCabe, G. Horn, Learning-related changes in Fos-like immunoreactivity in the chick forebrain after imprinting, Proc. Natl. Acad. Sci. U. S. A. 91 (1994) 11417–11421.
[186] B.J. McCabe, G. Horn, P.P.G. Bateson, Effects of restricted lesions of the chick forebrain on the acquisition of filial preferences during imprinting, Brain Res. 205 (1981) 29–37, http://dx.doi.org/10.1016/0006-8993(81)90717-4.
[187] C. Lieshoff, J. Große-Ophoff, H.-J. Bischof, Sexual imprinting leads to lateralized and non-lateralized expression of the immediate early gene zenk in the zebra finch brain, Behav. Brain Res. 148 (2004) 145–155, http://dx.doi.org/10.1016/S0166-4328(03)00189-X.
[188] M. Sadananda, H.-J. Bischof, Enhanced fos expression in the zebra finch (Taeniopygia guttata) brain following first courtship, J. Comp. Neurol. 448 (2002) 150–164, http://dx.doi.org/10.1002/cne.10232.
[189] M. Sadananda, H.-J. Bischof, C-fos induction in forebrain areas of two different visual pathways during consolidation of sexual imprinting in the zebra finch (Taeniopygia guttata), Behav. Brain Res. 173 (2006) 262–267, http://dx.doi.org/10.1016/j.bbr.2006.06.033.
[190] G. Horn, B.J. McCabe, Predispositions and preferences. Effects on imprinting of lesions to the chick brain, Anim. Behav. 32 (1984) 288–292, http://dx.doi.org/10.1016/S0003-3472(84)80349-8.
[191] S.W. Newman, The medial extended amygdala in male reproductive behavior. A node in the mammalian social behavior network, Ann. N. Y. Acad. Sci. 877 (1999) 242–257.
[192] S.W. Newman, The medial extended amygdala in male reproductive behavior. A node in the mammalian social behavior network, Ann. N. Y. Acad. Sci. 877 (1999) 242–257.
[193] N. Aste, J. Balthazart, P. Absil, R. Grossmann, E. Mülhbauer, C. Viglietti-Panzica, G.C. Panzica, Anatomical and neurochemical definition of the nucleus of the stria terminalis in Japanese quail (*Coturnix japonica*), J. Comp. Neurol. 396 (1998) 141–157.
[194] Y. Atoji, J.M. Wild, Fiber connections of the hippocampal formation and septum and subdivisions of the hippocampal formation in the pigeon as revealed by tract tracing and kainic acid lesions, J. Comp. Neurol. 475 (2004) 426–461, http://dx.doi.org/10.1002/cne.20186.
[195] J. Balthazart, V. Dupiereux, N. Aste, C. Viglietti-Panzica, M. Barrese, G.C. Panzica, Afferent and efferent connections of the sexually dimorphic medial preoptic nucleus of the male quail revealed by in vitro transport of DiI, Cell Tissue Res. 276 (1994) 455–475.
[196] J. Balthazart, P. Absil, A. Foidart, M. Houbart, N. Harada, G.F. Ball, Distribution of aromatase-immunoreactive cells in the forebrain of zebra finches (*Taeniopygia guttata*): implications for the neural action of steroids and nuclear definition in the avian hypothalamus, J. Neurobiol. 31 (1996) 129–148.
[197] F. Briganti, L. Beani, G.C. Panzica, Connections of the dorsomedial part of the nucleus intercollicularis in a male non-songbird, the Grey partridge: a tract-tracing study, Neurosci. Lett. 221 (1996) 61–65.
[198] M. Cheng, M. Chaiken, M. Zuo, H. Miller, Nucleus taenia of the amygdala of birds: anatomical and functional studies in ring doves (*Streptopelia risoria*) and European starlings (*Sturnus vulgaris*), Brain. Behav. Evol. 53 (1999) 243–270.
[199] J.L. Goodson, A.K. Evans, L. Lindberg, Chemoarchitectonic subdivisions of the songbird septum and a comparative overview of septum chemical anatomy in jawed vertebrates, J. Comp. Neurol. 473 (2004) 293–314, http://dx.doi.org/10.1002/cne.20061.
