Sensitive periods for social development: Interactions between predisposed and learned mechanisms

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Abstract

We analysed research that makes use of precocial species as animal models to describe the interaction of predisposed mechanisms and environmental factors in early learning, in particular for the development of social cognition. We also highlight the role of sensitive periods in this interaction, focusing on domestic chicks as one of the main animal models for this field. In the first section of the review, we focus on the emergence of early predispositions to attend to social partners. These attentional biases appear before any learning experience about social stimuli. However, non-specific experiences occurring during critical periods of the early post-natal life determine the emergence of these predisposed mechanisms for the detection of social partners. Social predispositions have an important role for the development learning-based social cognitive functions, showing the interdependence of predisposed and learned mechanisms in shaping social development. In the second part of the review we concentrate on the reciprocal interactions between filial imprinting and spontaneous (not learned) social predispositions. Reciprocal influences between these two sets of mechanisms ensure that, in the natural environment, filial imprinting will target appropriate social objects. Neural and physiological mechanisms regulating the sensitive periods for the emergence of social predispositions and for filial imprinting learning are also described.

Keywords: sensitive periods, predispositions, learning, social cognition, domestic chicks

Glossary

Altricial: animal born or hatched in a very immature condition so that the young require intense parental care.

c-Fos: protein product of the corresponding Immediate Early Gene *c-fos* that is acting as a transcription factor and is commonly used as a marker to quantify neural activity and plasticity.

Deprivation experiment: involves keeping an animal in an environment that has been systematically impoverished of a given type of stimuli. The rationale of these experiments is usually to deprive animals of a certain experience, to see whether the behaviour or trait of interest is nonetheless displayed.

Filial imprinting: rapid form of learning by exposure, through which the young of precocial bird species learn to recognize the object(s) to which they are exposed during a sensitive period. By this process, the young chick restricts its affiliative behaviour towards the first salient object(s) it encounters. In the natural environment, filial imprinting usually results in social attachment towards the mother hen and/or the brood mates.

Immediate Early Genes (IEG): a class of genes that are rapidly expressed in response to neural activation. Their products are often used as neural activity markers.

IMM (Intermediate Medial Mesopallium): associative brain region of the avian pallium (homolog to mammalian cortexes), involved in the memory storage for filial imprinting learning in domestic chicks.

Mesotocin: this hormone, which regulates many social behaviours, is the oxytocin-equivalent of nonmammalian tetrapods. Receptors for these neuropeptides are present in areas of the Social Behaviour Network.

Point-light display: animation created by placing light-points on the major joints of a walking body and obscuring the rest of the image. This sort of stimulus conveys many of the dynamic properties of the portrayed motion while removing most information on the configuration and appearance of the moving body.

Precocial: animal born or hatched in a very mature condition so that the young do not need intensive care, being able to perform autonomously many behavioural and physiological functions.

Predispositions: unlearned tendencies to react in predetermined ways (e.g., with approach or avoidance) to stimuli featuring specific characteristics (motion, colour, configuration, etc.). Predispositions are displayed by newborn or newly-hatched animals or by naïve animals, deprived of any experience with a given category of stimuli. Usually, the features that elicit predispositions are typical of objects of great biological significance, such as potential social companions, preys or predators.

Self-propulsion: propulsion powered by an energy source internal to the moving object. It is one of the main features that distinguish animate creatures from inanimate objects, which can be set in motion only by the action of external forces.

Sensitive period: limited periods during which specific mechanisms are more likely to take place and the effects of experience on developing organisms are stronger than in the rest of the lifespan.

Semi-rigid motion: Kind of movement, typically associated with biological motion. Some points maintain a fixed distance from each other, while their distance to other points varies. This motion pattern is exhibited by vertebrates and other legged animals and differs from the cinematics of rigid translation and random movement shown by most inanimate objects.

Social Behaviour Network: a set of interconnected subcortical areas, rich of sex-steroid hormone receptors, highly conserved across vertebrates and in charge of many social behaviours.

T3 (triiodothyronine): tyrosine-based hormone synthesized by the thyroid gland involved in the regulation of many physiological processes in the body. T3 represents the primary metabolically active thyroid hormone in avian species and has been recently implicated in the control of the sensitive window for filial imprinting.

1. General introduction

Throughout the tradition of developmental psychology, the role of predispositions (spontaneous preferences and behaviours) and experience-based learning mechanisms in determining cognitive development has been a central topic. The writings of Jacques Melher pay a special attention towards the way evolution equipped infants with specialised mechanisms, predisposed to perform specific tasks of great adaptive value. These mechanisms provide pre-representations at the basis of all subsequent knowledge (Mehler & Dupoux, 1994). Interestingly, although the early predisposed mechanisms envisioned by Mehler and Dupoux do not depend on direct learning experience, they are not experience-independent. On the contrary, environmental influences act by selecting, triggering and regulating them. Here, we provide an overview of the research on the dynamic interplay of predisposed and learned mechanisms in the development of social cognition during the early post-natal life. In doing so, we focus on the temporal dynamics of these interactions.

Experiences occurring during specific ontogenetic stages are particularly influential on subsequent cognitive, social and neural development (Bateson & Gluckman, 2012; Chan, 2014; Charil et al., 2010; Hubel & Wiesel, 1970; Kalcher-Sommersguter et al., 2015; Lorenz, 1937; Zeanah et al., 2009), as shown by the influential notion of sensitive periods. These are time windows in which the effects of environmental stimuli on developing organisms are stronger than in the rest of the lifespan ((Bodin, Yeates, & Cass, 2011) for the distinction between sensitive and critical periods, Dehorter & Del

Pino, 2020; Knudsen, 2004). We describe the sensitive periods in which different environmental factors are particularly effective and how they are modulated by genetic or environmental influences. This shows how the timing of events occurring in the species-typical environment can shape social development. As model systems, we will mostly refer to domestic chicks and their social development (Di Giorgio, Loveland, et al., 2017; Lorenzi et al., 2020; Rosa-Salva, Mayer, & Vallortigara, 2015). Precocial birds offer advantages such as the presence of a mature sensory-motor system and of fast learning mechanisms already in hatchlings (e.g., filial imprinting). For these reasons, they have been central to understand the interface between predisposed and learned mechanisms at the beginning of life.

Research in precocial birds revealed that, even in the pre-hatching phase, experience and genetically determined mechanisms interact in the development of socio-cognitive skills. Thanks to the *in ovo* development and the possibility to test behavioural responses already shortly after hatching, precocial birds (Versace, 2017) provide optimal models for the investigation of pre-natal influences on behavioural outcomes. This has been exploited by studies on the development of neuroanatomical and functional lateralization in domestic chicks, revealing how the interaction of genetic and experience-based mechanism within specific critical periods of the pre-natal life can modulate cognitive functions ((Rogers, 1982, 1997); (Deng & Rogers, 1997; Rogers & Bolden, 1991; Rogers & Deng, 1999; Rogers & Sink, 1988); (Deng & Rogers, 2002a); (Rogers, 1990); (Dharmaretnam & Rogers, 2005) (Lorenzi et al., 2019); (Chiandetti, 2011; Chiandetti & Vallortigara, 2019); (Chiandetti et al., 2013)).

In this review, however, we analyse how social and cognitive development are affected by the interplay between predisposed and learning mechanisms during the first stages of post-natal life. The review is divided into two main sections that follow an ontogenetic order, describing mechanisms occurring in the early postnatal life and then in the filial imprinting phase. In the first section, we focus on the mechanisms underlying the emergence of early predispositions to attend to social partners. These predispositions develop in the earliest stages of the postnatal life, in visually naïve chicks. To clarify whether a behaviour is spontaneous or acquired, researchers have used deprivation experiments. This method consists in depriving animals of a certain experience to see whether the behaviour of interest is displayed nonetheless (Lorenz, 1965). Animals are either tested before they have performed the activity, at birth or hatching, or reared in isolation to eliminate opportunities for learning through observation. These procedures are facilitated when embryos can be directly controlled and animals hatch individually, making deprivation experiments particularly suitable for oviparous species. Hence, it comes as no surprise that avian species have been central to investigate the ontogenetic origins of behaviour. The ethological tradition has emphasized stereotypical and species-specific fixed action patterns that do not depend on experience (Schleidt, 2010). Originally, behavioural biologists focused on the notion of instinct and complex sequences of relatively fixed adult behaviour (Burghardt & Bowers, 2017; Eibl-Eibesfeldt, 1975). More recently, scientists have identified early cognitive traits and spontaneous preferences (predispositions) that orient the behaviour of neonate, inexperienced animals, towards particular stimuli. As detailed below (see 2.1), converging evidence across neonates of different amniote species (e.g. domestic chicks, human infants, tortoise hatchlings) tested with the deprivation method suggests the presence of predisposed preferences to attend to stimuli associated with the presence of animate, living beings, the so-called "animacy detectors" (Di Giorgio et al., 2017a; Rosa-Salva et al., 2015; Vallortigara, 2012; Vallortigara, *in press*). These preferences, in the literature on domestic chicks and human infants, are often called "social predispositions". This is because, in the natural environment of social species, these early predispositions will result in preferential attention towards appropriate social partners. Differently from the fully structured, species-specific behaviours targeted by classical behavioural biologists, early predispositions appear as building blocks of the developing cognitive abilities of the vertebrate mind. These early social predispositions, whose neural basis we are starting to uncover in chicks (2.2), appear to contribute to the development and specialization of the brain circuits that, in adults, carry out sophisticated social information processing (Johnson, 2005). This may be achieved even by simply directing visual attention towards appropriate social stimuli, biasing the visual input received by the subject during a critical period of the postnatal development. Indeed, anomalies of early social predispositions have been associated with abnormalities in the development of social cognition, such as those associated with disorders of the autistic spectrums (Di Giorgio et al., 2016). However, even though social predispositions do not require any specific learning experience about social stimuli, their emergence unfolds also through the action of environmental influences. In the first section of the review, we thus describe how non-specific experiences occurring during well-defined critical periods of the early post-natal life determine the emergence of predisposed mechanisms for the detection of social partners (and animate creatures in general) (see 2.2). These predispositions have an important role in shaping the future development of more sophisticated, learning-based social cognitive functions. This literature beautifully shows the crucial interdependence of predisposed and learned mechanisms in shaping social development.