[200] C.M. Montagnese, A.D. Székely, A. Adám, A. Csillag, Efferent connections of septal nuclei of the domestic chick (*Gallus domesticus*): an anterograde pathway tracing study with a bearing on functional circuits, J. Comp. Neurol. 469 (2004) 437–456, http://dx.doi.org/10.1002/cne.11018.
[201] C.M. Montagnese, G. Zachar, E. Bálint, A. Csillag, Afferent connections of septal nuclei of the domestic chick (*Gallus domesticus*): a retrograde pathway tracing study, J. Comp. Neurol. 511 (2008) 109–150, http://dx.doi.org/10.1002/cne.21837.
[202] C.M. Montagnese, T. Székely, D. Gray, T. Balázsa, G. Zachar, Immunoreactivity distribution of vasotocin and vasoactive intestinal peptide in brain nuclei of two songbird species with different breeding systems, Brain. Behav. Evol. 83 (2014) 140–149, http://dx.doi.org/10.1159/000357831.
[203] G.C. Panzica, C. Viglietti-Panzica, J. Balthazart, The sexually dimorphic medial preoptic nucleus of quail: a key brain area mediating steroid action on male sexual behavior, Front. Neuroendocrinol. 17 (1996) 51–125, http://dx.doi.org/10.1006/frne.1996.0002.
[204] J.T. Watson, E. Adkins-Regan, Testosterone implanted in the preoptic area of male Japanese quail must be aromatized to activate copulation, Horm. Behav. 23 (1989) 432–447.
[205] L.A. O'Connell, H.A. Hofmann, The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis, J. Comp. Neurol. 519 (2011) 3599–3639, http://dx.doi.org/10.1002/cne.22735.
[206] M. Bamshad, M.A. Novak, G.J. de Vries, Cohabitation alters vasopressin innervation and paternal behavior in prairie voles (*Microtus ochrogaster*), Physiol. Behav. 56 (1994) 751–758.
[207] D. Caroline Blanchard, R.J. Blanchard, L.K. Takahashi, T. Takahashi, Septal lesions and aggressive behavior, Behav. Biol. 21 (1977) 157–161, http://dx.doi.org/10.1016/S0091-6773(77)92407-5.
[208] J.P. Curley, C.L. Jensen, B. Franks, F.A. Champagne, Variation in maternal and anxiety-like behavior associated with discrete patterns of oxytocin and vasopressin 1a receptor density in the lateral septum, Horm. Behav. 61 (2012) 454–461, http://dx.doi.org/10.1016/j.yhbeh.2012.01.013.
[209] C.F. Ferris, L. Gold, G.J. De Vries, M. Potegal, Evidence for a functional and anatomical relationship between the lateral septum and the hypothalamus in the control of flank marking behavior in Golden hamsters, J. Comp. Neurol. 293 (1990) 476–485, http://dx.doi.org/10.1002/cne.902930310.
[210] C.F. Ferris, Y. Delville, Z. Grzonka, J. Luber-Narod, T.R. Insel, An iodinated vasopressin (V1) antagonist blocks flank marking and selectively labels neural binding sites in golden hamsters, Physiol. Behav. 54 (1993) 737–747.
[211] C.F. Ferris, Y. Delville, R.W. Irvin, M. Potegal, Septo-hypothalamic organization of a stereotyped behavior controlled by vasopressin in golden hamsters, Physiol. Behav. 55 (1994) 755–759.
[212] J.L. Goodson, Territorial aggression and dawn song are modulated by septal vasotocin and vasoactive intestinal polypeptide in male field sparrows (*Spizella pusilla*), Horm. Behav. 34 (1998) 67–77, http://dx.doi.org/10.1006/hbeh.1998.1467.
[213] J.L. Goodson, Vasotocin and vasoactive intestinal polypeptide modulate aggression in a territorial songbird, the violet-eared waxbill (Estrildidae: *Uraeginthus granatina*), Gen. Comp. Endocrinol. 111 (1998) 233–244, http://dx.doi.org/10.1006/gcen.1998.7112.
[214] J.L. Goodson, The vertebrate social behavior network: evolutionary themes and variations, Horm. Behav. 48 (2005) 11–22, http://dx.doi.org/10.1016/j.yhbeh.2005.02.003.
[215] J.L. Goodson, E. Adkins-Regan, Effect of intraseptal vasotocin and vasoactive intestinal polypeptide infusions on courtship song and aggression in the male zebra finch (*Taeniopygia guttata*), J. Neuroendocrinol. 11 (1999) 19–25.
[216] J.L. Goodson, R. Eibach, J. Sakata, E. Adkins-Regan, Effect of septal lesions on male song and aggression in the colonial zebra finch (*Taeniopygia guttata*) and the territorial field sparrow (Spizella pusilla), Behav. Brain Res. 101 (1999) 167–180.
[217] J.L. Goodson, S.E. Schrock, J.D. Klatt, D. Kabelik, M.A. Kingsbury, Mesotocin and nonapeptide receptors promote estrildid flocking behavior, Science 325 (2009) 862–866, http://dx.doi.org/10.1126/science.1174929.
[218] Y.F. Guzmán, N.C. Tronson, V. Jovasevic, K. Sato, A.L. Guedea, H. Mizukami, K. Nishimori, J. Radulovic, Fear-enhancing effects of septal oxytocin receptors, Nat. Neurosci. 16 (2013) 1185–1187, http://dx.doi.org/10.1038/nn.3465.

[219] A.M. Kelly, J.L. Goodson, Hypothalamic oxytocin and vasopressin neurons exert sex-specific effects on pair bonding, gregariousness, and aggression in finches, Proc, Natl. Acad. Sci. U. S. A. 111 (2014) 6069–6074, http://dx.doi.org/10.1073/pnas.1322554111.
[220] J.D. Klatt, J.L. Goodson, Oxytocin-like receptors mediate pair bonding in a socially monogamous songbird, Proc. Biol. Sci. 280 (2013) 20122396, http://dx.doi.org/10.1098/rspb.2012.2396.
[221] S. Kollack-Walker, S.W. Newman, Mating and agonistic behavior produce different patterns of Fos immunolabeling in the male Syrian hamster brain, Neuroscience 66 (1995) 721–736.
[222] S. Kollack-Walker, S.J. Watson, H. Akil, Social stress in hamsters: defeat activates specific neurocircuits within the brain, J. Neurosci. Off. J. Soc. Neurosci. 17 (1997) 8842–8855.
[223] Y. Kondo, A. Shinoda, K. Yamanouchi, Y. Arai, Role of septum and preoptic area in regulating masculine and feminine sexual behavior in male rats, Horm. Behav. 24 (1990) 421–434.
[224] R. Landgraf, R. Gerstberger, A. Montkowski, J.C. Probst, C.T. Wotjak, F. Holsboer, M. Engelmann, V1 vasopressin receptor antisense oligodeoxynucleotide into septum reduces vasopressin binding social discrimination abilities, and anxiety-related behavior in rats, J. Neurosci. Off. J. Soc. Neurosci. 15 (1995) 4250–4258.
[225] G. Liebsch, C.T. Wotjak, R. Landgraf, M. Engelmann, Septal vasopressin modulates anxiety-related behaviour in rats, Neurosci. Lett. 217 (1996) 101–104, http://dx.doi.org/10.1016/0304-3940(96)13069-X.
[226] Y. Liu, J.T. Curtis, Z. Wang, Vasopressin in the lateral septum regulates pair bond formation in male prairie voles (*Microtus ochrogaster*), Behav. Neurosci. 115 (2001) 910–919.
[227] M. Lukas, I. Toth, A.H. Veenema, I.D. Neumann, Oxytocin mediates rodent social memory within the lateral septum and the medial amygdala depending on the relevance of the social stimulus: male juvenile versus female adult conspecifics, Psychoneuroendocrinology 38 (2013) 916–926, http://dx.doi.org/10.1016/j.psyneuen.2012.09.018.