In the second section of the review (section 3), we will focus on filial imprinting (Vallortigara & Versace, 2018), a very prominent form of learning, which is crucial for the survival and subsequent social adaptation of young chicks. Through filial imprinting, young precocial birds learn to recognize the object(s) to which they are exposed during a sensitive period. By this process, in the absence of any overt reinforcement, the young chick restricts its affiliative behaviour towards the first salient object(s) it encounters. In the natural environment, filial imprinting usually results in social attachment towards the mother hen and/or the brood mates (Bateson, 1966; Bolhuis, 1991; McCabe, 2019). This has, of course, crucial implications for social development, allowing chicks not only to receive parental care from the mother hen, but also to maintain group cohesion. Filial imprinting can thus provide the foundations for the formation and maintenance of stable social groups, whose internal hierarchy (pecking order) regulates “chicken societies”. By being exposed to conspecifics during development, chickens develop sophisticated social skills. These include the ability to recognize familiar conspecifics and their dominance hierarchy (Deng & Rogers, 2002b; Rogers & Workman, 1989; Vallortigara & Andrew, 1994; Vallortigara & Andrew, 1991; Vallortigara, 1992), the capacity to acquire information about food sources by observing others’ behaviour (Nicol, 2004) and even forms of perspective-taking and social deception (Marino, 2017). In the last part of the review, we will describe how experience-driven mechanisms and social predispositions can influence the course of filial imprinting, directing it towards appropriate objects. We will discuss how the emergence of social predispositions facilitates imprinting also towards non-predisposed features of the stimuli. Moreover, we will see that even after an initial imprinting towards an inanimate object, predispositions can emerge, which then direct subsequent secondary imprinting to appropriate social companions. We will see how experience occurring in specific time windows of the perinatal life in turn affects the duration of the sensitive period for imprinting. At least some of the brain regions involved in filial imprinting have been identified with a good degree of certainty (e.g., the Intermediate Medial Mesopallium, or IMM, see Horn, 2004). Some of the physiological mechanisms that control the opening and closing of the sensitive period for filial imprinting, though the actions of specific hormones and neurotransmitters, have been recently identified also (Aoki et al., 2018; Yamaguchi et al., 2012). This literature reveals the presence of interdependent relationships between experience-based and predisposed mechanisms.

2. Early post-natal life: sensitive periods for the emergence of predispositions

2.1 The study of early predispositions as adaptive responses

In this section, we analyse the evidence of preparedness to attend to social stimuli in the early post-natal life, as revealed by social predispositions in domestic chicks (the main model considered in this review). Early predispositions to orient towards and engage with particular stimuli have been observed for both static features and motion dynamics. Interestingly, the preferred features are associated with the presence of animate creatures (see Figure 1). Among static features, preferences have been observed for particular colours (e.g. red and blue are preferred to yellow and green (Kovach, 1971; Miura, Nishi, & Matsushima, 2020; Salzen, Lily, & McKeown, 1971; Salzen & Meyer, 1968; Taylor, Sluckin, & Hewitt, 1969), shapes (Hess & Goodwin, 1969; Salzen & Meyer, 1968; Schulman, Hale, & Graves, 1970), for hollow objects (Versace et al., 2016), for faces and for face-like configurations (in newborns, Johnson & Morton, 1991; Morton & Johnson, 1991; chicks, Rosa-Salva, Regolin, & Vallortigara, 2010, 2012; Rosa Salva et al., 2011; monkeys, Sugita, 2008; and tortoises Versace, Damini, & Stancher, 2020). A seminal work by Johnson and Horn (Johnson & Horn, 1988) has shown that, in the first hours after hatching, dark-reared chicks deprived from experience with conspecifics exhibit a preference to orient towards a stuffed fowl compared to a disassembled version of a similar fowl (Bolhuis, Johnson, & Horn, 1989; Egorova & Anokhin, 2003; Rosa-Salva et al., 2015; Versace et al., 2017). Subsequent experiments have shown that this predisposition is not specifically tuned to hens or fowls, but is based on low-level cues present in the area of the neck and face (Johnson & Horn, 1988; Rosa-Salva, Mayer & Vallortigara, 2019).

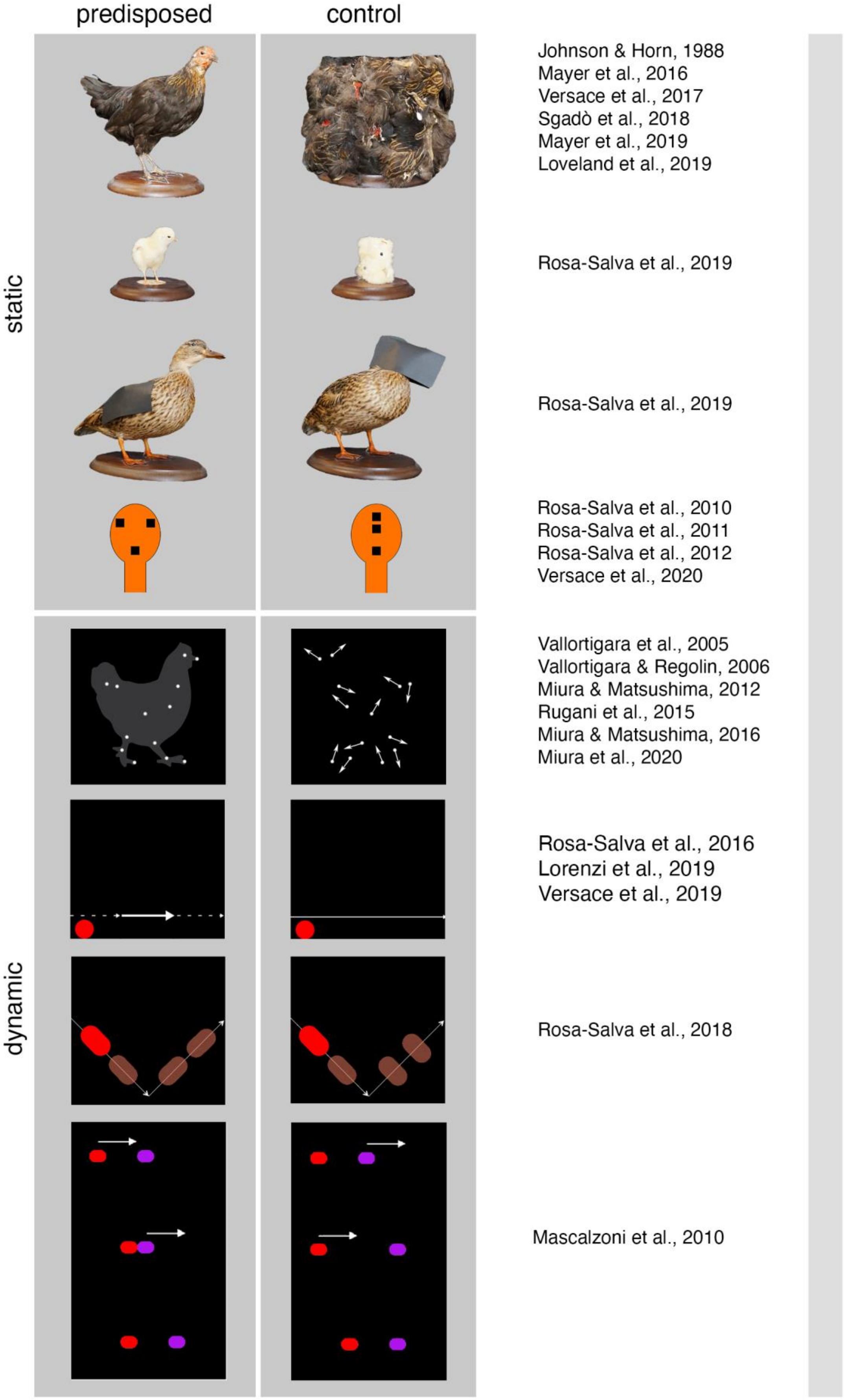

Fig. 1. Schematic representation of the main classes of stimuli used to test social predispositions for

static and dynamic features typical animate objects. For each pair of stimuli, the preferred object featuring the predisposed trait and a control stimulus are presented side by side, followed by a selection of papers reporting a behavioural preference for the predisposed object in naïve animals. From above, the first two images of the first panel represent the stimuli used to test the preference for hen-like objects (a stuffed junglefowl-like hen versus a scrambled version of a similar specimen). In the following rows: a pair of similar stimuli obtained from stuffed chick models; a stuffed duck with her wings occluded compared to a similar exemplar with the head region occluded; a schematic face-like stimulus and a non-face control image. The first two images of the second panel represent a point light display of a walking hen and a control stimulus with random motion of the same dots (the silhouette of the hen has been added for illustrative purposes). In the following two rows: a schematic representation of a speed changing stimulus and its speed-constant control; an object that always moves in the direction of its main body axis and its control stimulus. In the last row, we represented on the left the sequence of movement of a self-propelled red object hitting and putting in motion a non-self-propelled purple object (the sequence has to be read from above to below). In this case, chicks preferentially imprint on the red objects. On the right, both objects appear self-propelled and chicks display no preferences between the two. In all dynamic stimuli arrows have been added for illustrative purposes.

Deprivation studies on social predispositions have been conveniently conducted on domestic chicks and other precocial species, thanks to the ease of testing precocial animals that are born with a mature sensory and motor system (Versace, 2017). However, the preference for faces and face-like configurations has been extensively observed also in human infants (Buiatti et al., 2019; Di Giorgio et al., 2016; Goren, Sarty & Wu, 1975; Morton & Johnson, 1991; Simion & Di Giorgio, 2015), human fetuses (Reid et al., 2017), monkeys (Sugita, 2008) and recently in tortoise hatchlings (Versace et al., 2020). This suggests the presence of an ancient mechanism for the detection of faces, which is tuned to low-level features associated with the presence of faces. This mechanism, active soon after birth or hatching, does not specify the species-specific or individual details of faces, but increases the chances that newborn animals orient towards other animals by directing their attention toward any face-like configuration.

Dynamic patterns are also very effective in attracting the attention of newborn animals. Although precocial avian species can exhibit affiliative responses to still objects, the phenomenon of filial imprinting is enhanced by the presence of moving objects (ten Cate, 1986). This suggests that the first orienting responses of animals, before they developed affiliative responses to particular objects they have experienced, might be driven by cues of animacy, the property of "being alive". In line with this idea, we have observed early preferences of visually inexperienced animals for motion dynamics associated with the presence of animate, living beings. This supports the idea of an animacy-detector tuned to some of the features that distinguish the biological motion of animate creatures (Mascalzoni, Regolin, & Vallortigara, 2010; Rosa-Salva et al., 2016; Rosa-Salva et al., 2018; Vallortigara, Regolin, & Marconato, 2005). Vallortigara and colleagues (2005) have initially discovered a spontaneous preference for point-light displays that move according to semi-rigid biological motion. In this kind of movement, points located on different parts of the body move relative to one another within an elastic, constrained range. This is different from the cinematics of rigid translation and random movement shown by most inanimate objects. The preference for biological motion has been documented in human neonates too (Simion, Regolin, & Bulf, 2008). Social predispositions for animate motion can be observed using very simplified visual stimuli. For instance, visually naïve chicks prefer to imprint on objects that start to move on their own, rather than being pushed in motion by a collision with another object (Mascalzoni et al., 2010; Simion et al., 2008). Likewise, the ability to spontaneously start to move from a resting state (“start from rest”) elicits visual preferences also in human newborns (Di Giorgio et al., 2017b). Similarly, both chicks and human infants prefer to approach objects that change in speed and, in the case of chicks, rotate autonomously (Frankenhuis et al., 2013; Hernik, Fearon, & Csibra, 2014; Rosa-Salva et al., 2016, 2018). These are all features that signal the presence of an internal energy source in self-propelled objects (a defining feature for the discrimination of animate creatures). Moreover, a predisposition for objects that move in the direction of their main body-symmetry axis, as most bilaterians, is present in both infants (Hernik et al., 2014) and visually-inexperienced chicks (Rosa-Salva et al., 2018). Overall, compelling evidence suggests that early approach responses are facilitated by cues associated with animate objects.

An important function of early preferences might be to direct the attention of the young animals towards the animate objects that will provide care, and towards which young animals should develop affiliative responses and sexual responses later on (Morton & Johnson, 1991; Versace et al., 2018). As mentioned in the introduction, this would also enable the subsequent development of neural mechanisms specialised for the processing of various aspects of social information (Di Giorgio et al., 2016; Johnson, 2005). This idea is supported by evidence of enhanced imprinting responses elicited by predisposed stimuli, such as red colour on the head of a creature that moves according to biological motion (Lemaire et al., 2020; Miura et al., 2020; Miura & Matsushima, 2016) or such as ”start from rest” (Mascalzoni et al., 2010). However, similar early predispositions have been found in solitary animals with no parental care, such as land tortoises (Versace et al., 2020). This suggests that mechanisms to direct attention towards animate objects might respond to a general need of identifying living agents to gain information about important aspects of life, including the presence of resources, preys and predators (Lorenzi & Vallortigara, 2020; Vallortigara, 2012; Versace et al., 2020). The predispositions for some stimuli exhibited at the beginning of life, though, are not rigidly prescriptive, as revealed by the fact that both chicks (Versace et al., 2017) and young tortoises (Versace et al., 2018) can show exploration of alternative stimuli. The propensity to focus only on the predisposed stimuli or explore alternative stimuli has a genetic basis in chicks, as shown by the differences in perseverance in approaching a stuffed hen in visually naïve chicks (Versace et al., 2017).

In line with the idea that predispositions direct attention to stimuli relevant for an individual’s fitness, we have recently shown that spontaneous responses that do not require experience include anti-predator defensive behaviours. Although this topic has received less attention than social predispositions, to date studies in chicks (and mallard ducklings, Dessborn et al., 2012) have shown that precocial birds are able to recognize and appropriately react to various threats, and this in the absence of previous experience. A few decades ago, Schiff reported that dark-hatched and -reared chicks escape a stimulus rapidly looming in front of them (Schiff, 1965). Recently, we have shown that young chicks reared with no experience with moving stimuli spontaneously assess the difference between distant and approaching threats posed by stimuli moving overhead. Being presented with stimuli that mimicked either an approaching threat (a ‘looming’ stimulus increasing in size like an approaching predator) or a distant threat (a 'sweeping' stimulus moving at a constant distance like a cruising prey bird), naïve chicks modulated their defensive responses accordingly (Hébert, Versace, & Vallortigara, 2019). They ran away from an approaching stimulus and froze in the presence of a distant threat (see Fig. 2). Static visual stimuli can also trigger innate anti-predatory responses: while chicks are attracted by 'face-like' stimuli (a silhouette containing three dark blobs organized in a triangular fashion) over a control stimulus (Rosa-Salva et al., 2009) (Fig. 1), they avoid stimuli with a black 'pupil-like' feature (Rosa-Salva, Regolin, & Vallortigara, 2012) (see Fig. 2) (see also (Gagliardi, Gallup, & Boren, 1976; Jones, 1980; Scaife, 1976) and (Rosa-Salva, Regolin, & Vallortigara, 2007)).

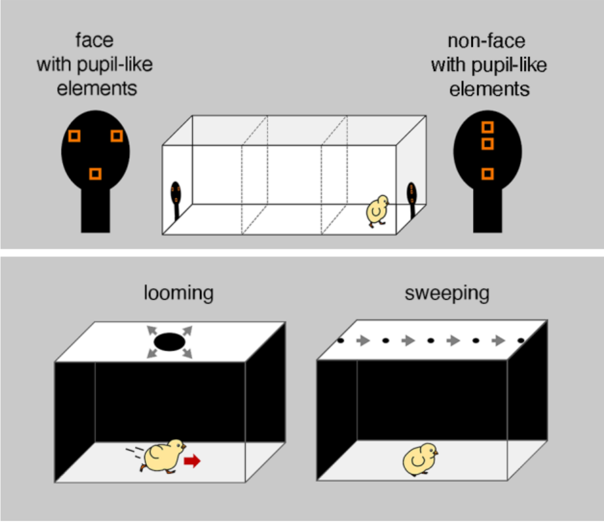

Fig. 2 Illustration of stimuli and setups used to test predisposed anti-predator responses in naïve chicks. In the upper panel, a face-like and a non-face-like schematic stimulus are shown, both featuring three internal features with a central pupil-like element. Only in the face-like configuration these resemble a pair of predator eyes. Naïve chicks tend to avoid the face-like stimulus in this test. In the lower panel, prototypical chicks' reactions to looming and sweeping stimuli (fleeing and freezing, respectively) are shown.

2.2 Neural and physiological mechanisms underlying early predispositions

Our recent research started to shed some light on the neural mechanism underlying early predispositions for social stimuli. We did this visualising c-Fos to map neural activation. In one of our first studies on this regard we found higher activation of IMM in chicks that preferred a scrambled version of a stuffed fowl hen compared to chicks that preferred the normal fowl. It was already known that the IMM (Bolhuis & Honey, 1998; Horn, 1986, 1990; Horn & McCabe, 1984; McCabe & Horn, 1994; McCabe, Horn, & Bateson, 1981) is not required for the preference for hen-like objects. Bilateral lesions of the IMM impair the recognition of imprinting objects, but do not suppress the predisposed preference for hen-like objects (Horn & McCabe, 1984). However, although this region does not cause the expression of the predisposition, IMM responds differently to naturalistic and artificial stimuli in inexperienced chicks (Mayer et al., 2016). At least three explanations are possible for this finding. The mismatch between the template provided by the predisposition for hen-like objects and the artificial object experienced may require increased plasticity to imprint on the scrambled stimulus. This could cause increased c-Fos expression in the chicks that choose the non-predisposed stimulus, since c-Fos is a marker of learning and memory related plasticity (Lanahan & Worley, 1998; Okuno, 2011; Sauvage, Kitsukawa, & Atucha, 2019). Another possibility is that the choice to approach the scrambled fowl reflects the lack of a predisposed preference for hen-like objects and that c-Fos expression in IMM could be systematically higher individuals with this abnormal developmental outcome. Last but not least, it has been proposed that the neural circuits responsible for the expression of predispositions in chicks with hen preference suppress the neuronal activity in the IMM (McCabe, 2019).