[228] G. Nagarajan, B.A. Tessaro, S.W. Kang, W.J. Kuenzel, Identification of arginine vasotocin (AVT) neurons activated by acute and chronic restraint stress in the avian septum and anterior diencephalon, Gen. Comp. Endocrinol. 202 (2014) 59–68, http://dx.doi.org/10.1016/j.ygcen.2014.04.012.
[229] K. Nishizawa, E.-I. Izawa, S. Watanabe, Neural-activity mapping of memory-based dominance in the crow: neural networks integrating individual discrimination and social behaviour control, Neuroscience 197 (2011) 307–319, http://dx.doi.org/10.1016/j.neuroscience.2011.09.001.
[230] D.E. Olazábal, L.J. Young, Species and individual differences in juvenile female alloparental care are associated with oxytocin receptor density in the striatum and the lateral septum, Horm. Behav. 49 (2006) 681–687, http://dx.doi.org/10.1016/j.yhbeh.2005.12.010.
[231] J.M. Ramirez, C. Salas, M. Portavella, Offense and defense after lateral septal lesions in *Columba livia*, Int. J. Neurosci. 41 (1988) 241–250.
[232] M. Taziaux, C.A. Cornil, C. Dejace, L. Arckens, G.F. Ball, J. Balthazart, Neuroanatomical specificity in the expression of the immediate early gene c-fos following expression of appetitive and consummatory male sexual behaviour in Japanese quail, Eur. J. Neurosci. 23 (2006) 1869–1887, http://dx.doi.org/10.1111/j.1460-9568.2006.04719.x.
[233] M.L. Tomaszycki, S.B. Banerjee, E. Adkins-Regan, The role of sex steroids in courtship, pairing and pairing behaviors in the socially monogamous zebra finch, Horm. Behav. 50 (2006) 141–147, http://dx.doi.org/10.1016/j.yhbeh.2006.02.005.
[234] A.H. Veenema, D.I. Beiderbeck, M. Lukas, I.D. Neumann, Distinct correlations of vasopressin release within the lateral septum and the bed nucleus of the stria terminalis with the display of intermale aggression, Horm. Behav. 58 (2010) 273–281, http://dx.doi.org/10.1016/j.yhbeh.2010.03.006.
[235] A.H. Veenema, R. Bredewold, G.J. De Vries, Vasopressin regulates social recognition in juvenile and adult rats of both sexes, but in sex- and age-specific ways, Horm. Behav. 61 (2012) 50–56, http://dx.doi.org/10.1016/j.yhbeh.2011.10.002.
[236] Z. Wang, C.F. Ferris, G.J. De Vries, Role of septal vasopressin innervation in paternal behavior in prairie voles (*Microtus ochrogaster*), Proc. Natl. Acad. Sci. U. S. A. 91 (1994) 400–404.
[237] I. Zoicas, D.A. Slattery, I.D. Neumann, Brain oxytocin in social fear conditioning and its extinction: involvement of the lateral septum, Neuropsychopharmacology 39 (2014) 3027–3035, http://dx.doi.org/10.1038/npp.2014.156.
[238] U. Mayer, O. Rosa-Salva, F. Morbioli, G. Vallortigara, Septal response to the first exposure to the motion of an Alive conspecific In naive domestic chicks, in: Proc 8th Eur. Conf. Comp. Neurobiol., ECCN, Munich, Germany, 2016, p. 34.
[239] E. Lorenzi, U. Mayer, O. Rosa-Salva, G. Vallortigara, A neuronal activity marker c-fos reveals higher activity in septum of chicks exposed to animacy motion cues, in: TSPC Proc. Trieste Symp Percept. Cogn., EUT Edizioni Università di Trieste, Trieste, Italy, 2015, p. 65.
[240] B. De Groef, S.V. Grommen, V.M. Darras, Hatching the cleidoic egg: the role of thyroid hormones, Front. Endocrinol. 4 (2013) 63.
[241] G. Gvaryahu, N. Snapir, B. Robinzon, G. Goodman, M.E. El Halawani, V.E. Grimm, The gonadotropic-axis involvement in the course of the filial following response in the domestic fowl chick, Physiol. Behav. 38 (1986) 651–656.