Other studies have investigated the involvement of the social behaviour network in chicks' predispositions. This network includes interconnected brain regions that are rich in sex-steroid receptors and modulate various social behaviours in adult vertebrates (Goodson, 2005; Newman, 1999; O'Connell & Hofmann, 2011). Until recently, however, it was unclear whether areas of this network participate in the expression of early social behaviours in newborn animals too. We found activation of important social behaviour network nodes, such as septum, preoptic area and amygdaloid areas (arcopallium and nucleus taeniae of the amygdala) in visually naïve chicks exposed for the first time to social stimuli (Lorenzi et al., 2017; Mayer et al., 2017, 2019; Mayer, Rosa-Salva, & Vallortigara, 2017). Among the amygdaloid nuclei, nucleus taeniae of the amygdala and parts of arcopallium selectively responded to the static features of predisposed stimuli (e.g., hen-like objects) (Mayer et al., 2019). This is similar to what happens in humans, where amygdala has been implicated in early orienting responses towards face-like configurations (Johnson, 2005). An interesting dissociation appeared when we tested the response to the animate motion of social companions. In this case, the amygdaloid nuclei were not responsive, while the activation of septum and preoptic area was increased. In a first study, we found that septum was responsive to the motion of a living conspecific compared to the rigid motion of a similarly stimulus (a stuffed chick rotating at a constant speed) (Mayer et al., 2017). In a follow-up work, we found that both septum and preoptic area were also activated by a highly controlled stimulus showing speed changes in the motion of a simple object (Lorenzi et al., 2017). Overall, these nodes of the social behaviour network show selective responses to features of animate objects already in visually naïve animals. Previous visual experience and specific learning events do not seem to be necessary to establish these functions, in line with what has been recently reported for cortical areas specialised for face processing in humans (Ratan Murty et al., 2020). Areas of the social behaviour network might be involved in processing the social valence of, and bonding to, social stimuli in the absence of previous social experience.

In mammals and birds, social behaviours are mediated by neuropeptide signalling based on vasopressin and oxytocin receptors, present in medial amygdala and lateral septum (Goodson et al., 2009). A recent study investigated the role of vasotocin and mesotocin (the avian homologs of vasopressin and oxytocin) in mediating the social predisposition for hen-like objects. This revealed that intracranial mesotocin administration increased the level of preference for the stuffed fowl model compared to saline-injected controls (Loveland, Stewart, & Vallortigara, 2019). This suggests that mesotocin signalling may regulate the expression of social predispositions, probably acting on areas of the social behaviour network.

Intriguingly, in two of our works investigating the physiological substrate of chicks' predispositions for social stimuli, we found that their development can be disrupted exposing embryos to valproic acid during the last week of incubation (Lorenzi et al., 2019; Sgadò et al., 2018). In humans, prenatal exposure to this drug increases the risk to develop disorders of the autistic spectrum (Christensen et al., 2013). For this reason, embryonic exposure to valproic acid is used to develop models of autism in rodents

(Nicolini & Fahnestock, 2018) and chicks (Lorenzi et al., 2019; Nishigori et al., 2013; Sgadò et al., 2018). The embryonic administration of valproic acid to chicks induces selective anomalies in social aggregation behaviours (Nishigori et al., 2013), impairment in the recognition of familiar conspecifics (Zachar et al., 2019), a loss of the predisposition for hen-like objects (Sgadò et al., 2018) and speed-changing stimuli (Lorenzi et al., 2019). These results support the idea that, in chicks like in human newborns (Di Giorgio et al., 2016), disturbances of early social predisposition may derail the normal development of social cognition, causing abnormal developmental outcomes such as those observed in autistic disorders. The mechanisms subtending to the effects of valproic acid in chicks are currently unknown. However, in mammals, valproic acid seems to act on an inhibitory pathway (GABAergic parvalbumine cells) that controls critical periods for cortical plasticity (eg., Gervain et al., 2013; Gogolla et al., 2009; Lauber, Filice, & Schwaller, 2016; Reh et al., 2020; Silingardi et al., 2010). This opens the way for future studies investigating how valproic acid may affect similar pathways in birds, deepening our understanding of the mechanisms that control sensitive periods in non-mammalian species.

Overall, evidence suggests that the neural mechanisms to detect living animals are widespread across species and might fulfill a range of adaptive functions from the first stages of life.

2.3 Transient time windows for the emergence of early predispositions and their hormonal correlates

Early predispositions are not fixed and crystallised responses that are present throughout life (differently from the fixed-action patterns investigated by classical ethologists) (see (Shultz, Klin, & Jones, 2018 for a review on human neonates).

The preference for face-like stimuli, for instance, changes during the first months of life. This preference is apparent in human neonates in the first hours after birth, declines at around two months of age before reappearing again at five months for more complex stimuli (Buiatti et al., 2019; Johnson et al., 1991; Shultz et al., 2018; Simion & Di Giorgio, 2015) and being detectable up to adulthood (Tomalski, Csibra, & Johnson, 2009). Likewise, at hatching, chicks of both sexes have a spontaneous preference to approach other females (Pallante, Rucco, & Versace, in preparation). This preference rapidly fades when chicks are expose to other chicks. The loss of this preference occurs at the age in which in the will chicks leave the nest. This dynamic may be important to promote social cohesion with the flock, that is composed of both male and female chicks.

Transient time windows in the appearance of predispositions have been well documented for chicks' preferences to approach stuffed hens (Bolhuis, Johnson, & Horn, 1985; Egorova & Anokhin, 2003; Horn, Bolhuis, & Hampton, 1995; Johnson, Bolhuis, & Horn, 1985). This preference emerges only after the animals have been stimulated through some activating experience, such as motoric activity, exposure to unrelated visual patterns, handling or acoustical stimulation. These activating experiences do not provide any specific information about the predisposed visual stimuli. Indeed, the activating experiences can even involve modalities other than vision. To have an effect, the activating experiences that trigger the appearance of the predisposition for hen-like objects must happen within a specific time window in the early post-natal life (between 24 and 36 hours after hatching) (Bolhuis & Horn, 1997; Bolhuis et al., 1989; Davies, Johnson, & Horn, 1992; Johnson, Davies, & Horn, 1989). Moreover, the ensuing predisposition will be detectable only at precise time points after the activating experiences (between 5 and 24h after the stimulation, Davies et al., 1992). This timing, however, is modulated by the type of activating experience to which chicks are exposed. For instance, if chicks also receive visual stimulation while performing motoric activity, the preference for hen-like objects is detectable already after 2 hours (Bolhuis et al., 1985). However, it is unclear whether this acceleration depends on the level of arousal or the sensory modality stimulated by the activating experience (see also Lickliter, 2000; Rosa-Salva et al., 2015). Studies on the role of stimulating experiences during sensitive developmental periods also revealed information on the physiological mechanisms involved. An intriguing case is that of noradrenaline, which is not directly involved in the expression of the preference for hen-like objects (Bolhuis, McCabe, & Horn, 1986; Davies, Horn, & McCabe, 1985; Davies et al., 1992; see Rosa-Salva et al., 2015 for a review). This neurotransmitter, however, seems to play a role in the opening of the sensitive period related to its emergence. Indeed, the administration of a noradrenaline antagonist delays the onset of the sensitive period during which activating experiences cause the subsequent emergence of the predisposition for hen-like objects (Davies et al., 1992; for similar evidence after the administration of the anaesthetic equithisin see Bolhuis & Horn, 1997).

Similar developmental properties also characterise the predispositions for self-propelled objects and biological motion. The preference for objects that change in speed is present 24 hours after hatching, but fades two days later (Versace, Ragusa, & Vallortigara, 2019). The development of a preference for the semi-rigid biological motion typical of legged animals may require previous exposure to moving visual stimuli (Miura & Matsushima, 2012) or motoric activity such as walking on a treadmill (Vallortigara et al., 2005). In the case of biological motion, the behavioural preference is detectable already thirty minutes after the exposure to moving visual stimuli and persists one day late. A sensitive period was also present for the preference for biological motion, which was visible in two- but not in five-day old chicks (Miura et al., 2020).

In some studies, the development of biological motion preferences were limited to males (Miura & Matsushima, 2012). This is in line with the evidence of the involvement of sex hormones, such as testosterone, in the expression of the predisposed preference for hen-like objects (e.g., Bolhuis et al., 1986; see Rosa-Salva et al., 2015 for a review). This may indicate that at least some of the underlying physiological mechanisms may be shared between different social predispositions.

Thyroid hormones too have been implicated in the development of social predispositions for animate motion. These hormones play essential roles in the brain development of vertebrate species (McNabb & King, 1993). Among thyroid hormones, 3,5,3′-triiodothyronine (T3) has the highest affinity with avian thyroid receptors and is, therefore, the primary metabolically active thyroid hormone (Bellabarba et al., 1988;

Weirich & McNabb, 1984). We recently obtained preliminary evidence that T3 affects the emergence of chicks' predisposition for speed-changing objects, by modulating its timing (Lorenzi et al., 2020). Blocking the thyroid hormone receptors with an antagonist, at the age when domestics chicks normally show a preference for speed changing objects (day 1 post-hatching), leads to the disappearance of the preference. Contrariwise, injecting T3 when the sensitive period normally terminates (day 3 post-hatching), reinstates the preference for self-propelled objects, at least in females (Lorenzi et al., 2020). Whether T3 only controls the emergence of the predisposition for self-propelled objects or it acts on a more general brain mechanism common to most predispositions, remains however to be univocally determined.

3. Experience-driven effects and the control of sensitive periods for imprinting

The predisposed preference for biological motion has facilitating effects on filial imprinting for non-predisposed features, such as the colour of the moving stimulus. Chicks that developed a stronger preference for a biological motion stimulus are better able to imprint on the colour in which this stimulus was depicted (Miura & Matsushima, 2016). Miura and Matsushima (2020) found evidence of a complex interaction between the predisposition for biological motion, the predisposition for the red colour (typical of hens' combs and junglefowl faces) and filial imprinting. This work revealed a predisposed preference for approaching and imprinting on stimuli in which the biological motion of a walking hen is associated with the colour red. On the contrary, the same stimulus presented in yellow or performing a simple linear motion is a less effective imprinting stimulus. This might reflect a predisposed preference for a walking animal with a red comb/crest or a reddish face. Notably, this effect seemed driven by the movement of the hen’s head, since presenting only the head of the stimulus was as effective as presenting the whole body, whereas the tail region was not effective. Crucially, however, the capacity to imprint on biological motion stimuli presented in a yellow colour could be rescued, if chicks were pre-exposed to visual moving stimuli. When chicks had been stimulated by exposure to moving objects before imprinting, they could also imprint on a biological motion stimulus with the less predisposed yellow colour. Similarly, previous visual exposure to a group of conspecifics enhances imprinting preferences (Deng & Rogers, 2002b). Only chicks that were exposed to a group of conspecifics, in a later test showed a preference for the individual chick with whom they had been subsequently reared. This effect was due to an improvement of the performance of the right-eye system (left hemisphere), in line with the dominance of the right hemisphere in biological motion processing (Rugani et al., 2015) or in familiarity recognition (Vallortigara & Rogers, 2005). On the contrary, the left eye-system showed a stably superior performance, also in the absence of this priming experience. See also (Lickliter, Dyer, & McBride, 1993; Lickliter & Gottlieb, 1985; Lickliter & Gottlieb, 1988) for similar effects in ducklings.

Overall, the studies reviewed so far suggest a dynamic and potentially enhancing interplay between experience-based and predisposed mechanisms. On the one hand, as we saw in the previous paragraph, non-specific experiences, occurring within specific sensitive periods, drive the emergence of predispositions for animate stimuli. On the other hand, predispositions are associated with enhanced learning of additional features of the stimulus.

A well-known feature of filial imprinting is the presence of a limited sensitive period during which this form of learning can occur. Behaviourally, the sensitive period for imprinting begins as soon as precocial birds start following an object and terminates once the birds start to avoid unfamiliar ones (Bolhuis, 1991). The sensitive period for imprinting usually lasts a couple of days after hatching; for instance, Yamaguchi et al. (2012) reported that 4 day-old, dark-reared chicks can no longer be imprinted (but see Case & Graves, 1978; Sluckin, 1972 for reports of imprintability up to 7 days in dark reared chicks, indicating potential inter-breed variability). However, the duration of the sensitive period can substantially vary, being influenced by different factors (Bateson, 1966; Bolhuis, 1991; Sluckin, 1972). Both pre-hatch and post-hatch experiences influence the determination of the sensitive period (Dimond, 1968; Landsberg, 1976; Simner, 1973). For instance, rearing ducklings in diffuse, non-patterned light (preventing structured visual experiences) extends the sensitive period in this species (Moltz & Stettner, 1961).

At the neurophysiological level, an increase of the concentration of the neurotransmitter glutamate extends the imprinting period, suggesting a possible role of NMDA glutamate receptors (Parsons & Rogers, 1997, 2000). The sensitive period for filial imprinting may be influenced by hormones too (Bateson, 1983; Knudsen, 2004). For instance, in ducklings a rise of corticosterone has been described around the end of the sensitive period for imprinting (Weiss, Köhler, & Landsberg, 1977). This hormonal change may be the source for the increasing fear observed when imprinting terminates (Bolhuis, 1991).

Recently, a role of thyroid hormones has been identified in domestic chicks. In precocial galliform birds, the thyroid hormones T4 and T3 peak around hatching and then gradually decrease (Lu, McMurtry, & Coon, 2007; McNabb, 2006; Yamaguchi et al., 2012). The level of T3 in the brain correlates with the strength of imprinting and artificially injecting T3 facilitates it. The action of T3 appears to be quick, being detectable already in 30 minutes, similarly to what reported above for the induction of the predisposition for biological motion. Importantly, T3 is strongly implicated in the control of the sensitive period for imprinting in chicks. Inhibiting it (either systemically or via brain injections) impairs visual imprinting, whereas injecting it extends and even re-opens its sensitive period up to 8 days after hatching. After this age, the capability to form imprinting attachment cannot be rescued by T3, indicating the presence of further, yet unknown, closing mechanisms (Yamaguchi et al., 2012). Recent studies have also elucidated the neural mechanisms subtending to the action of T3, which seem to be specifically localised to IMM (a region classically implicated in imprinting, Horn, 2004) (summarised in Fig. 3). Blockage of the nucleotide diphosphate kinase 2 in IMM impairs the reopening of the sensitive window by T3 (Yamaguchi et al., 2016). Likewise, blocking the Wnt-2b glycoprotein, related to neuronal growth, in an area connected to IMM (IMHA, intermediate medial hyperpallium apicale) also prevents T3 action (Aoki et al., 2015; Yamaguchi et al., 2018) (see Fig. 3).

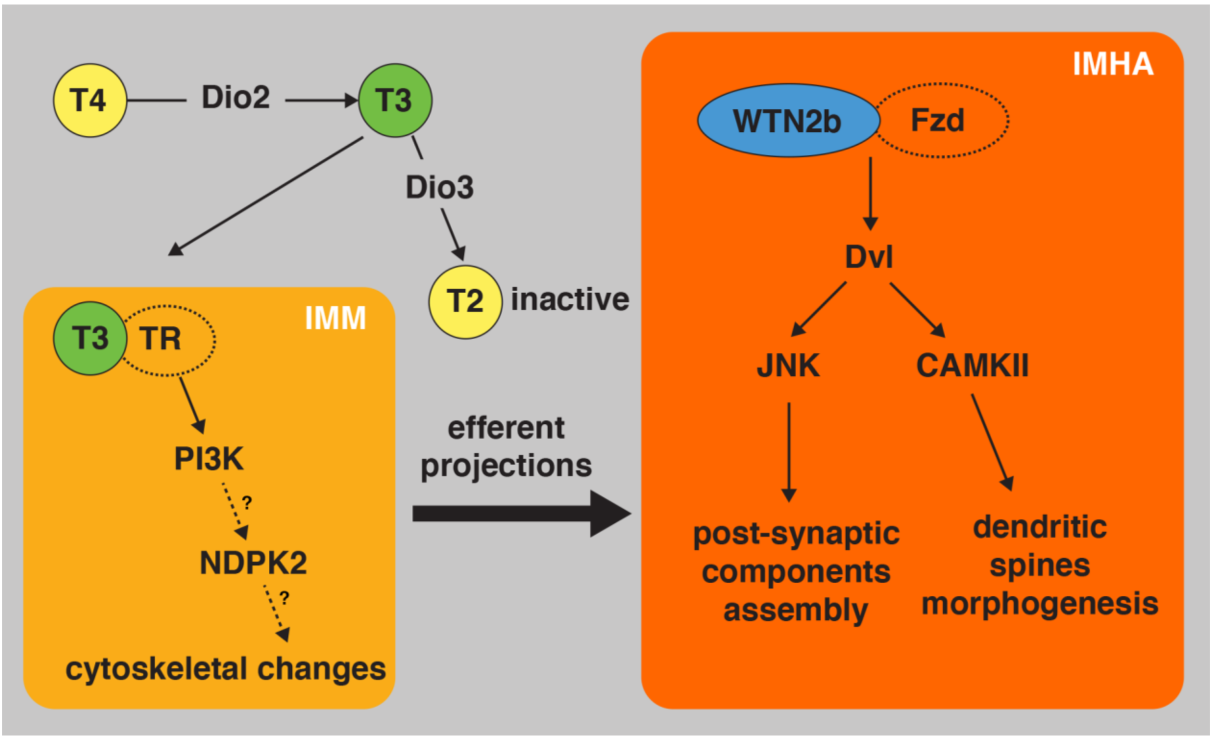

Fig. 3. Known pathways for the action of T3 on IMM (Intermediate Medial Mesopallium) and its efferent IMHA (Intermediate Medial Hyperpallium Apicale). The concentration of the thyroid hormone T3 (3,5,3′-triiodothyronine) is balanced in the brain by the enzyme Dio2 (type 2 iodothyronine deiodinase), which converts T4 into T3 (the active form) and by Dio3, which converts T3 into its inactive metabolite T2 (3,3′-diiodothyronine). In IMM, T3 binds a thyroid hormone receptor (TR), which activates the enzyme phosphatidylinositol 3′-kinase (PI3K). PI3K is hypothesised (dotted arrow) to act on another enzyme, NDPK2 (Nucleoside diphosphate kinase II), which would in turn interact with proteins that regulate the actin cytoskeleton, potentially leading to changes in the dendritic spines, supporting learning related plasticity. In IMHA, the molecular mechanisms that regulate the sensitive period for imprinting may involve the Wnt2b protein, which binds to a Fzd (frizzled) receptor, causing the activation of Dvl (Dishvelled) protein. This in turn modulates the activity of two enzymes, JNK (c-Jun N-terminal kinase) and CAMKII (Ca2+/calmodulin-dependent protein kinase II). The activation of this pathway induces changes in actin and reorganization of the microtubules, modulating the morphogenesis of dendritic spines and post-synaptic components assembly. Overall, the activation of the Wtn pathway in IMHA, concurrently with the input that this structure receives from the IMM that has been activated by T3

influx, may strengthen the connectivity between these two areas, contributing to the opening of the critical period for imprinting.