[242] S. Yamaguchi, N. Aoki, T. Kitajima, E. Iikubo, S. Katagiri, T. Matsushima, K.J. Homma, Thyroid hormone determines the start of the sensitive period of imprinting and primes later learning, Nat. Commun. 3 (2012) 1081.
[243] J. Nordgreen, A.M. Janczak, M. Bakken, Effects of prenatal exposure to corticosterone on filial imprinting in the domestic chick, *Gallus gallus domesticus*, Anim. Behav. 72 (2006) 1217–1228.
[244] J.J. Bolhuis, B.J. McCabe, G. Horn, Androgens and imprinting: differential effects of testosterone on filial preference in the domestic chick, Behav. Neurosci. 100 (1986) 51–56, http://dx.doi.org/10.1037/0735-7044.100.1.51.
[245] A.M. Kelly, M.A. Kingsbury, K. Hoffbuhr, S.E. Schrock, B. Waxman, D. Kabelik, R.R. Thompson, J.L. Goodson, Vasotocin neurons and septal V1a-like receptors potently modulate songbird flocking and responses to novelty, Horm. Behav. 60 (2011) 12–21, http://dx.doi.org/10.1016/j.yhbeh.2011.01.012.
[246] R.R. Thompson, J.C. Walton, R. Bhalla, K.C. George, E.H. Beth, A primitive social circuit: vasotocin–substance P interactions modulate social behavior through a peripheral feedback mechanism in goldfish, Eur. J. Neurosci. 27 (2008) 2285–2293.
[247] J.L. Loveland, G. Vallortigara, Neurobiology of social predispositions in newly hatched chicks: c-fos expression in dopamine neurons and substance P effect, in: Proc 8th Eur. Conf. Comp. Neurobiol., ECCN, Munich, Germany, 2016, p. 84.
[248] M.H. Johnson, A. Senju, P. Tomalski, The two-process theory of face processing: modifications based on two decades of data from infants and adults, Neurosci. Biobehav. Rev. 50 (2015) 169–179.
[249] A. Senju, M.H. Johnson, Atypical eye contact in autism: models, mechanisms and development, Neurosci. Biobehav. Rev. 33 (2009) 1204–1214.
[250] G. Dawson, S.J. Webb, J. McPartland, Understanding the nature of face processing impairment in autism: insights from behavioral and electrophysiological studies, Dev. Neuropsychol. 27 (2005) 403–424.
[251] N.M. Kleinhans, T. Richards, L.C. Johnson, K.E. Weaver, J. Greenson, G. Dawson, E. Aylward, fMRI evidence of neural abnormalities in the subcortical face processing system in ASD, Neuroimage 54 (2011) 697–704.
[252] F.R. Volkmar, Understanding the social brain in autism, Dev. Psychobiol. 53 (2011) 428–434, http://dx.doi.org/10.1002/dev.20556.
[253] L. Zwaigenbaum, S. Bryson, T. Rogers, W. Roberts, J. Brian, P. Szatmari, Behavioral manifestations of autism in the first year of life, Int. J. Dev. Neurosci. 23 (2005) 143–152.
[254] B.S. Abrahams, D.H. Geschwind, Advances in autism genetics: on the threshold of a new neurobiology, Nat. Rev. Genet. 9 (2008) 341–355, http://dx.doi.org/10.1038/nrg2346.
[255] S. Ozonoff, G.S. Young, A. Carter, D. Messinger, N. Yirmiya, L. Zwaigenbaum, S. Bryson, L.J. Carver, J.N. Constantino, K. Dobkins, et al., Recurrence risk for autism spectrum disorders: a baby siblings research consortium study, Pediatrics 128 (2011) e488–e495.
[256] K. Chawarska, S. Macari, F. Shic, Decreased spontaneous attention to social scenes in 6-month-old infants later diagnosed with autism spectrum disorders, Biol. Psychiatry 74 (2013) 195–203.
[257] E.J.H. Jones, K. Venema, R. Earl, R. Lowy, K. Barnes, A. Estes, G. Dawson, S.J. Webb, Reduced engagement with social stimuli in 6-month-old infants with later autism spectrum disorder: a longitudinal prospective study of infants at high familial risk, J. Neurodev. Disord. 8 (2016) 1.