Moreover, it has been recently shown that the expression of $GABA_A$-$GABA_B$ receptors within IMM defines the opening and closing of the sensitive period downstream to T3. While $GABA_B$ initiates imprinting, $GABA_A$ contributes to its termination (Aoki et al., 2018; see also McCabe, 2019 for a comprehensive review of this literature). In mammals, the brain-region specific maturation parvalbumin-positive GABAergic inhibitory interneurons have a crucial role in the neurobiology of sensitive periods. This allows the refinement of cortical circuits that build up advanced cognitive functions (reviewed in Reh et al., 2020). Once again, similar mechanisms might be present in avian species (e.g., Aoki et al., 2018, see above), opening the way for exciting comparative investigations.

Similar to what described for the behavioural effects of the biological motion preference, the relationship between imprinting and T3 hormonal levels seems to be a circular one. The process of imprinting increases the forebrain concentration of T3 hormone, by increasing the expression of Dio2, the enzyme that converts T4 to T3 (the active form) (see also Takemura et al., 2018). This “primes” the mechanisms for the development of further secondary imprinting learning. As a consequence, after this initial priming even chicks as old as 4-8 days became susceptible to further imprinting (Yamaguchi et al., 2012). The similarity with the mechanisms described above for the action of the biological motion preference is not only a superficial one. Indeed, the induction of the predisposition for biological motion is linked to an increase in the gene expression of Dio2 (Miura et al., 2018; Takemura et al., 2018). The level of preference for biological motion developed by chicks primed with exposure to moving stimuli correlates with the level of telencephalic Dio2 expression (Takemura et al., 2018). Moreover, injections of IOP (iopanoic acid, that inhibits Dio2) reduced the level of biological motion preference developed by newly-hatched chicks after priming with motion stimuli (Miura et al., 2018). This reveals a direct causal link between the action of thyroid hormones and predispositions for biological motion. According to the model proposed by Miura and Matsushima (2020), the first encounter of an animal with a salient moving object would cause a surge of telencephalic T3 concentration. This would have consequences both at the level of inborn predispositions (causing the rapid emergence of the predisposition for biological motion), and at the level of learning mechanisms (causing the acute activation of imprinting learning and priming the memory system for further imprinting learning in the later days). Thanks to the induction of the predisposition for biological motion, even if the first moving object seen by the chick would be an inanimate object, the subsequent imprinting would be directed towards more biologically plausible objects. Please note that secondary imprinting towards naturalistic stimuli overrides previous imprinting learning on artificial ones, but not vice versa (Boakes & Panter, 1985; Bolhuis & Trooster, 1988). Moreover, the first "wave" of imprinting will determine at least some degree of following behaviour (i.e., motoric and visual stimulation). Thus, this first visual experience with any moving object is also likely to activate the emergence of the predispositions for hen-like objects, and specifically for their red face region (Fig. 4).

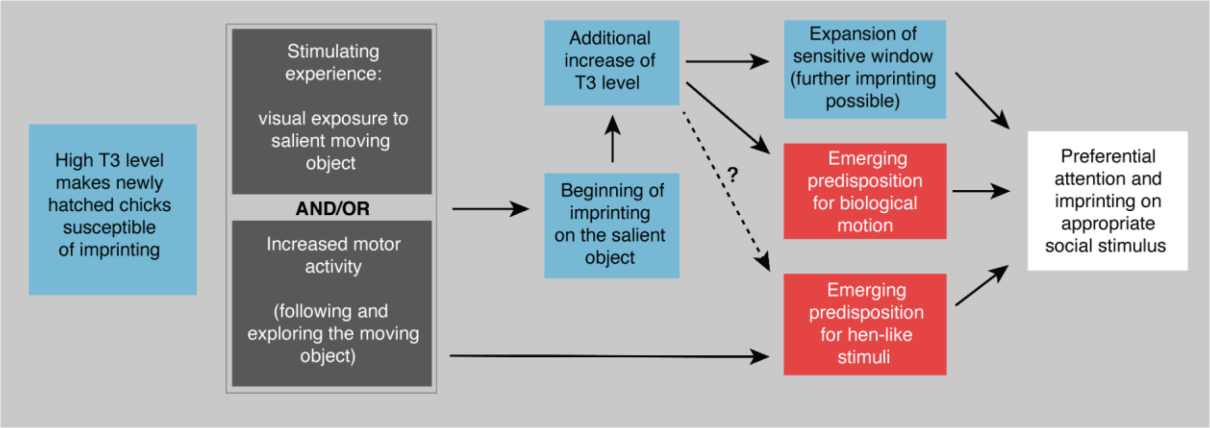

Fig. 4. Schematic illustration of a model representing the emergence of multiple social predispositions as a consequence of the exposure to any salient moving stimulus, in newly hatched chicks. T3 level peak at hatching, making these animals susceptible to imprinting. The exposure to the stimulus and the associated motoric activity will cause the emergence of the predisposition for the head region of hen-like stimuli. Moreover, by being exposed to a salient stimulus the animals will start to learn its features through filial imprinting. This process will cause an additional increase in the concentration of T3. This will have two consequences: extending the sensitive window for imprinting and causing the emergence of the predisposition for biological motion. (It is unknown whether T3 has any effect on the predisposition for hen-like object, dotted arrow). The combined presence of the two predispositions will direct chicks' attention towards appropriate social stimuli (e.g., the mother hen) if they are at all available in the environment. Since the animals are still susceptible to (secondary) imprinting learning, this will ensure filial attachment towards the mother hen.

It seems that multiple mechanisms evolved to ensure this crucial step of social development (Versace et al., 2018). Filial attachment towards the mother hen has important short-term beneficial consequences for the chicks, that gain heat, protection and guidance from the hen. Thanks to their notable social-learning abilities, chicks can also acquire crucial information (e.g., on the position and palatability of various food sources) from the hen and other brood-mates (e.g., Marino, 2017; Nicol, 2004).

Unfortunately, compared to the earlier developmental stages, less is known about how these interactive processes extend to later stages of chicks' life. For instance, there is relatively little evidence of the impact of these early environmental influences on the social adaptation of adult chickens (but see Rogers & Workman, 1989 for longitudinal data on lateralization and social interaction in chicks up to 16 days of age; see also Leonard et al., 1993; Leonard, Zanette, & Wayne Fairfull, 1993; Widowski, Lo Fo Wong, & Duncan, 1998 for the long-term effect of group composition on adult mating and agonistic behaviours). This aspect has been perhaps better studied in other bird species such as zebra finches, where sexual imprinting has been the object of numerous studies (see Bischof, 1994, 2018; ten Cate & Vos, 1999 for reviews). In sexual imprinting, the early experience the birds have with social companions, within a specific sensitive period of the post-natal life, affects their mate choice later in life. After this early acquisition phase, the formation of stable mate-preferences by sexual imprinting involves a second sensitive period, at the time when the young bird performs its first courtship. The availability of an appropriate partner to court can modify or consolidate the preference acquired in the earlier phase, crystallising it in its definitive form. It has been proposed that the first stage of sexual imprinting in zebra finches could correspond to filial imprinting as described for altricial birds. In this phase, the young bird would acquire general information that allow it to recognise parents, siblings and other members of its social group. During the subsequent consolidation phase, its first courtship attempts are directed towards individuals resembling this template, if at all available, and the tendency is further consolidated. Similar to what we saw for filial imprinting, also in sexual imprinting the preferences of young birds are not completely unconstrained, revealing the presence of genetic biases or unlearned predispositions. Indeed, cross-fostering experiments with birds of different species revealed that sexual imprinting is usually easier to achieve for the own species. This two-phase process, involving the interaction of predisposed and learned mechanisms, thus increases the chances to obtain sexual imprinting towards the bird's own species, while allowing still sufficient behavioural flexibility to cope with different environmental circumstances (Bischof, 2018). The neural correlates of learning occurring in sexual imprinting during the consolidation phase have been also well investigated (Bischof, 2007). In the case of visual sexual imprinting, changes occurring during the second sensitive period involved mostly an irreversible reduction of dendritic spines in the Lateral Nido-Mesopallium (LNM). Similarities with the processes observed for filial imprinting include a clear involvement of hormonal signalling (testosterone, in this case) in the opening of the sensitive window for the consolidation phase, and of GABAergic inhibition for its closing. Future studies should be devoted to compare how predispositions and learning mechanisms interact during the earlier stages of life and later in development (see Vidal, 1980 for a behavioural study of the relationship between sexual and filial imprinting in chicks). It would thus be important to perform longitudinal developmental studies, targeting how early environmental influences shape adult social behaviour.

4. Conclusions

In a world rich in stimuli, social predispositions help young animals to direct their attention and learning toward social partners, which provide protection and guidance, and to ignore less relevant stimuli. Predispositions are not fixed and immutable mechanisms, though, but respond in different ways to the environmental and social stimulation present at specific time-points during the ontogenetic development. We have described how the relation between predisposed and environmental factors in the first phases of life has profound influences on subsequent development (see also Versace et al., 2018; Versace & Vallortigara, 2015). However, long term effects have just started to be elucidated.

We have shown how distinct sensitive periods shape the development of social behaviour via complex interactions of environmental and genetic influences. This is apparent, for instance, in the development of affiliative responses for the mother through predispositions that orient the newborn towards animate objects (reviewed in Di Giorgio et al., 2017a) and enhance learning of the particular features of the social partners. The latter mechanism is shown for example by the enhancement of imprinting in chicks whose predispositions for biological motion have been activated by previous exposure to moving objects (Miura & Matsushima, 2016; Miura et al., 2020). Importantly, we have shown how environmental events can modulate the timing and duration of sensitive periods, maximising the chances of optimal developmental outcomes. This is well-exemplified by in the surge of T3 elicited by the first wave of imprinting learning after encountering a salient object, which allows subsequent secondary imprinting to take place (Yamaguchi et al., 2012).

Domestic chicks are currently an elective model system to investigate connection between predispositions and learning at the behavioural and neurobiological level. This is mostly due to the advantages of precocial animals that respond to behavioural tests immediately after birth, as well as to the opportunity to investigate the fast learning mechanism of filial imprinting. These advantages allowed researchers to shed some light on the neural and physiological bases of the early mechanisms (e.g., Horn, 2004; Lorenzi et al., 2017; Loveland et al., 2019; Mayer et al., 2016, 2017a, 2017b, 2019), including those for the opening and closing of sensitive periods (Aoki et al., 2018; Yamaguchi et al., 2012). While the notion of sensitive period has been traditionally applied to filial imprinting, mounting evidence shows that specific time windows regulate the emergence of predispositions too (e.g., (Bolhuis & Horn, 1997; Bolhuis et al., 1989; Davies, Johnson, & Horn, 1992; Johnson, Davies & Horn, 1989; Miura et al., 2020; Versace, Ragusa & Vallortigara, 2019).

More recently, chicks have been used for the study of how predispositions influence typical and pathological development, as they are being proposed as a model for the social impairment of autism spectrum disorders (Sgadò et al., 2018; Lorenzi al., 2019; see also Di Giorgio et al., 2016; Zachar et al., 2019). This is facilitated by the fact that predispositions appear to be very similar across taxa. In fact, organisms as different as human babies, chicks and tortoises display similar social predispositions (e.g., Johnson, 2005; Rosa-Salva et al., 2010; Versace et al., 2020). This further points at the adaptive value of mechanisms that enable young animals to cope with their environment from the early stages of life, as already envisioned in the pre-representations conceptualised by Mehler and Dupoux for human infants (Mehler & Dupoux, 1994).

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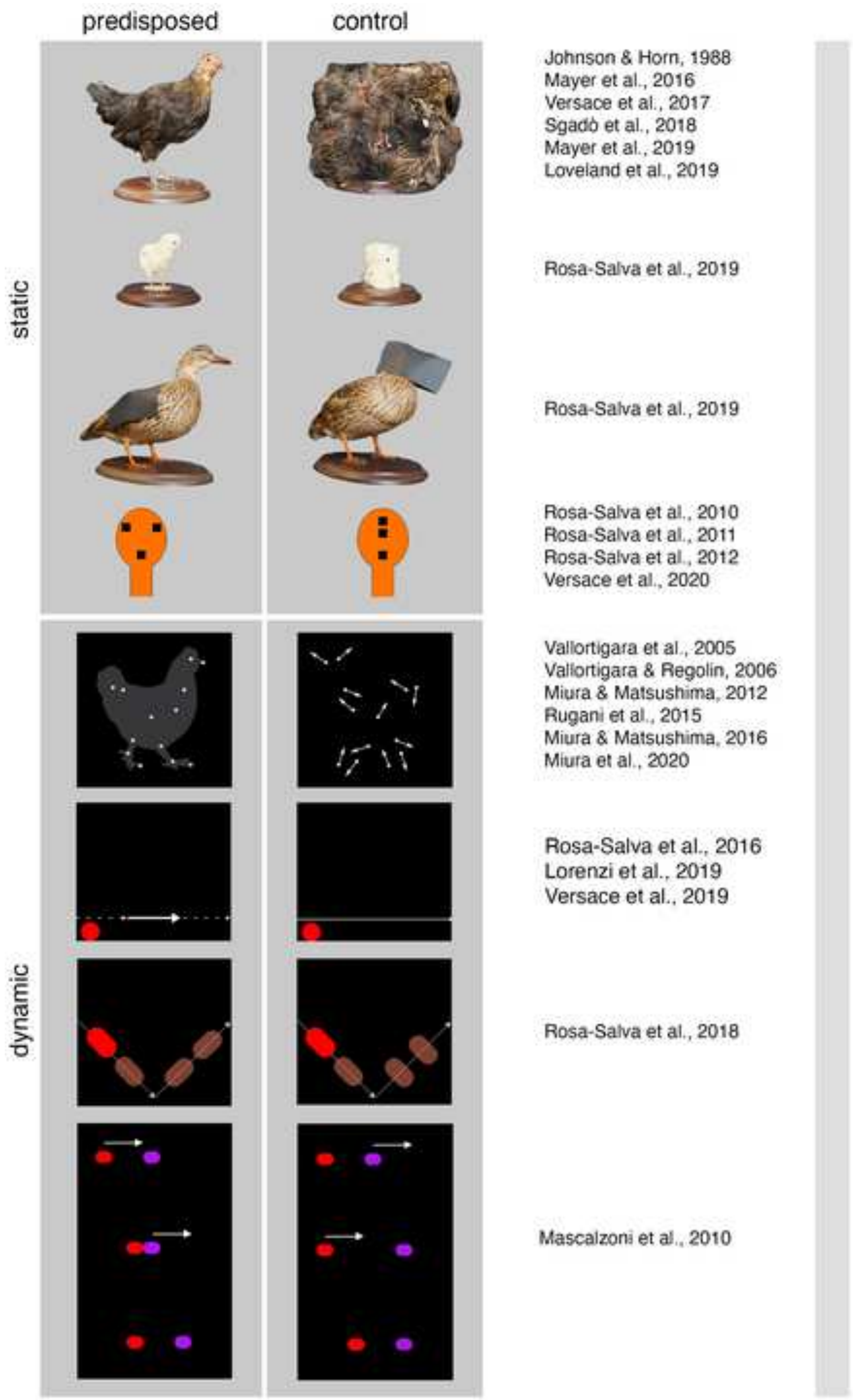
- precocial avian species are optimal models to study social cognition development
- predisposed and environmental factors interact in the development of domestic chicks
- social predispositions require activating experiences, occurring in critical periods
- social predispositions and filial imprinting are reciprocally interacting mechanisms
- hormonal and neural mechanisms control critical periods for social development

Figure 1


predisposed
control
static
dynamic
Johnson & Horn, 1988
Mayer et al., 2016
Versace et al., 2017
Sgadò et al., 2018
Mayer et al., 2019
Loveland et al., 2019
Rosa-Salva et al., 2019
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Versace et al., 2020
Vallortigara et al., 2005
Vallortigara & Regolin, 2006
Miura & Matsushima, 2012
Rugani et al., 2015
Miura & Matsushima, 2016
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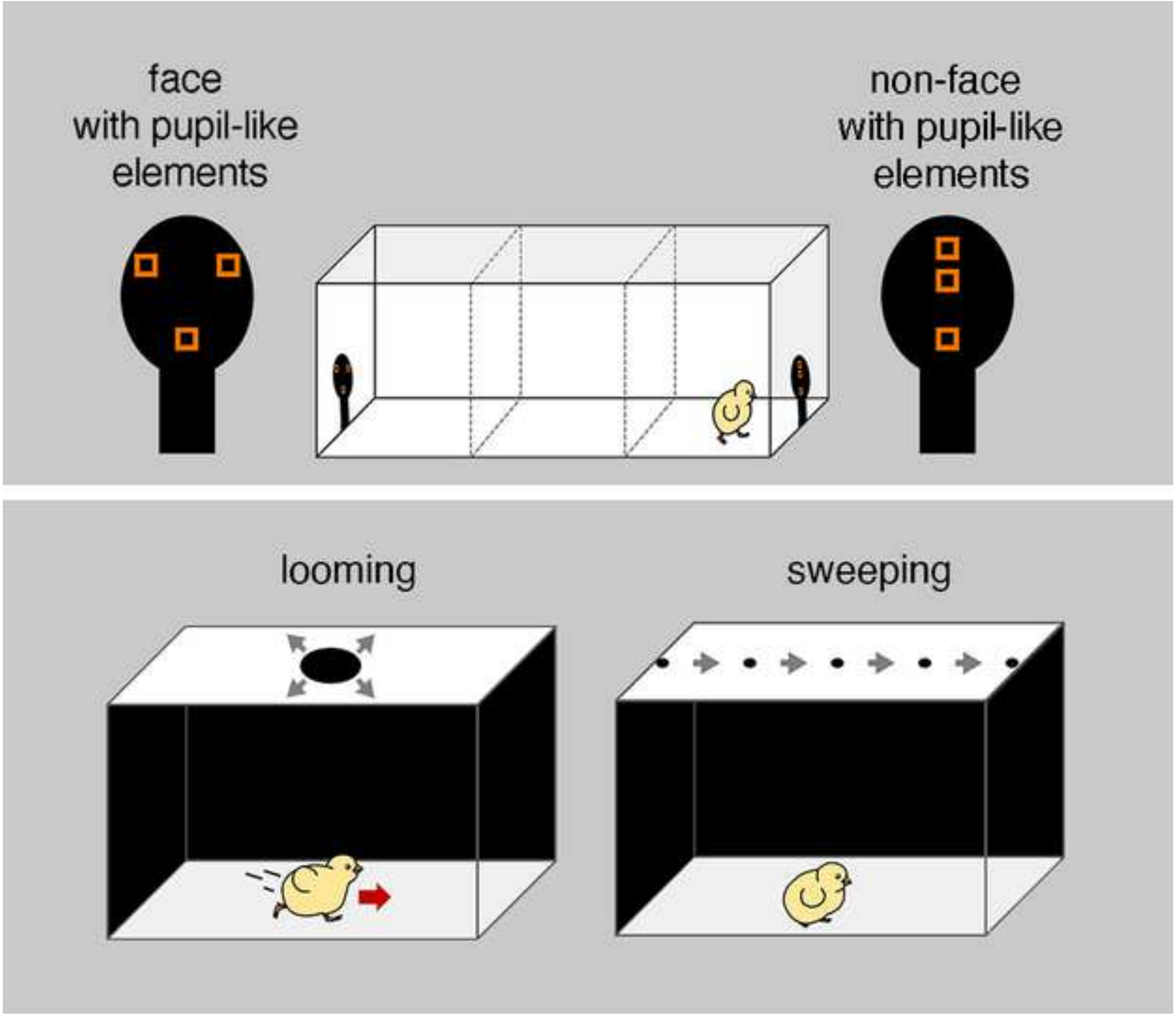