[258] F. Shic, S. Macari, K. Chawarska, Speech disturbs face scanning in 6-month-old infants who develop autism spectrum disorder, Biol. Psychiatry 75 (2014) 231–237.
[259] A. Estes, L. Zwaigenbaum, H. Gu, T.S. John, S. Paterson, J.T. Elison, H. Hazlett, K. Botteron, S.R. Dager, R.T. Schultz, et al., Behavioral, cognitive, and adaptive development in infants with autism spectrum disorder in the first 2 years of life, J. Neurodev. Disord. 7 (2015) 1.
[260] K. Libertus, K.A. Sheperd, S.W. Ross, R.J. Landa, Limited fine motor and grasping skills in 6-month-old infants at high risk for autism, Child Dev. 85 (2014) 2218–2231.
[261] M. Elsabbagh, T. Gliga, A. Pickles, K. Hudry, T. Charman, M.H. Johnson, B Team, others, The development of face orienting mechanisms in infants at-risk for autism, Behav. Brain Res. 251 (2013) 147–154.
[262] W. Jones, A. Klin, Attention to eyes is present but in decline in 2–6-month-old infants later diagnosed with autism, Nature 504 (2013) 427–431.
[263] E. Valenza, F. Simion, V.M. Cassia, C. Umiltà, Face preference at birth, J. Exp. Psychol. Hum. Percept. Perform. 22 (1996) 892.
[264] T. Farroni, G. Csibra, F. Simion, M.H. Johnson, Eye contact detection in humans from birth, Proc. Natl. Acad. Sci. U. S. A. 99 (2002) 9602–9605, http://dx.doi.org/10.1073/pnas.152159999.
[265] H. Tager-Flusberg, The origins of social impairments in autism spectrum disorder: studies of infants at risk, Neural Netw. 23 (2010) 1072–1076.
[266] M.H. Johnson, Functional brain development in humans, Nat. Rev. Neurosci. 2 (2001) 475–483.
[267] M.H. Johnson, Interactive specialization: a domain-general framework for human functional brain development? Dev. Cogn. Neurosci. 1 (2011) 7–21.
[268] M.H. Johnson, T. Grossmann, K.C. Kadosh, Mapping functional brain development: building a social brain through interactive specialization, Dev. Psychol. 45 (2009) 151.
[269] E.J. Jones, T. Gliga, R. Bedford, T. Charman, M.H. Johnson, Developmental pathways to autism: a review of prospective studies of infants at risk, Neurosci. Biobehav. Rev. 39 (2014) 1–33.

[270] S.L. Andersen, A. Tomada, E.S. Vincow, E. Valente, A. Polcari, M.H. Teicher, Preliminary evidence for sensitive periods in the effect of childhood sexual abuse on regional brain development, J. Neuropsychiatry Clin. Neurosci. 20 (2008) 292–301, http://dx.doi.org/10.1176/jnp.2008.20.3.292.
[271] M.H. Teicher, A. Tomoda, S.L. Andersen, Neurobiological consequences of early stress and childhood maltreatment: are results from human and animal studies comparable? Ann. N. Y. Acad. Sci. 1071 (2006) 313–323.
[272] H.T. Chugani, M.E. Behen, O. Muzik, C. Juhász, F. Nagy, D.C. Chugani, Local brain functional activity following early deprivation: a study of postinstitutionalized romanian orphans, NeuroImage 14 (2001) 1290–1301, http://dx.doi.org/10.1006/nimg.2001.0917.
[273] C.A. Nelson, C.H. Zeanah, N.A. Fox, P.J. Marshall, A.T. Smyke, D. Guthrie, Cognitive recovery in socially deprived young children: the Bucharest early intervention project, Science 318 (2007) 1937–1940.
[274] U. Mayer, O. Rosa-Salva, G. Vallortigara, First exposure to an alive conspecific activates septal and amygdaloid nuclei in visually-naïve domestic chicks (*Gallus gallus*), Behav. Brain. Res. (in press).