face
with pupil-like
elements
non-face
with pupil-like
elements
looming
sweeping

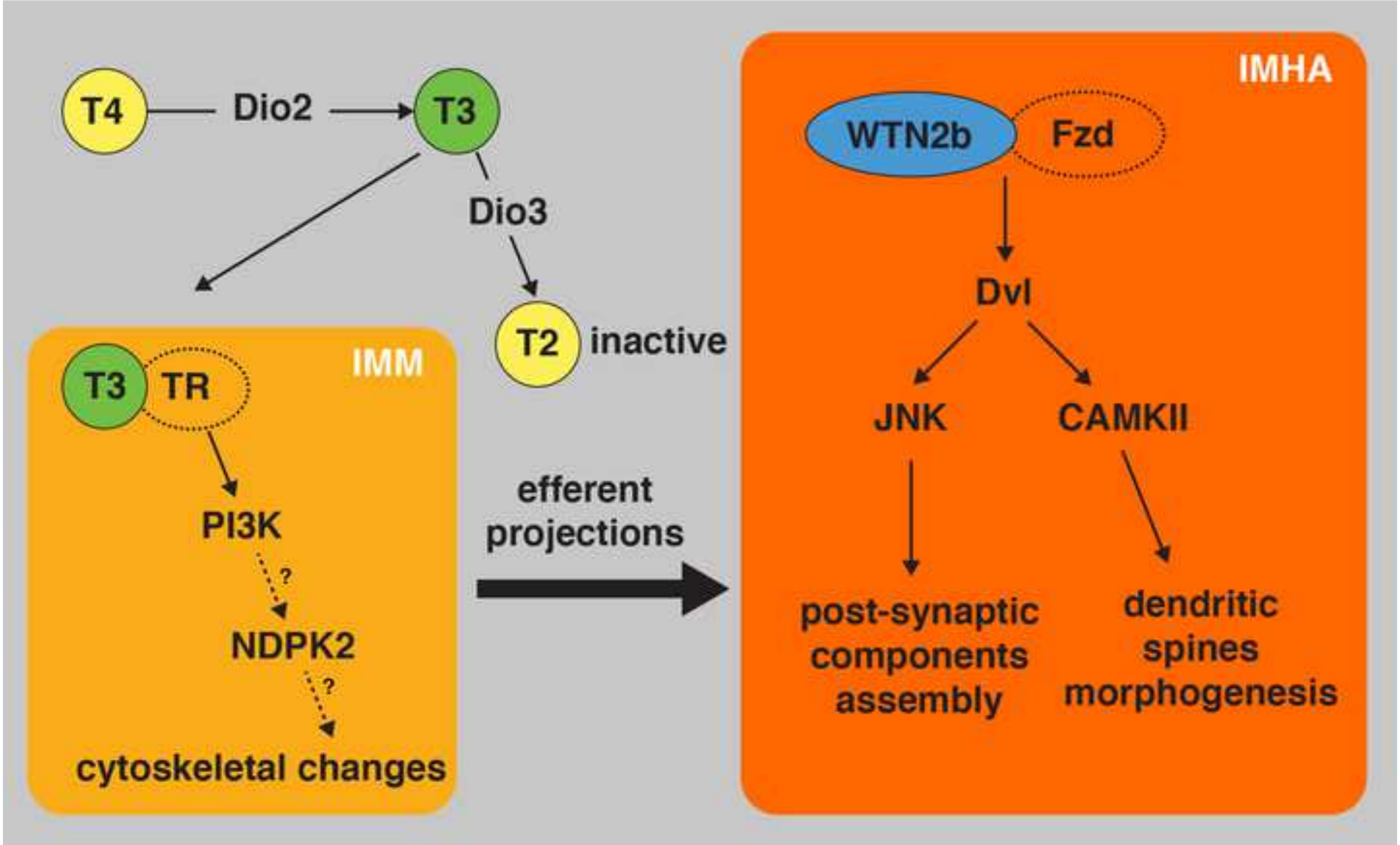
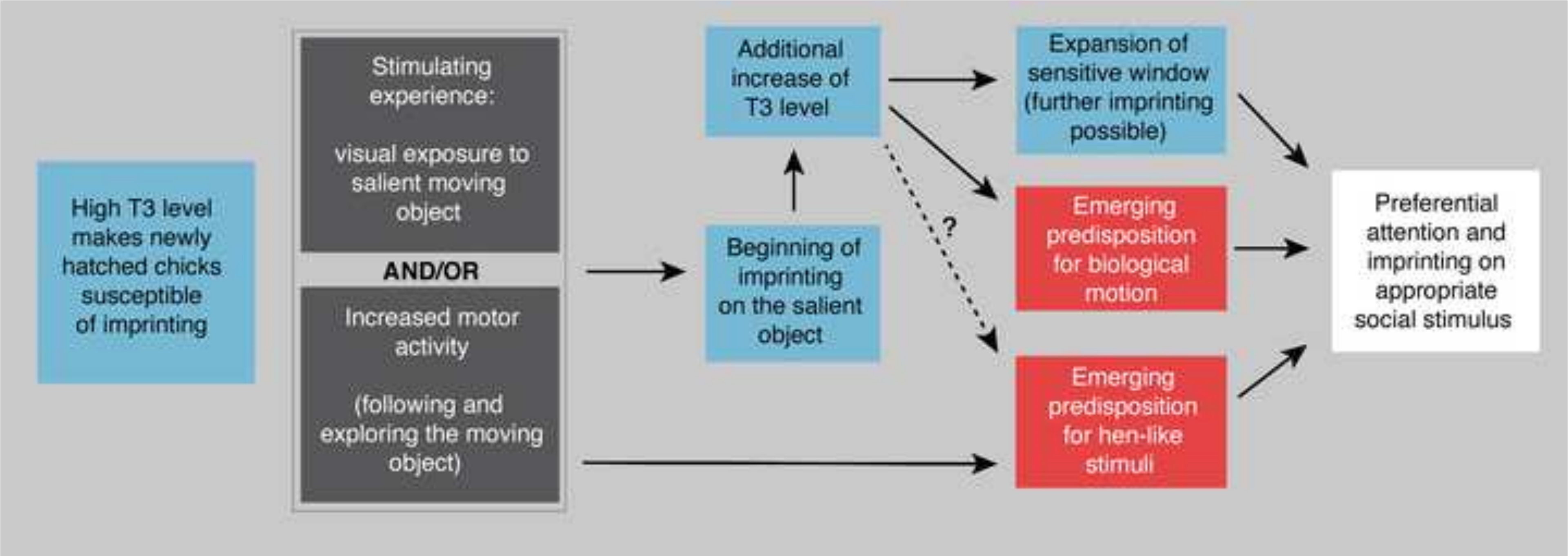

T4
Dio2
T3
Dio3
T2
inactive
IMM
T3
TR
PI3K
?
NDPK2
?
cytoskeletal changes
efferent projections
IMHA
WTN2b
Fzd
Dvl
JNK
CAMKII
post-synaptic components assembly
dendritic spines morphogenesis

Figure 4


High T3 level makes newly hatched chicks susceptible of imprinting
Stimulating experience:
visual exposure to salient moving object
AND/OR
Increased motor activity
(following and exploring the moving object)
Additional increase of T3 level
Beginning of imprinting on the salient object
?
Expansion of sensitive window (further imprinting possible)
Emerging predisposition for biological motion
Emerging predisposition for hen-like stimuli
Preferential attention and imprinting on appropriate social stimulus